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1 Multiple branching and attachment structures in  
2 cloudinomorphs, Nama Group, Namibia

3 Amy Shore<sup>1\*</sup>, Rachel Wood<sup>1</sup>, Andrew Curtis<sup>1</sup>, and Frederick Bowyer<sup>1,2</sup>

4 <sup>1</sup>*School of GeoSciences, University of Edinburgh, James Hutton Road, Edinburgh EH9 3FE,*  
5 *UK.*

6 <sup>2</sup>*School of Earth and Environment, University of Leeds, Leeds, LS2 9JT*

7 \*E-mail: [amy.shore@ed.ac.uk](mailto:amy.shore@ed.ac.uk)

8

9 **ABSTRACT**

10 The Ediacaran-Cambrian cloudinomorphs, which include *Cloudina*, are the first putative  
11 skeletal metazoans. They have a benthic ecology and tubular, organic or biomineralized  
12 stacked funnel morphologies, but an unresolved phylogenetic affinity. Rare dichotomous  
13 branching has been described in *Cloudina*, but here we demonstrate the presence of multiple  
14 (polytomous), dichotomous branching in cloudinomorphs from a microbial mat-community  
15 from the Nama Group, Namibia, as revealed by 3D models created from serial sections.  
16 Branches share an open, central cavity, and branching is achieved via external budding.  
17 These cloudinomorphs show attachment and mutual cementation to each other, and also to  
18 *Namacalathus*, via extratubular skeletal structures to potentially form a horizontal  
19 framework. Polytomous branching excludes a bilaterian affinity as proposed for other  
20 cloudinomorphs. This raises the possibility that the Ediacaran tubular, funnel morphology is  
21 convergent, and that cloudinomorphs may, in fact, represent taxa of diverse affinity.

22

23

24

## 25 INTRODUCTION

26 Significant evolutionary innovations in metazoans such as biomineralization, reef-  
27 building, and motile behavior appear during the terminal Ediacaran. The most studied  
28 Ediacaran skeletal taxa is *Cloudina* (ca. 550-540 Ma), due to its widespread distribution and  
29 potential index fossil status (Grant, 1990).

30 *Cloudina* and other similar tubular skeletal and organic taxa (informally known as  
31 ‘cloudinids’ and ‘cloudinomorphs’) have a sinuous, tube-like morphology formed of  
32 eccentrically stacked funnels that lack transverse cross-walls but which can flare to form  
33 outer wall flanges (Germs, 1972; Hua et al., 2005; Selly et al., 2020). To date, at least seven  
34 genera have been attributed to cloudinomorphs (Yang et al., 2020), and as a group they are  
35 transitional across the Ediacaran-Cambrian boundary. Cloudinomorphs can have a closed or  
36 open base, a smooth inner wall, and an aperture (Germs, 1972; Cai et al., 2011; Schiffbauer et  
37 al., 2020). The size of *Cloudina* is highly variable globally, cited as ranging from 0.3 to 6.5  
38 mm wide and 1.5 to 150 mm in length; dimensions may be determined by environmental as  
39 well as systematic factors (Wood et al., 2017). *Cloudina* communities occupied a range of  
40 different carbonate substrates including microbial mats, thrombolites, and reefs (Cai et al.,  
41 2014; Penny et al, 2014; Becker-Kerber et al., 2017; Wood et al., 2017, Álvaro et al., 2019,  
42 but see Mehra and Maloof, 2018). Dichotomous branching has been observed in a few cases  
43 in *Cloudina* (Hua et al., 2005; Penny et al, 2014) and also budding of daughter tubes between  
44 two adjacent tubes (Cortijo et al., 2010), both suggestive of asexual reproduction. Evidence  
45 for mutual attachment and cementation of *Cloudina* individuals has been noted in the Nama  
46 Group, Namibia, where two forms of attachment are documented: apical terminations serving  
47 as attachment sites and ‘meniscus cements’ between adjacent individuals (Penny et al., 2014).

48 The affinity of cloudinomorphs is problematic, with the group variously attributed to  
49 calcareous algae, cnidarians or annelids (Terleev et al., 2004, e.g. Vinn and Zaton, 2012;

50 Schiffbauer et al., 2020). A cnidarian affinity is supported by the deep-seated division of  
51 *Cloudina* tubes within the parent tube (Hua et al., 2005; Cortijo et al., 2014). However, the  
52 general nested funnel morphology and skeletal ultrastructure of some cloudinomorphs are  
53 similar to modern annelids (Vinn and Zaton, 2012; Yang et al., 2020), and preservation of a  
54 central, tubular, pyritized structure in a cloudinomorph inferred to be a gut would support a  
55 stem-annelid, affinity (Schiffbauer et al., 2020). Indeed many skeletal features of  
56 cloudinomorphs are in fact present in diverse invertebrate groups.

57 Here we describe the first recorded instance of multiple (polytomous) branching, and the  
58 form of attachment sites, in cloudinomorphs. This informs the debate as to the potential  
59 affinities of this global and transitional Ediacaran-Cambrian group.

60

## 61 **GEOLOGICAL SETTING**

62 The Nama Group (ca. 550–541 Ma) is a fossiliferous Ediacaran-Cambrian sedimentary  
63 ramp succession deposited in two sub-basins (Germs, 1983, and see Supplementary Material  
64 and Fig. DR1 in the Data Repository), consisting of the Kuibis Subgroup overlain by the  
65 Schwarzrand (Germs, 1983; Saylor et al., 1995). Ash bed dates and inferred sedimentation  
66 rates suggest the basal Nama unconformity is ca. 550–553 Ma (Saylor et al., 1998) and the top  
67 of the Schwarzrand Subgroup is younger than at least  $539.64 \pm 0.19$  Ma (Linnemann et al.,  
68 2019).

69

## 70 **MATERIAL AND METHODS**

71 Samples from *in-situ* bedding planes were collected from near the top of the Upper  
72 Omkyk Member of the Kuibis Subgroup, at Omkyk Farm and Driedoornvlagte in the Zaris  
73 Subbasin (Table DR1; Fig. DR1). An ash bed from the overlying Hoogland Member is dated  
74 at  $547.32 \pm 0.65$  Ma (Grotzinger et al., 1995; Schmitz, 2012). Driedoornvlagte is a shallow

75 reef complex that formed in a mid-ramp setting that contains abundant skeletal taxa,  
76 *Cloudina*, *Namacalathus*, and *Namapoikia*. At Omkyk Farm, strata record deposition at an  
77 inner ramp position close to the Osis Arch, into increasingly shallow, very low-energy,  
78 lagoonal settings containing *Cloudina* and *Namacalathus* (Wood et al., 2015).

79 Cloudinomorph specimens were serially ground in increments of either 10  $\mu\text{m}$  (Figs. DR2  
80 and 3), or 25  $\mu\text{m}$  (Fig. DR4), using a Buehler Petrothin thin sectioning system and imaged  
81 using a binocular microscope. Processed images were imported as a virtual stack into Avizo 9  
82 software to create 3D models composed of between 50-123 2D images and smoothed to  
83 reduce noise. Cloudinomorph walls and the open cavity were manually segmented separately  
84 (Fig. DR5). Highly polished thin sections were imaged by standard petrographic and  
85 cathodoluminescence microscopy, and ImageJ software was used for all measurements. See  
86 the GSA Data Repository<sup>1</sup> for further details of localities and methods.

87

## 88 **RESULTS**

### 89 **Microbial mat metazoan communities**

90 Bedding planes of flaggy, wackestone to packstone grading into friable, dolomitized  
91 wackestone to mudstone from Omkyk Farm, 12-30 mm thick, show abundant aggregations of  
92 sinuous, straight, and apparently branching cloudinomorphs and *Namacalathus* associated  
93 with inferred microbial mats (Figs. 1A and B; Fig. 2). Inferred microbial mats are dark or  
94 covered in iron oxides and have irregular or patchy edges distinct from the yellow, micritic  
95 mudstone with skeletal bioclasts. Mats are usually <1 mm thick and undulating, and occur  
96 parallel to bedding at a spacing of 2-5 mm.

97 Tubular fossils from Omkyk Farm show a distinct annulated outer wall structure (Fig. 1C)  
98 but recrystallization obscures any internal stacked, funnel organization. They are therefore

99 attributed to cloudinomorphs. Material from Driedoornvlagte can be attributed to *Cloudina*  
100 (Grant, 1990).

101 Cloudinomorph individuals range from 1.2-21.7 mm in length, and 0.1-2.3 mm in width  
102 (n=604) as measured on bedding planes, and are inferred to be attached to mats, as they are  
103 most abundant within inferred mats and some individuals appear to radiate from them (Fig.  
104 1A). *In-situ Namacalathus* are present as clusters of small individuals within the mats (Fig.  
105 1A), and as larger individuals outside the mats, which show close aggregation and radiate  
106 from a smaller area of attachment with deformation between individuals (Fig. 1B).

107

### 108 **Cloudinomorph growth patterns**

109 The diameter of cloudinomorphs measured from bedding surfaces shows an initial fast  
110 rate of inflation within the first 1 mm of extensional growth but remains constant thereafter  
111 (Fig. 1D). While bedding plane surfaces show examples of potential attachment sites and/or  
112 branching cloudinomorphs (Fig. 2), evidence for bifurcating tubes can only be proven by the  
113 presence of a shared cavity.

114 Polished surfaces reveal that cloudinomorph tubes are infilled first by a cloudy,  
115 isopachous cement (21-587  $\mu\text{m}$  thick; mean = 110  $\mu\text{m}$ ; Fig. DR7), then remaining internal  
116 space by sparry calcite (Figs. DR2 and DR4). Cathodoluminescence reveals an earlier, thin  
117 (up to 200  $\mu\text{m}$ ) generation of acicular cement (Fig. DR6C). The isopachous cement is either  
118 patchy or zoned, and sparry calcite cements distinctly zoned (Figs. 3G, H, J). The presence of  
119 a shared cavity is evidenced by the absence of a wall or any associated skeletal breakage that  
120 might imply post-depositional compaction, and also that the isopachous cement crust forms a  
121 continuous crust connecting both tubes, as well as continuous sparry calcite cement infill  
122 (Figs. 3G, H).

123 One 3D model of the cloudinomorph outer wall, highlighted by the micritic envelope or  
124 the outer edge of the cavity lining isopachous cement, confirms the presence of multiple  
125 branches with differing orientations along one parent tube (Figs. 3A, B; Figs. DR2). These  
126 diverge from the parental tube at angles of 35 to 299° (Table DR2; Fig. DR8). The plunge  
127 angle of the branches and attachment site, are consistently shallow, from 1.4 to 7.1°. Models  
128 of the cavity as defined by the extent of sparry calcite confirms this multiple branching  
129 structure (Figs. 3C, D). The diameter of cloudinomorph branches measured directly from the  
130 3D models also shows an initial fast rate of inflation within the first 1 mm of growth but  
131 constant diameter thereafter (Fig. 1D).

132 Branches grow from the outer wall of the parent tube, i.e. with no intra-calar bifurcation  
133 (Figs. 3A-D). Models also reveal attachment sites of small cloudinomorph individuals, as  
134 indicated by the presence of the parental tube outer wall and no shared cavity (Figs. 3A, B;  
135 Fig. DR2D, G). The attached tube is often initially more narrow than the width of the tube to  
136 which it attaches (Figs. 3A, B), but the tube inflates also rapidly to form a cavity (Fig. 1D).  
137 Individuals can therefore be reconstructed with both multiple branches and attachment sites  
138 (Fig. 3E).

139

#### 140 **Cloudinomorph attachment structures**

141 Cementation can present as one tube attached either at the base (attachment) or along the  
142 length of the shell (mutual cementation). On the bedding surface, potential cemented/attached  
143 tubes are indicated by a gap between apparently branching tubes (Fig. 2E). This is inferred to  
144 represent either the isopachous cement crust or sediment infill between the parent and  
145 inflating daughter tube, or two attached tubes which are differently orientated in 3D relative  
146 to one another.

147 Mutual cementation is also observed at both Omkyk Farm and Driedoornvlagte between  
148 adjacent or near parallel tubes in close proximity ( $< 0.3$  mm) (Fig. 4A). At Driedoornvlagte,  
149 *Cloudina* walls are composed of brown, inclusion-rich dolomite and dolomitized extra-  
150 tubular structures, with geopetal dolomitized micrite present within the tube (Fig. 4D). Under  
151 cathodoluminescence, *Cloudina* walls show bright luminescence and neomorphosed calcite  
152 with the same bright luminescence is also present between the adjacent tubes suggesting that  
153 the *Cloudina* walls and the extra-tubular structure share the same diagenetic signature (Fig.  
154 4E). This structure predates the formation of a further distinctive, slightly bluish, dull  
155 luminescent neomorphosed calcite with patchy areas of brighter luminescence, that forms  
156 both adjacent to *Cloudina* walls and within the inner tube adjacent to the contact structure  
157 (Fig. 4E). An inclusion rich, non-luminescent sparry calcitic cement and a later clear sparry  
158 calcite postdate these cements (Fig. 4E).

159 Similar mutual cementation is also noted between cloudinomorphs and the outer wall of a  
160 fragment of *Namacalathus* (Fig. 4B; Fig. DR4), reaching 0.4 mm thickness. Attachment is  
161 further confirmed via serial sectioning and 3D modeling (Fig. 4C).

162

## 163 **DISCUSSION**

164 The low energy, inner ramp environment of the Upper Omkyk Member at Omkyk Farm  
165 has allowed for the preservation of an inferred microbial mat community of delicate, in-situ  
166 branching or cemented cloudinomorphs and *Namacalathus*.

167 The presence of a shared cavity in these cloudinomorphs shows that the parent and  
168 daughter branches shared the same living space. The continuation of early cement between  
169 the parent and daughter tube and the lack of evidence for breakage of the tube walls suggest  
170 this is a growth feature. This style of branching is unlike that previously recorded where the  
171 tube splits into two half cylinders within the parent tube, i.e. intra-parietal budding, or



172 dichotomous branching (Hua et al., 2005; Cortijo et al., 2010). We see no evidence of a  
173 dividing wall along the midline within the parent tube, suggesting a different form of  
174 reproduction, here conforming to external budding.

175 We find multiple examples of apical and longitudinal attachment accompanied by a  
176 neomorphosed calcite extratubular structure, which aided mutual cloudinomorph attachment.  
177 We further show the occurrence of attachment between cloudinomorph and *Namacalathus*.  
178 These structures pre-date all inorganic cements, including pseudomorphed aragonitic cement  
179 botryoids where present (Penny et al., 2014). Given that these structures are only found  
180 associated with cloudinomorphs, and also have multiple positions relative to the tubular  
181 growth form, it is likely that they have a biological origin. These structures may have formed  
182 by extra-tubular secretion, perhaps via extracellular polymeric substances (EPS) or an organic  
183 template, which became calcified. The close proximity of individuals appears to have  
184 encouraged mutual cementation allowing for the formation of a horizontal, multi-component,  
185 rigid structure associated with microbial mat surfaces (Fig. 4F). This confirms that the ability  
186 to gain secure, mutual, attachment was present by the terminal Ediacaran.

187 The observation of multiple branching in cloudinomorphs suggests a non-bilaterian  
188 affinity for these representatives. Modern cnidarians, in particular hydrozoans, show various  
189 forms of asexual reproduction, including longitudinal fission and external budding, rapid  
190 daughter branch diameter increase after branching, similar diameters of parent and daughter  
191 tubes, and multiple branching (Vinn and Zaton, 2012; Han et al., 2017; Yang et al., 2020).  
192 Such a non-bilaterian affinity would be counter to that implied by the presence of an inferred  
193 gut in cloudinomorphs from Nevada, USA (Schiffbauer et al., 2020), as well as the  
194 organized, lamellar microstructure of organic-walled cloudinomorphs from Mongolia (Yang  
195 et al., 2020). This apparent contradiction therefore raises the possibility that the common

196 Ediacaran-Cambrian tubular and stacked, funnel morphology is convergent, and that  
197 cloudinomorphs may, in fact, represent taxa of diverse affinity.

198

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204

## 205 **REFERENCES CITED**

- 206 Álvaro, J.J., Cortijo, I., Jensen, S., Mus, M.M. and Palacios, T., 2020. *Cloudina*-microbial  
207 reef resilience to substrate instability in a Cadomian retro-arc basin of the Iberian  
208 Peninsula. *Precambrian Research*, v. 336, p. 105479.
- 209 Becker-Kerber, B., Pacheco, M. L. A. F., Rudnitzki, I. D., Galante, D., Rodrigues, F., and de  
210 Moraes Leme, J., 2017, Ecological interactions in *Cloudina* from the Ediacaran of  
211 Brazil: implications for the rise of animal biomineralization: *Scientific Reports*, v. 7,  
212 p. 5482-5488.
- 213 Cai, Y., Hua, H., Schiffbauer, J. D., Sun, B., and Yuan, X., 2014, Tube growth patterns and  
214 microbial mat-related lifestyles in the Ediacaran fossil *Cloudina*, Gaojiashan  
215 Lagerstätte, South China: *Gondwana Research*, v. 25, p. 1008-1018.
- 216 Cai, Y., Schiffbauer, J. D., Hua, H., and Xiao, S., 2011, Morphology and paleoecology of the  
217 late Ediacaran tubular fossil *Conotubus hemiannulatus* from the Gaojiashan  
218 Lagerstätte of southern Shaanxi Province, South China: *Precambrian Research*, v.  
219 191, p. 46-57.

220 Cortijo, I., Cai, Y., Hua, H., Schiffbauer, J. D., and Xiao, S., 2014, Life history and  
221 autecology of an Ediacaran index fossil: development and dispersal of Cloudina:  
222 Gondwana Research, v. 28, p. 419-424.

223 Cortijo, I., Mus, M. M., Jensen, S., and Palacios, T., 2010, A new species of Cloudina from  
224 the terminal Ediacaran of Spain: Precambrian Research, v. 176, p. 1-10.

225 Germs, G. J., 1972, New shelly fossils from Nama Group, south west Africa: American  
226 Journal of Science, v. 272, p. 752-761.

227 Germs, G., 1983, Implications of a sedimentary facies and depositional environmental  
228 analysis of the Nama Group in South West Africa/Namibia: Special Publications of  
229 the Geological Society of South Africa, v. 11, p. 89-114.

230 Grant, S., 1990, Shell structure and distribution of Cloudina, a potential index fossil for the  
231 terminal Proterozoic: American Journal of Science, v. 290, p. 261-294.

232 Grotzinger, J. P., Bowring, S. A., Saylor, B. Z., and Kaufman, A. J., 1995, Biostratigraphic  
233 and geochronologic constraints on early animal evolution: Science, v. 270, p. 598-  
234 604.

235 Han, J., Cai, Y., Schiffbauer, J. D., Hua, H., Wang, X., Yang, X., Uesugi, K., Komiya, T.,  
236 and Sun, J., 2017, A Cloudina-like fossil with evidence of asexual reproduction from  
237 the lowest Cambrian, South China: Geological Magazine, v. 154, p. 1294-1305.

238 Hua, H., Chen, Z., Yuan, X., Zhang, L., and Xiao, S., 2005, Skeletogenesis and asexual  
239 reproduction in the earliest biomineralizing animal Cloudina: Geology, v. 33, p. 277-  
240 280.

241 Linnemann, U., Ovtcharova, M., Schaltegger, U., Gärtner, A., Hautmann, M., Geyer, G.,  
242 Vickers-Rich, P., Rich, T., Plessen, B., and Hofmann, M., 2019, New high-resolution  
243 age data from the Ediacaran–Cambrian boundary indicate rapid, ecologically driven  
244 onset of the Cambrian explosion: Terra Nova, v. 31, p. 49-58.

245 Mehra, A. and Maloof, A., 2018. Multiscale approach reveals that Cloudina aggregates are  
246 detritus and not in situ reef constructions. *Proceedings of the National Academy of*  
247 *Sciences*, 115(11), p. E2519-E2527.

248 Penny, A. M., Wood, R., Curtis, A., Bowyer, F., Tostevin, R., and Hoffman, K.-H., 2014,  
249 Ediacaran metazoan reefs from the Nama Group, Namibia: *Science*, v. 344, p. 1504-  
250 1506.

251 Saylor, B. Z., Grotzinger, J. P., and Germs, G. J., 1995, Sequence stratigraphy and  
252 sedimentology of the Neoproterozoic Kuibis and Schwarzrand subgroups (Nama  
253 Group), southwestern Namibia: *Precambrian Research*, v. 73, p. 153-171.

254 Saylor, B. Z., Kaufman, A. J., Grotzinger, J. P., and Urban, F., 1998, A composite reference  
255 section for terminal Proterozoic strata of southern Namibia: *Journal of Sedimentary*  
256 *Research*, v. 68, p. 1223-35.

257 Schiffbauer, J.D., Selly, T., Jacquet, S.M., Nelson, L.L., Strange, M.A., Cai, Y., and Smith,  
258 E.F., 2020, Discovery of bilaterian-type through-guts in cloudinomorphs from the  
259 terminal Ediacaran Period: *Nature Communications*, v.11, p. 205.

260 Schmitz, M., 2012, Radiogenic isotope geochronology, *The Geologic Time Scale*, Elsevier,  
261 p. 115-126.

262 Selly, T., Schiffbauer, J.D., Jacquet, S.M., Smith, E.F., Nelson, L.L., Andreasen, B.D.,  
263 Huntley, J.W., Strange, M.A., O'Neil, G.R., Thater, C.A., Bykova, N., Steiner, M.,  
264 Yang, B., and Cai, Y., 2020, A new cloudinid fossil assemblage from the terminal  
265 Ediacaran of Nevada, USA: *Journal of Systematic Palaeontology*, v.18, p. 357-379.

266 Terleev, A., Luchinina, V., Sosnovskaya, O., and Bagmet, G., 2004, Calcareous algae and  
267 lower boundary of the Cambrian in the western Altai-Sayan Folded Area: *Geologiya i*  
268 *Geofizika*, v. 45, p. 485-491.

269 Vinn, O., and Zaton, M., 2012, Inconsistencies in proposed annelid affinities of early  
270 biomineralized organism Cloudina (Ediacaran): structural and ontogenetic evidences:  
271 Carnets De Geologie, p. 39-47.

272 Wood, R., Curtis, A., Penny, A., Zhuravlev, A. Y., Curtis-Walcott, S., Iippinge, S., and  
273 Bowyer, F., 2017a, Flexible and responsive growth strategy of the Ediacaran skeletal  
274 Cloudina from the Nama Group, Namibia: Geology, v. 45, p. 259-262.

275 Wood, R., Poulton, S., Prave, A., Hoffmann, K.-H., Clarkson, M., Guilbaud, R., Lyne, J.,  
276 Tostevin, R., Bowyer, F., and Penny, A., 2015, Dynamic redox conditions control late  
277 Ediacaran metazoan ecosystems in the Nama Group, Namibia: Precambrian Research,  
278 v. 261, p. 252-271.

279 Yang, B., Steiner, M., Schiffbauer, J.D., Selly, T., Wu, X., Zhang, C. and Liu, P., 2020.  
280 Ultrastructure of Ediacaran cloudinids suggests diverse taphonomic histories and  
281 affinities with non-biomineralized annelids. Scientific Reports, 10(1), pp.1-12.

282

### 283 **FIGURE CAPTIONS**

284 Figure 1: Bedding surfaces from Upper Omkyk Member, Omkyk Farm, Namibia. A: *In-situ*  
285 cloudinomorphs and *Namacalathus* (black arrows) on two generations of microbial mat  
286 surfaces (1 and 2) with projecting cloudinomorphs (red arrows), and bioclasts in inter-mat  
287 mudstone (3). B: Cluster of large *Namacalathus* in inter-mat area (arrow). C: Cloudinomorph  
288 with annulated morphology (funnels arrowed). D: Width of cloudinomorph tubes measured  
289 from 2D bedding planes and multiple branching 3D model.

290

291 Figure 2: Cloudinomorphs with multiple attachment sites and branches. A, C, E: Bedding  
292 plane images; B, D, F: Trace through inferred central axes of tubes. E, multiple attachment

293 sites with isopachous cements or sediment infill defining the contact between tubes (single  
294 arrows) and inner tube wall (double arrow).

295

296 Figure 3: Multiple branching cloudinomorph with the parent tube (1, white arrow), branching  
297 daughter tube (2; shared cavities, orange arrow), indirect evidence of branching where the  
298 cavity does not extend to the full tube (green arrow), and attachment sites (3, red arrow). A:  
299 Upper, plan view of 3D model (from bedding surface) of outer tube with 5% smoothing. B:  
300 Lower, rear view of same model. C: Upper, plan view of 3D model (from bedding surface) of  
301 open cavity, D: Lower, plan view of same model. E: Reconstruction of multiple branching  
302 cloudinomorph (Artist: Astrid Robertsson). F: PPL photomicrograph and G:  
303 Cathodoluminescent photomicrograph of branching cloudinomorph, showing continuity of  
304 isopachous (I) and sparry calcite (S) cements in parent and daughter tube. H: Inset of G,  
305 showing continuity of isopachous cement between the two tubes (blue arrows) and later  
306 sparry cement infilling both (orange arrows). I: PPL photomicrograph and J:  
307 Cathodoluminescent photomicrograph of cloudinomorph tube where arrows mark successive  
308 funnels, with isopachous (I) and sparry calcite (S) cement infill.

309

310 Figure 4: Cloudinomorph attachment. A: Plan view of attached parallel cloudinomorph tubes  
311 (white arrow) with stacked funnel morphology (red arrows indicate funnels). B: Plan view of  
312 extra-tubular structure between cloudinomorph tube and *Namacalathus* (white arrow). C: 3D  
313 model showing cementation between *Namacalathus* and a cloudinomorph (white arrow), blue  
314 arrow indicates way up. D: PPL photomicrograph of two *Cloudina* tubes from  
315 Driedoornvlagte, with inclusion rich extra tubular structure (ETS) between the tubes.  
316 Geopetal dolomitic geopetal micrite (DM), and calcitic spar infill (CS). E:  
317 Cathodoluminescent image of same area as D, showing two generations within the ETS,

318 bright luminescence (ETS<sup>1</sup>) then dull luminescence with patches of bright luminescence  
319 (ETS<sup>2</sup>). Both pre-date the inclusion-rich cement (IC) and latest sparry cements (CS). F:  
320 Reconstruction of inferred microbial mat-community with in-situ skeletal metazoans (1)  
321 Microbial mat; (2) *Namacalathus* cluster; (3) Isolated *Namacalathus* outside microbial mat;  
322 (4) Branching cloudinomorph with horizontal habit; (5) Multiple attachment sites of  
323 cloudinomorph; (6) Mutual attachment of cloudinomorph by extra-tubular structures; (7)  
324 Attachment between cloudinomorph and *Namacalathus*. (Artist: Astrid Robertsson).