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

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ABSTRACT

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

INTRODUCTION

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

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

The affinity of cloudinomorphs is problematic, with the group variously attributed to calcareous algae, cnidarians, or annelids (Terleev et al., 2004; e.g., Vinn and Zaton, 2012; Schiffbauer et al., 2020). A cnidarian affinity is supported by the deep-seated division of *Cloudina* tubes within the parent tube (Hua et al., 2005; Cortijo et al., 2014). However, the general nested funnel morphology and skeletal ultrastructure of some cloudinomorphs are similar to modern annelids (Vinn and Zaton, 2012; Yang et al., 2020), and preservation of a central, tubular, pyritized structure in a cloudinomorph inferred to be a gut would support a stem-annelid affinity (Schiffbauer et al., 2020). Indeed, many skeletal features of cloudinomorphs are in fact present in diverse invertebrate groups.

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

GEOLOGICAL SETTING

The Nama Group (ca. 550–541 Ma) is a fossiliferous Ediacaran–Cambrian sedimentary ramp succession deposited in two subbasins (Germs, 1983; see also the Supplemental Material[1] and Fig. S1 therein), consisting of the Kuibis Subgroup overlain by the Schwarzrand Subgroup (Germs, 1983; Saylor et al., 1995). Ash bed dates and inferred sedimentation rates suggest the basal Nama unconformity has an age of ca. 550–553 Ma (Saylor et al., 1998), and the top of the Schwarzrand Subgroup is younger than at least 539.64 ± 0.19 Ma (Linnemann et al., 2019).

MATERIAL AND METHODS

Samples from *in situ* bedding planes were collected from near the top of the Upper Omkyk Member of the Kuibis Subgroup, at Omkyk Farm and Driedoornvlagte in the Zaris Subbasin (Table S1; Fig. S1). An ash bed from the overlying Hoogland Member is dated at

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[1]Supplemental Material. Geological setting of the study sites within the Nama Group, Namibia; methods used for serial sectioning and 3-D model reconstruction; additional photomicrographs; and cloudinomorph tube measurements. Please visit https://doi.org/10.1130/GEOL.S.12307427 to access the supplemental material, and contact editing@geosociety.org with any questions.

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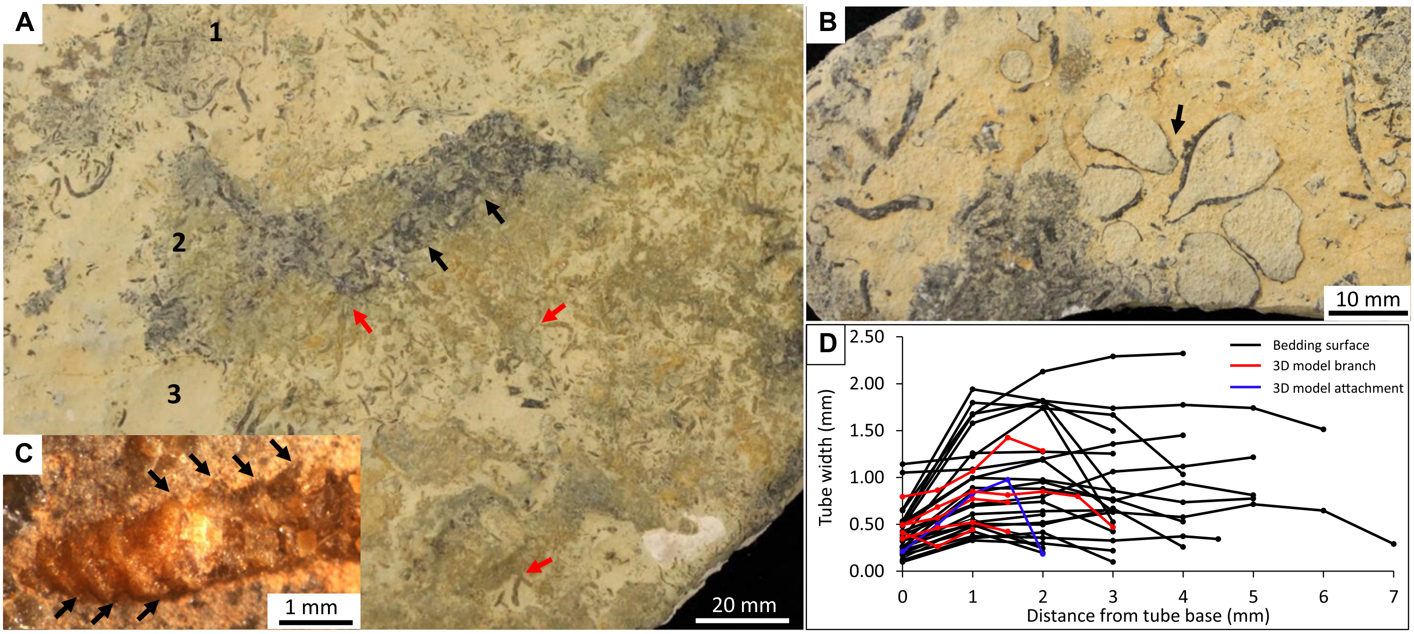

Figure 1. Bedding surfaces from the Upper Omkyk Member, Omkyk Farm, Namibia. (A) *In situ* cloudinomorphs and *Namacalathus* (black arrows) on two generations of microbial mat surfaces (1 and 2) with projecting cloudinomorphs (red arrows), and bioclasts in intermat mudstone (3). (B) Cluster of large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

547.32 ± 0.65 Ma (Grotzinger et al., 1995; Schmitz, 2012). Driedoornvlagte is a shallow reef complex that formed in a midramp setting that contains abundant skeletal taxa, *Cloudina*, *Namacalathus*, and *Namapoikia*. At Omkyk Farm, strata record deposition at an inner-ramp position close to the Osis Arch, into increasingly shallow, very low-energy, lagoonal settings containing *Cloudina* and *Namacalathus* (Wood et al., 2015).

Cloudinomorph specimens were serially ground into increments of either 10 µm (Figs. S2 and S3) or 25 µm (Fig. S4), using a Buehler Petrothin thin-sectioning system, and imaged using a binocular microscope or flatbed scanner. Processed images were imported as a virtual stack into Avizo 9 software to create three-dimensional (3-D) models composed of between 50 and 123 two-dimensional images and smoothed to reduce noise. Cloudinomorph walls and the open cavity were manually segmented separately (Fig. S5). Highly polished thin sections were imaged by standard petrographic and cathodoluminescence microscopy, and ImageJ software (https://imagej.net/) was used for all measurements. See the Supplemental Material for further details of localities and methods.

RESULTS

Microbial Mat Metazoan Communities

Bedding planes of flaggy wackestone to packstone grading into friable, dolomitized wackestone to mudstone from Omkyk Farm, 12–30 mm thick, showed abundant aggregations of sinuous, straight, and apparently branching cloudinomorphs and *Namacalathus* associated with inferred microbial mats (Figs. 1A, 1B, and 2). Inferred microbial mats were dark or covered in iron oxides and had irregular or patchy edges distinct from the yellow, micritic mudstone with skeletal bioclasts. Mats were usually <1 mm thick and undulating, and they occurred parallel to bedding at a spacing of 2–5 mm.

Tubular fossils from Omkyk Farm showed a distinct annulated outer wall structure (Fig. 1C), but recrystallization obscured any internal stacked, funnel organization. They were therefore attributed to cloudinomorphs. Material from Driedoornvlagte can be attributed to *Cloudina* (Grant, 1990).

Cloudinomorph individuals ranged from 1.2 to 21.7 mm in length and from 0.1 to 2.3 mm in width ($n = 604$), as measured on bedding planes, and they were inferred to be attached to mats, because they are most abundant within inferred mats, and some individuals appeared to radiate from the mats (Fig. 1A). *In situ Namacalathus* specimens were present as clusters of small individuals within the mats (Fig. 1A), and as larger individuals outside the mats, which showed close aggregation and radiated from a smaller area of attachment with deformation between individuals (Fig. 1B).

Cloudinomorph Growth Patterns

The diameter of cloudinomorphs measured from bedding surfaces showed an initial fast rate of inflation within the first 1 mm of extensional growth but remained constant thereafter

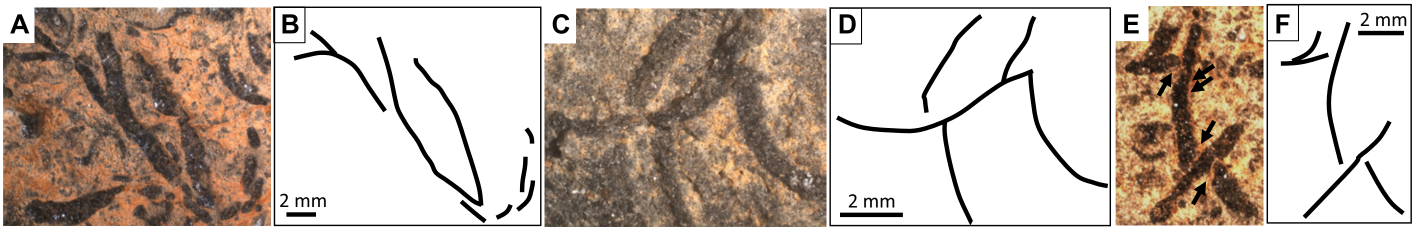

Figure 2. Cloudinomorphs with multiple attachment sites and branches. (A, C, E) Bedding plane images. (B, D, F) Trace through inferred central axes of tubes. Multiple attachment sites with isopachous cements or sediment infill in E define contact between tubes (single arrows) and inner tube wall (double arrow).

(Fig. 1D). While bedding plane surfaces showed examples of potential attachment sites and/or branching cloudinomorphs (Fig. 2), evidence for bifurcating tubes can only be proven by the presence of a shared cavity.

Polished surfaces revealed that cloudinomorph tubes were infilled first by a cloudy, isopachous cement (21–587 µm thick; mean = 110 µm; Fig. S7) and then by sparry calcite in the remaining internal space (Figs. S2 and S4). Cathodoluminescence revealed an earlier, thin (up to 200 µm) generation of acicular cement (Fig. S6C). The isopachous cement is either patchy or zoned, and sparry calcite cements are distinctly zoned (Figs. 3G, 3H, and 3J). The presence of a shared cavity is evidenced by the absence of a wall or any associated skeletal breakage that might imply postdepositional compaction, and also by the isopachous cement crust that forms a continuous crust connecting both tubes, as well as continuous sparry calcite cement infill (Figs. 3G and 3H).

One 3-D model of the cloudinomorph outer wall, highlighted by the micritic envelope or the outer edge of the cavity-lining isopachous cement, confirmed the presence of multiple branches with differing orientations along one parent tube (Figs. 3A and 3B; Fig. S2). These diverged from the parental tube at angles of 35° to 299° (Table S2; Fig. S8). The plunge angles of the branches and attachment site were consistently shallow, from 1.4° to 7.1°. Models of the cavity as defined by the extent of sparry calcite confirmed this multiple branching structure (Figs. 3C and 3D). The diameter of cloudinomorph branches measured directly from the 3-D models also showed an initial fast rate of inflation within the first 1 mm of growth but constant diameter thereafter (Fig. 1D).

Branches grew from the outer wall of the parent tube, i.e., with no intracalar bifurcation (Figs. 3A–3D). Models also revealed attachment sites of small cloudinomorph individuals, as indicated by the presence of the parental tube outer wall and no shared cavity (Figs. 3A and 3B; Figs. S2D and S2G). The attached tube was often initially more narrow than the width of the tube to which it was attached (Figs. 3A and 3B), but the tube also inflated rapidly to form a cavity (Fig. 1D). Individuals could therefore be reconstructed with both multiple branches and attachment sites (Fig. 3E).

Cloudinomorph Attachment Structures

Cementation was observed as one tube attached either at the base (attachment) or along the length of the shell (mutual cementation). On the bedding surface, potential cemented/attached tubes were indicated by a gap between apparently branching tubes (Fig. 2E). This was inferred to represent either the isopachous cement crust or sediment infill between the parent and inflating daughter tube, or two attached tubes that were differently oriented in 3-D relative to one another.

Mutual cementation was also observed at both Omkyk Farm and Driedoornvlagte between adjacent or near-parallel tubes in close proximity (<0.3 mm; Fig. 4A). At Driedoornvlagte, *Cloudina* walls were composed of brown, inclusion-rich dolomite and dolomitized extratubular structures, with geopetal dolomitized micrite present within the tube (Fig. 4D). Under cathodoluminescence, *Cloudina* walls showed bright luminescence and neomorphosed calcite with the same bright luminescence that was also present between the adjacent tubes, suggesting that the *Cloudina* walls and the extratubular structure shared the same diagenetic signature (Fig. 4E).

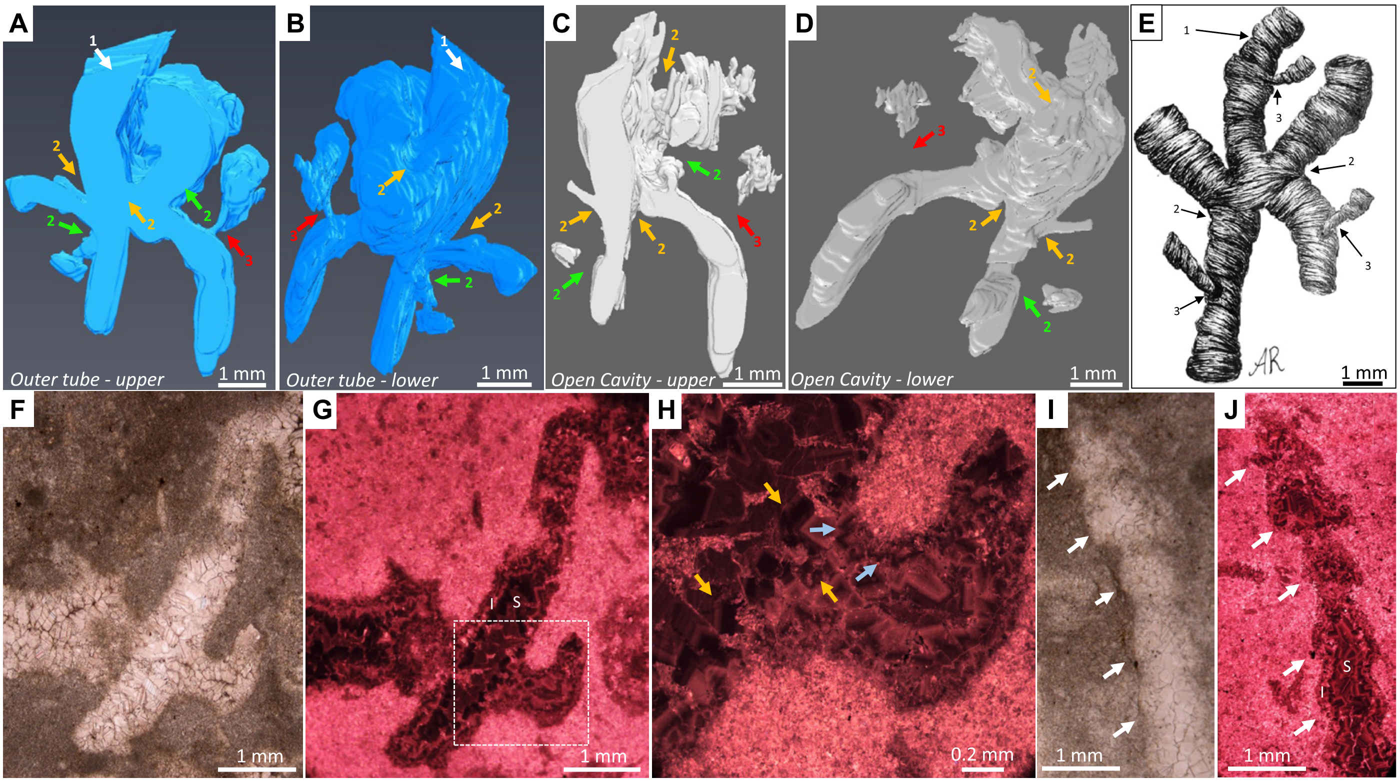

Figure 3. Multiple branching cloudinomorph with parent tube (1, white arrow), branching daughter tube (2, shared cavities, orange arrows), indirect evidence of branching where cavity does not extend to full tube (green arrows), and attachment sites (3, red arrows). (A) Upper, plan view of three-dimensional (3-D) model (from bedding surface) of outer tube with 5% smoothing. (B) Lower, rear view of same model. (C) Upper, plan view of 3-D model (from bedding surface) of open cavity. (D) Lower, plan view of same model. (E) Reconstruction of multiple branching cloudinomorph (artist: Astrid Robertsson). (F) Plane-polarized light (PPL) photomicrograph and (G) cathodoluminescent photomicrograph of branching cloudinomorph, showing continuity of isopachous (I) and sparry calcite (S) cements in parent and daughter tubes. (H) Inset of G, showing continuity of isopachous cement between two tubes (blue arrows) and later sparry cement infilling both tubes (orange arrows). (I) PPL photomicrograph and (J) cathodoluminescent photomicrograph of cloudinomorph tube where arrows mark successive funnels, with isopachous (I) and sparry calcite (S) cement infill.

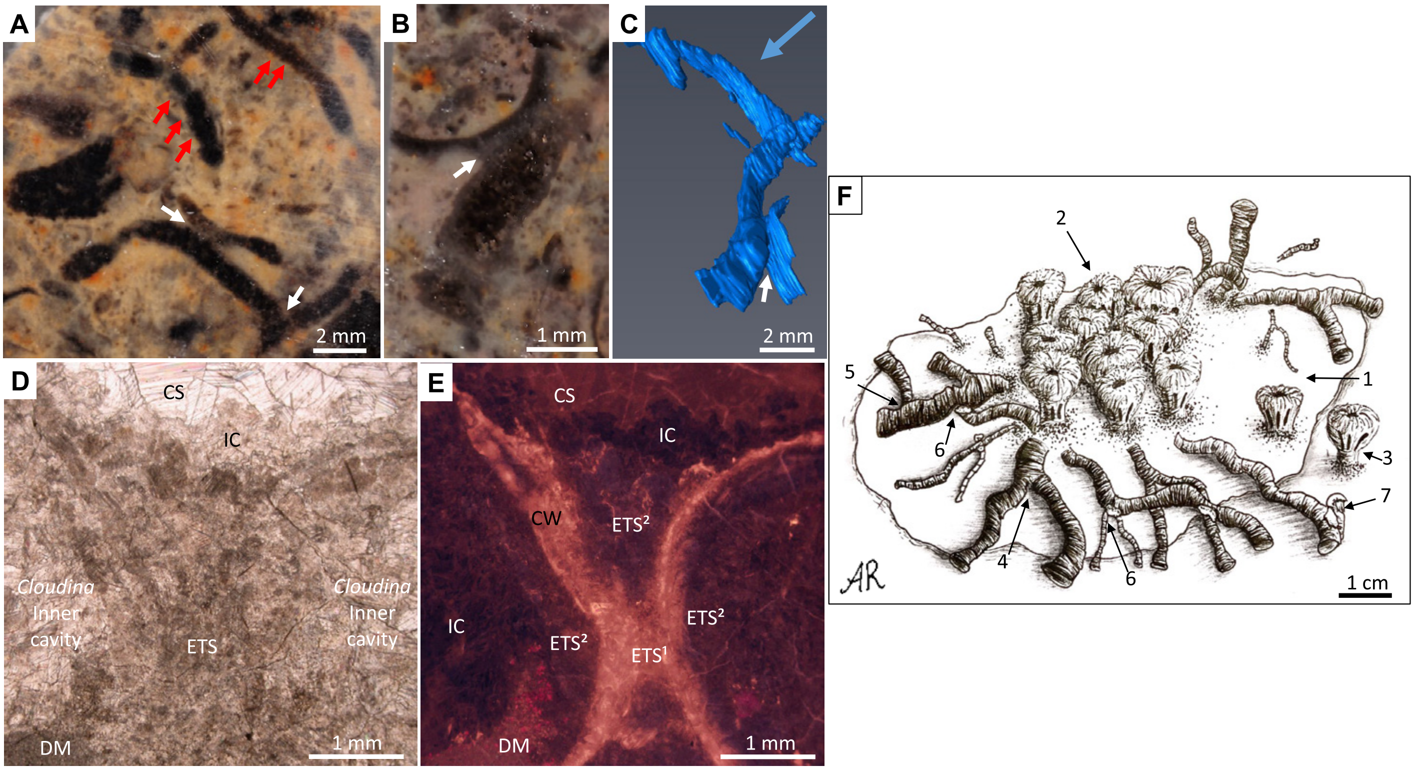

Figure 4. Cloudinomorph attachment. (A) Plan view of attached parallel cloudinomorph tubes (white arrows) with stacked funnel morphology (red arrows indicate funnels). (B) Plan view of extratubular structure between cloudinomorph tube and *Namacalathus* (white arrow). (C) Three-dimensional (3-D) model showing cementation between *Namacalathus* and cloudinomorph (white arrow), where blue arrow indicates way up. (D) Plane-polarized light (PPL) photomicrograph of two *Cloudina* tubes from Driedoornvlagte, with inclusion-rich extratubular structure (ETS) between tubes, geopetal dolomitic micrite (DM), inclusion-rich cement (IC), and calcitic spar infill (CS). (E) Cathodoluminescence image of same area as D, showing two generations within ETS: bright luminescence (ETS^1) and then dull luminescence with patches of bright luminescence (ETS^2). Both predate inclusion-rich cement (IC) and latest sparry cements (CS). (F) Reconstruction of inferred microbial mat community with *in situ* skeletal metazoans: (1) microbial mat; (2) *Namacalathus* cluster; (3) isolated *Namacalathus* outside microbial mat; (4) branching cloudinomorph with horizontal habit; (5) multiple branching cloudinomorph; (6) mutual attachment of cloudinomorph by extratubular structures; (7) attachment between cloudinomorph and *Namacalathus* (artist: Astrid Robertsson).

This structure predated the formation of a further distinctive, slightly bluish, dully luminescent neomorphosed calcite with patchy areas of brighter luminescence, which formed both adjacent to *Cloudina* walls and within the inner tube adjacent to the contact structure (Fig. 4E). An inclusion-rich, nonluminescent sparry calcitic cement and a later clear sparry calcite postdate these cements (Fig. 4E).

Similar mutual cementation was also noted between cloudinomorphs and the outer wall of a fragment of *Namacalathus* (Fig. 4B; Fig. S4), reaching 0.4 mm thickness. Attachment was further confirmed via serial sectioning and 3-D modeling (Fig. 4C).

DISCUSSION

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

The presence of a shared cavity in these cloudinomorphs shows that the parent and daughter branches shared the same living space. The continuation of early cement between the parent and daughter tubes and the lack of evidence for breakage of the tube walls suggest that this is a growth feature. This style of branching is unlike that previously recorded, where the tube splits into two half cylinders within the parent tube, i.e., intraparietal budding, or dichotomous branching (Hua et al., 2005; Cortijo et al., 2010). We saw no evidence of a dividing wall along the midline within the parent tube, suggesting a different form of reproduction, here conforming to external budding.

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

The observation of multiple branching in cloudinomorphs suggests a non-bilaterian affinity for these representatives. Modern cnidarians, in particular hydrozoans, show various forms of asexual reproduction, including longitudinal fission and external budding, rapid daughter branch diameter increase after branching, similar diameters of parent and daughter tubes, and multiple branching (Vinn and Zaton, 2012; Han et al., 2017; Yang et al., 2020).

Such a non-bilaterian affinity would be counter to that implied by the presence of an inferred gut in cloudinomorphs from Nevada (Schiffbauer et al., 2020), as well as the organized, lamellar microstructure of organic-walled cloudinomorphs from Mongolia (Yang et al., 2020).

This apparent contradiction therefore raises the possibility that the common Ediacaran-Cambrian tubular and stacked, funnel morphology is convergent, and that cloudinomorphs may, in fact, represent taxa of diverse affinity.

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