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

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11 **ABSTRACT**

12 The Ediacaran skeletal tubular putative metazoan *Cloudina* occurs globally in  
13 carbonate settings, which provided both lithified substrates and minimized the cost of  
14 skeletonization. Habitat and substrate preferences, and the relationship of *Cloudina* to  
15 other metazoans, have not been fully documented so we know little as to its ecological  
16 demands or community dynamics. *In situ Cloudina* from the Nama Group, Namibia (ca.  
17 550–541 Ma) formed mutually-attached reefs composed of successive assemblages in  
18 shallow, high-energy environments, and also communities attached to either stromatolites  
19 in storm-influenced deep inner-ramp settings or thin microbial mats in lower energy  
20 habitats. Each assemblage shows statistically distinct tube diameter cohorts, but in sum  
21 *Cloudina* shows an exponential frequency distribution of diameter size. In reefs, we  
22 document a periodicity of size variation, where mean, minimum and maximum tube

23 diameters vary together and show a systematic increase toward the top of each  
24 assemblage. We conclude that most Nama Group *Cloudina* represent one ecologically  
25 generalist taxon with highly variable size, that size was environmentally mediated, and  
26 that *Cloudina* could respond rapidly to periodic environmental changes. While Nama  
27 Group skeletal metazoans coexisted with soft-bodied biota, there was no apparent  
28 ecological interaction as they were segregated into lithified carbonate, and non-lithified  
29 clastic microbial mat communities, respectively. We infer that ecological flexibility  
30 allowed *Cloudina* to form varied communities that colonized diverse carbonate substrates  
31 under low levels of interspecific substrate competition. This is in notable contrast to the  
32 earliest Cambrian skeletal epibenthos that formed biodiverse reef communities with  
33 specialist niche occupancy.

#### 34 **INTRODUCTION**

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

42         The non-uniformitarian Ediacaran marine world was characterized by a  
43 heterogeneous redox landscape (e.g., Wood et al., 2015), and carbonate and clastic  
44 seafloors were covered by extensive microbial mats in the absence of deep bioturbation  
45 (Droser et al., 2005). All known Ediacaran biomineralized metazoans are exclusively

46 benthic and found in carbonate settings where the physiological cost of skeletonization  
47 may have been minimized by both high carbonate supersaturation and the low metabolic  
48 demand of an immobile habit (Wood, 2011).

49 Here we consider the in situ distribution of the putative metazoan *Cloudina* in the  
50 Nama Group, Namibia (ca. 550–541 Ma) (Fig. 1). While *Cloudina* has been documented  
51 to occupy diverse carbonate habitats globally (e.g., Grotzinger et al., 2005; Hua et al.,  
52 2005; Warren et al. 2011), we know little as to its environmental distribution, substrate  
53 preferences, and community dynamics, even though these are critical elements in the  
54 survival and success of benthic metazoans. Here, we use size data and ecological  
55 associations to explore the environmental controls on *Cloudina* within the context of  
56 these early metazoan life habits and ecosystems.

## 57 **MORPHOLOGY AND GROWTH OF *CLOUDINA***

58 *Cloudina* is built of repeating funnel-like, adapically flaring tubes or cones set one  
59 within the next to form a distinctive cone-in-cone, eccentrically-built skeleton (Germs,  
60 1972). *Cloudina* may have been a filter or suspension feeder of possible Cnidarian  
61 affinity, where soft-parts probably occupied the youngest cones only (Wood, 2011).  
62 *Cloudina* was capable of multiple reproductive modes, including aggregation and  
63 episodic larval settlement (Wood and Curtis, 2015), and clonal reproduction (Hua et al.,  
64 2005). From the ancestral cone (Fig. 2F), *Cloudina* shows a variety of growth modes  
65 where cones can be added at variable intervals, often manifest as external annular ridges,  
66 and can grow in size (diameter and height) to varying degrees. Growth mode A has  
67 densely stacked cones with rapid early cone size increase to achieve maximum diameter,  
68 which then remains constant. Growth mode B shows densely stacked cones with

69 continuous cone size increase through the lifetime of the individual. Growth mode C has  
70 a constant cone size with widely spaced cones. *Cloudina* assemblages can show  
71 directional orientation, which may indicate preferential growth into a nutrient-rich current  
72 as might be expected of passive suspension feeders (Penny et al., 2014).

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

#### 79 **GEOLOGICAL SETTING OF THE NAMA GROUP**

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

89 Assemblages from three localities are considered in this study: Driedoornvlagte  
90 reef complex, Zebra River and Swartpunt (Fig. 1). Fe speciation, Fe/Al and cerium  
91 anomalies show these assemblages to have grown under stable, well-oxygenated

92 conditions (Wood et al., 2015; Tostevin et al., 2016). Localities span  $\geq 6$  m.y. from the  
93 Upper Omkyk Member ( $> 547$  Ma) to the top of the Spitskopf Member (ca. 541 Ma).

## 94 **METHODS**

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

## 106 **RESULTS**

### 107 ***Cloudina* Ecological Associations**

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

110 (1) Shallow-water, *Cloudina* reefs from the mid-ramp, high energy platform margin  
111 associated with coalesced thrombolite mounds of the final cycle of reef growth of the  
112 Upper Omkyk Member at Driedoornvlagte reef complex. Large *Cloudina* (*C.*  
113 *hartmanae*) reefs grew by mutual attachment (Fig. 2A), often via additional extra-  
114 tubular patches, or meniscus-like features (Penny et al., 2014). Individuals of small

115 *Cloudina* (*C. riemkeae*) formed reefs via attachment either to each other or to diffuse,  
116 micro-clotted, thrombolite (Wood and Curtis, 2015) (Fig. 2B). Early botryoidal  
117 cements are abundant and *Cloudina* has a variable, but dominantly sub-horizontal  
118 orientation. Both reefs types are composed of many repeated units or assemblages  
119 (Figs. 2A and 2B). These are 10–30 cm in height and laterally lens-shaped up to 3 m  
120 in length. The upper part of these units grade into a layer 5–32 mm thick, which is  
121 preferentially dolomitised, composed of an increasing density of micro-thrombotic  
122 clots, sediment and microbial laminae with *Cloudina* (Figs. 2A and B). The final  
123 microbial laminae often mark a sharp boundary before growth of the succeeding unit.  
124 More rarely a unit may be erosionally truncated (Fig. 2E). We noted at least 20 such  
125 units within one large *C. hartmanae* reef. The density of individuals within the *C.*  
126 *hartmanae* reefs have a mean of 48.34/100 mm<sup>2</sup> (range = 27–87/100 mm<sup>2</sup>; n = 435),  
127 *C. riemkeae* a mean of 482/100 mm<sup>2</sup> (range = 465–500/100mm<sup>2</sup>; n = 193). Smaller  
128 individuals often cluster in groups (Fig. 2E). Individuals ascribed to *C. hartmanae* are  
129 dominated by growth mode A, but B is also present. *C. riemkeae*, shows all growth  
130 modes A, B, and, more rarely, C.

131 (2) Elongate stromatolitic biostromes associated with packstones, cross-bedded  
132 grainstones and breccias from the storm-influenced deep inner ramp (Grotzinger et  
133 al., 2005) of the Upper Omkyk Member at Zebra River. *Cloudina* is found attached to  
134 large stromatolitic heads, often with encrusting botryoidal cement, in recumbent  
135 straight or sinuous form attached to the upper surfaces of, or embedded vertically or  
136 sub-horizontally within, stromatolite heads (Fig. 2C). The measured density of  
137 individuals on stromatolite heads have a mean of 7.86/100 mm<sup>2</sup> (range = 2–15/100

138 mm<sup>2</sup>; n = 228). Individuals show growth modes A and B. Inter-reef muds bear in situ,  
139 spiny *Namacalathus* (Penny et al., 2016) and *Cloudina* debris.

140 (3) Thin microbial mat communities from the low energy, flaggy wackstone units of both  
141 the outer and inner ramp highstand systems tract settings of the Spitzkopf Member at  
142 Swartpunt (Wood et al., 2015). Here, *Cloudina* grows horizontally attached to  
143 undulating microbial mats (Fig. 2D), often with a notable preferred orientation  
144 (Penny et al., 2014). The mean density on bedding planes is 5.40/100 mm<sup>2</sup> (range =  
145 2–19/100mm<sup>2</sup>; n = 293). Individuals show growth modes A and B.

#### 146 **Tube diameter Distribution of *Cloudina***

147 Normalized tube diameter distribution of all measured in situ *Cloudina* (n = 1145)  
148 follows an exponential distribution (Fig. 3A). By contrast, raw mean and range (Fig. 3C),  
149 and normalized distributions (Figs. 3B–3E) for each setting reveals size differences  
150 between assemblages. Shapiro-Wilk tests show that the size distributions of in situ  
151 assemblages are not normally distributed (Table DR2). Kolmogorov–Smirnov tests reject  
152 the null hypothesis that these size distributions are from the same population distribution.  
153 Differences between the *C. hartmanae* and *C. riemkeae* reefs, and the inter-stromatolite  
154 mud at Zebra River (Fig. 3D) are all statistically distinct at the 95% confidence level  
155 from each other and from all other settings (Table DR3). Other assemblages are  
156 significantly different to others at a 90% confidence level, except for Swartpunt –Upper  
157 which shows statistical similarities to several other assemblages.

158 Within a measured transect through the *C. hartmanae* reef, four successive  
159 assemblages (labeled 1–4) are distinguished by the position of final dolomitized layers  
160 with sharp tops (Fig. 4A). The transect reveals a marked periodicity in tube diameter,

161 where mean, maximum and minimum all vary synchronously through time within each  
162 successive assemblage (Fig. 4B). The largest minimum, mean and maximum tube sizes  
163 occur often, but not always, toward or within the final dolomitised layers of each  
164 assemblage. The intervals of notable increase and decrease of tube diameter occur over  
165 1.3–3.2 cm of restored vertical thickness. A further rise and fall of maximum  
166 measurements is also evident in Assemblage 3. We estimate most *Cloudina* individuals to  
167 range from 20 to 50 mm in length, with a dominant growth mode A where inflation to  
168 maximum tube diameter occurs within the first 10 mm of growth.

## 169 **DISCUSSION**

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

175 Statistical tests show that the *Cloudina* tube diameter distribution within inter-  
176 stromatolite mud at Zebra River is significantly different (95% confidence level) from all  
177 in situ cohorts (Figs. 3C and 3D). This confirms that detrital *Cloudina* size distribution  
178 should not be used as representative of any in situ community. Contrary to previous  
179 assessments (Germs, 1972), however, the exponential rather than bimodal distribution of  
180 tube diameter (Fig. 3A), shows that size should not be used as a species-specific trait. It is  
181 possible, however, that the restriction of growth mode C to some, small (<1 mm  
182 diameter) individuals, provides support for a separate species possessing a distinct growth

183 strategy. We also note that over the 6 m.y. interval explored here, *Cloudina* appears to be  
184 morphologically unchanged.

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

196         From these data we can conclude that individual size in *Cloudina* was controlled  
197 by the environment, and moreover that *Cloudina* could respond rapidly to changes in the  
198 environmental determinants of size. While it is possible that *Cloudina* was a rapidly-  
199 evolving specialist responding to environmental change, the fact that documented size  
200 changes were cyclical suggests that *Cloudina* shows considerable intraspecific size  
201 variation with a highly flexible and responsive growth pattern. Environmental controls on  
202 *Cloudina* size may include fluctuations in nutrient levels, hydrodynamic energy, space  
203 availability, or carbonate supersaturation. In addition, we note that *Cloudina* could  
204 produce varied skeletal innovations according to ecological need, such as the additional

205 skeletal structures between closely aggregating individuals in reef settings, inferred to  
206 impart rigidity (Penny et al., 2014; Wood and Curtis, 2015).

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

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

224         Ediacaran skeletal metazoan communities were of very low diversity, rarely  
225 reaching a maximum of three taxa (e.g., in the Nama Group - *Cloudina*, *Namacalathus*,  
226 and *Namapoikia*). This is in notable contrast to the first skeletal benthic metazoan  
227 communities of the early Cambrian Stage 2, which show up to seven taxa (Riding and

228 Zhuravlev, 1995). Although similarly attached to either microbial or other skeletal  
229 substrates, these metazoan communities were biogeographically distinct and also show  
230 specialist niche occupancy (Zhuravlev et al., 2015).

## 231 **CONCLUSIONS**

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

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### 302 **FIGURE CAPTIONS**

303 Figure 1. Locations and stratigraphic setting of the Nama Group, Namibia. A: Simplified  
304 map showing geological setting, subgroups, and sub-basins of the late Ediacaran to early  
305 Cambrian Nama Group of southern Namibia (modified after Grotzinger and Miller,  
306 2008). Locations: 1—Driedoornvlagte, 2—Zebra River, 3—Swartpunt. B: Stratigraphy of  
307 the northern Zaris and southern Witputs sub-basins with major sequences, dated ash beds,  
308 first and last appearances of *Cloudina* and Ediacaran biota, and major reefs (modified  
309 after Wood et al., 2015).

310

311 Figure 2. In situ *Cloudina* ecological associations from the Nama Group, Namibia. Reefs  
312 ascribed to *C. hartmanae* (A) and *C. riemkeae* (B) from the Upper Omkyk Member,  
313 Driedoornvlagte. The base and top of each assemblage is shown. C: Various orientations,  
314 including recumbent and sinuous *Cloudina* individuals (arrowed) attached to elongate  
315 stromatolite heads, from the Upper Omkyk Member, Zebra River. D: Many individuals  
316 (arrowed) attached horizontally to thin, patchy microbial mats (M) in the Spitzkopf

317 Member, Swartpunt. E: Clusters of small individuals (arrowed), and a truncation surface  
318 (double arrows) in reefs ascribed to *C. hartmanae*, Driedoornvlagte. F: Growth modes of  
319 *Cloudina*. From the ancestral cone, *Cloudina* can show either (A) rapid early cone size  
320 increase (diameter and height) to achieve maximum diameter which then remains  
321 constant, or (B) continuous cone size increase through the lifetime of the individual, or  
322 (C) no increase in cone size.

323

324 Figure 3. Normalized frequency distribution of *Cloudina* in binned tube diameter from  
325 the Nama Group, Namibia. A: Combined in situ data from Driedoornvlagte ('*C.*  
326 *hartmanae*' and '*C.riemkeae*' reefs), Zebra River and Lower and Upper Swartpunt. B:  
327 Distributions from in situ Driedoornvlagte (*C. hartmanae* and *C.riemkeae* reefs), Zebra  
328 River stromatolites and Upper and Lower Swartpunt. C: Box and whisker plots for  
329 Driedoornvlagte *C. hartmanae* (DR-H) and *C.riemkeae* reefs (DR-R), Zebra River  
330 stromatolites (ZR-S) and inter-reef mud (ZR-M), and Swartpunt - Lower (SWP-L) and  
331 Upper (SWP-U). D: Distribution of Zebra River stromatolites compared to individuals in  
332 inter-reef mud. E: Distribution of Lower and Upper Swartpunt assemblages.

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334 Figure 4. Size distribution of *Cloudina hartmanae* along a tangential 100 cm transect  
335 through a reef, Driedoornvlagte, Namibia. Continuous white line is base of dolomitized  
336 layer; dotted white line is top of dolomitized layer. A: Field image of transect showing  
337 successively numbered assemblages. The restored approximate vertical height for each  
338 successive assemblage is 15.4, 14.8, 22.5 and 7.1 cm, respectively. B: Maximum (black),

339 minimum (blue) and mean (red) at 2 cm intervals through transect. Shaded areas show  
340 dolomitized layers.

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342 <sup>1</sup>GSA Data Repository item 2017xxx, xxxxxxxx, is available online at

343 [www.geosociety.org/pubs/ft2017.htm](http://www.geosociety.org/pubs/ft2017.htm), or on request from [editing@geosociety.org](mailto:editing@geosociety.org).