A Revised Morphology of *Cloudina* with Ecological and Phylogenetic Implications

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Abstract

The conventional view of the Ediacaran index fossil *Cloudina*, as proposed by Grant (1990), depicts the shell structure as a series of nested test tubes. A digital serial-reconstruction of *Cloudina* and examination of thin sections indicates that only the bottom-most tube has a bottom and that the shell wall structure is not as well defined as previously thought. The conventional ecological reconstruction, as proposed by Seilacher (1999), puts *Cloudina* in a microbial mat framework. Evidence from fossils *in situ* and from the shape of *Cloudina* suggests that this interpretation is incorrect. Rather, I propose that *Cloudina* lived on seaweeds in the reef environment. I also introduce a new mode of inference in determining shell orientation based on gravitational forces. Given the morphological evidence, *Cloudina* appears to be more similar to pogonophoran or annelid worms and less similar than previously thought to cnidarian corals.

Introduction

Life in the Precambrian is seen by many in a Hobbesian view—sessile, benthic, and short. While this may accurately describe the functional behavior of Ediacaran communities, it overlooks the significant metazoan diversity that was present there, for within the Ediacaran period the first metazoans entered the fossil record and diversified. Even though the presence of metazoans in the Ediacaran has been known for over thirty years, relatively little is known about their phylogenic affinities, their structure, and their role in the ecosystem. *Cloudina* is one of these organisms, and this paper will provide a brief overview of what is known about *Cloudina* and then present a new interpretation based on detailed 3D morphological reconstruction.

Geological Setting of Cloudina

Cloudina is a small (0.3 to 6.5 mm in diameter and up to 3.5 cm long (Germs, 1972; Grant, 1990)), shelly metazoan that has been found worldwide, including Namibia (Germs, 1972), Oman (Conway Morris et al., 1990), China (Conway Morris et al., 1990; Bengtson and Zhao, 1992), Canada (Hofmann and Mountjoy, 2001), and Nevada (Hagadorn and Waggoner, 2000.) It has thus been proposed as an index fossil for the terminal Neoproterozoic (Grant, 1990), now called the Ediacaran Period (Knoll et al., 2004). *Cloudina* has never been found on the same bedding plane as the problematic soft-bodied fossils of the Ediacarans, but they are found interbedded in the same formation, indicating that they likely co-existed together, though perhaps in a different micro-habitat (Germs, 1972, 1983). *Cloudina* has been found in the same bed as other early shelled metazoans, such as *Namacalathus* and other unidentified—and likely undescribed—shelly metazoans (Grotzinger et al., 2000), indicating that it is but one part of a robust and diverse Ediacaran ecosystem. As a part of this larger community of metazoans, *Cloudina* is among the first organisms to form a shell, and this development appears to be worldwide and geologically instantaneous (Grant, 1990). *Cloudina* is also the first organism to exhibit traces of being predated upon (Bengtson and Zhao, 1992; Hua et al., 2003).

The specimens of *Cloudina* used in this study come from the Nama Group of southern Namibia. The general stratigraphy of the Nama Group was worked out by Martin (1965) and Germs (1972, 1974, 1983), and is presented in Figure 1. According to Grotzinger et al. (2000), "in general, the Nama Group consists of a number of marine-shelf siliciclastic and carbonate sequences (Kuibis and Schwarzrand Subgroups) overlain by alluvial to shallow marine molasse (Fish River Subgroup) that documents unroofing of the Damara/Gariep hinterlands…. Thrombolite-stromatolite reefs are well developed in the Kuibis Subgroup of the northern, Zaris

subbasin, and in the Huns platform of the southern, Witputs subbasin." Numerous reef structures, as described in Grotzinger et al. (2000), are present and the specimens for this analysis—as with all *Cloudina* specimens from Namibia—were found in a debris flow from the top of the reef. Grotzinger et al. (1995) dated the formation to the late Ediacaran. More information on the stratigraphy and geologic setting can be obtained from Grotzinger et al. (2000) and Germs (1972, 1974, 1983).

Current Thought on Cloudina

Cloudina has been problematic since its discovery by Germs (1972), who tentatively assigned it to the Cribricyathea Vologdin, 1961, a class known from the lower Cambrian. Germs further noted that *Cloudina* reproduced by budding (and perhaps by other means, but budding is the only form he observed). Glaessner (1976) accepted Germs' classification and further proposed that *Cloudina* was similar to the annelid worms (e.g. serpulid polychaetes). However, Hahn and Pflug (1985) expressed doubt as to whether Germs and Glaessner's classification was correct and did not propose a higher affinity than family (Cloudinidae, which they established). Conway Morris et al. (1990) discounted both Germs' and Glaessner's suggested relationships, unwilling to identify it to anything higher than family (Cloudinidae). Grant (1990), in a comprehensive review of the genus, concluded that *Cloudina*'s tubes each had their own bottom and thus suggested that it had "at least a cnidarian grade of organization" (p. 288). Grant also provided the first schematic reconstruction of *Cloudina* (Figure 2). Bengtson and Conway Morris (1992) do not comment on Grant's (1990) cnidarian suggestion but do discount the relationship between annelids (Glaessner, 1976) and cribricyathans (Germs, 1972; Glaessner, 1976). Conway Morris (1993), agreeing with Grant (1990), suggested that *Cloudina* could conceivably be a stem group cnidarian. More recent workers have not commented on any higher

affinities or relationships, though Gaucher (2000) and Hua et al. (2003) have further documented cases of budding on *Cloudina*, making the stem group cnidarian case stronger (Figure 3).

Seilacher (1999) was the first to propose a life habit for *Cloudina*, positing that it was a "mat-sticker" (Figure 4; Figure 5). Seilacher pointed out that, "while the taxonomic position of *Cloudina* and related forms remains problematic, conical shells with an obstructed apex fit the paradigm of 'sediment stickers.' Being immobile, members of this guild gain their stabilization by growing upward with the sediment, and at the same time moving the soft parts upward within the shell like an elevator" (Seilacher, 1999, p. 91). Seilacher et al. (2003) reiterated this view.

Seilacher's (1999) interpretation of lifestyle is based on the morphological reconstruction of Grant (1990), as can be seen clearly in Figure 5. Currently, this reconstruction is the best information available on *Cloudina*. Unfortunately, it is based on interpretation of thin sections, and while Bengtson and Zhao (1992) and Hua et al. (2003) have 3D specimens that confirm many of the findings of Grant (1990), they do not provide a full picture of the internal morphology of *Cloudina*. Neither Bengtson and Zhao (1992) nor Hua et al. (2003) specifically address the issue of the "test tube" bottoms, one of the key pieces of evidence in support of a stem group cnidarian identification. Though they claim that their findings support Grant's (1990) reconstruction, Figure 2B in Bengtson and Zhao (1992)—the only cross section they give in support of this claim—does not show the "test tube" bottoms, as would be expected from the Grant (1990) reconstruction. Thin section analysis and reconstruction, such as the work done by Grant (1990), is dependent on getting a correct cross section, and slight variations in the orientation of the cross section can lead to an inaccurate or incomplete reconstruction of the organism's shell. Given the pre-eminence of morphology in interpreting the role of *Cloudina* and other similar organisms in the Ediacaran reef environment, the only way to make significant

progress in our understanding of *Cloudina* is to obtain a comprehensive 3D reconstruction of the organism.

Materials and Methods

A 7.5 x 7.5 x 3 cm rock with specimens of *Cloudina*, collected by Grotzinger in 2000, was chosen for the degree of contrast between the fossils and the surrounding rock matrix. The rock was cut in half and mounted on a 0.55 cm thick metal plate and ground flat. Four parallel 1-mm diameter holes were drilled all the way through the rock for calibrating and orienting the images. A layer of mineral oil (CVS store brand) was then applied to the surface of the fossil to improve refraction and the fossil was scanned into the computer using a high-quality, color JPEG format (resulting image sizes ranged from 25 to 30 MB). Using a surface grinder, 50 microns were ground off from the sample, as described in Watters and Grotzinger (2001) and Watters (2000). Mineral oil was again applied and the fossil was scanned in. This process was repeated a total of 566 times, resulting in a total of 567 images. After image 509 the calibration holes had to be redrilled, and one needed to be relocated. The images were then loaded into MATLAB (6.5r1; Mathworks Corporation), the location of the calibration holes on each image were marked (so as to align each image with the ones above and below it), and the images were then subjected to a battery of image processing procedures. An enhanced, grayscale image was generated by combining intensity data from the red and green color channels, after which an image thresholding procedure transformed the grayscale image into a black and white image. A number of other procedures was also performed to eliminate unwanted image components (such as noise introduced by different color intensities in the original rock not related to the fossil organism) and to smooth fossil boundaries so as to simplify the contours obtained. Due to within-image color intensity variance, not all material that was part of the fossil was identified as

such by the computer; future work will have to focus on better differentiating fossil material from the matrix. Nonetheless, a good deal of the fossil was recognized as such by the software and thus included in the reconstruction. A region of interest, which in this case was in the shape of a rectangle, was selected and contours were obtained for that region from 509 images representing 2.545 cm (omitting those images taken after the re-drilling of the calibration holes). The contour file was transformed by the program NUAGES (Geiger, 1993) into a 3D inventor model, which became the reconstruction. Computer screenshots of the reconstructions were made, and the original inventor files are available from the author. Three different specimens were selected for the reconstruction and are displayed in Figures 6 and 7.

Advantages of 3D Digital Serial Sectioning

Besides obtaining a full 3D model of *Cloudina*, there are other advantages to creating a computerized 3D model of a fossil that are not otherwise discussed in this paper. The method of obtaining a region of interest is to select a polygon from the first picture; the polygon can be in any shape and thus allows for the examination of any chosen part of the organism's morphology. Furthermore, a catalogue of cross-sections can be compiled, allowing for easy identification in the field or in the laboratory. In addition, population statistics can be measured more accurately using the computer. For other advantageous uses of 3D serial sectioning, the reader is referred to Watters and Grotzinger (2001).

Results

The specimens chosen were oriented parallel to the bedding plane and thus their orientation is not significant in terms of deriving a life-habitat or in determining direction of growth with respect to the structure upon which it grew. No significant curvature in the

specimens was noted, similar to the phosphatic fossils of Bengtson and Zhao (1992) and Hua et al. (2003). The flange structure described by Grant (1990) and shown in Figures 2-3 is observed in this reconstruction; one is the structure observed at the very top right of Figure 7B and the other is a structure protruding from the upper-middle left of the specimen on the left in Figure 6B (indicated by an arrow). Concentric "test tube" structures are observed in the form of multiple shell walls; the constraints of the rock boundary prevent a definitive determination as to whether the multiple shell walls are actually part of a concentric "test tube" structure or instead indicate that the organism grew smaller with time. For example, were the shell walls observed in the specimen to the right in Figure 6B not part of a concentric "test tube" structure, they might indicate that the organism secreted a shell wall, decreased in diameter, and then secreted another shell wall; if it decreased in length it did not secrete a new shell bottom, perhaps implying that it retreated into its shell. In all cases the shell walls observed were contiguous structures. The width of the fossil walls is also highly variable.

Most significant is that the "test tube" bottoms as reported by Grant (1990) are not visible, nor is their presence indicated by any aspect of the fossil. Significantly, a "test tube" bottom-like structure, as diagrammed in Figure 2, was observed and photographed on the reconstruction sample (Figure 8). After the reconstruction was performed, it became clear that the presence of inner "test tube" bottoms was due to the intersection of the shell wall with the edge of the rock (as can be seen by the black, V-shaped structures in Figure 7B). No inner bottom layer was observed in the reconstruction, and it is suggested that such a bottom layer was never present but instead was an artifact of both preservation and cross-sectioning. To confirm, the thin sections used by Grant (1990) were examined; only one slide gave strong evidence of "test tube" bottoms, and that slide can also be explained as a cross section that cuts into the side

of the shell wall giving the artificial impression that there were "test tube" bottoms when, in fact, there were none.

Discussion

In the light of the new reconstruction, it would appear that *Cloudina* is not what it has been thought to be; this discovery has implications for both paleoecology and phylogeny.

PALEOECOLOGY

Seilacher (1999) hypothesized that *Cloudina* lived half-embedded into a microbial biomat / reef structure and that its growth rate was directly related to the sedimentation rate of the biomat. In such a reconstruction, *Cloudina*, which from the reconstruction presented here and in Grant (1990) has the characteristics of a suspension feeder, grew upwards solely in order to stay clear of the sediment layer and thus maintaining feeding. The soft body of *Cloudina* would not grow longer; it would simply elevate its position. This is similar to the growth patterns of some corals and makes sense given the old reconstruction.

With the new reconstruction, however, the mat-sticker habit becomes more difficult to justify. With no bottom to the nested inner tubes, a simpler explanation for the growth of *Cloudina*'s shell is that it simply grew longer and secreted new shell material to cover its new growth. In this case, Seilacher's suggestion that growth rates are dependent on sedimentation rates, while still possible, becomes less probable. It is still possible that *Cloudina* could be infaunal if sedimentation rates at early development stages were relatively quick so that sediment would stabilize the lower part of the shell allowing *Cloudina* to grow straight up. In either case, of all *Cloudina* specimens found, none of them have actually been found on the actual reef; they

have instead been found in debris flow to the side of the reef (A. Knoll, pers. comm.). Given this, it is unlikely that *Cloudina* was actually infaunal.

If *Cloudina* is not infaunal then it is either epifaunal or not located on the reef itself but in the larger reef environment.

I propose that the three epifaunal positions (horizontal, vertical, and curved) can be determined for *Cloudina* both by using the results of the reconstruction and by inferring orientation from the concentric shell rings seen in a cross-section. In the specimens observed for this study, the "test tube" rings (visible on the individual images) were either concentric or skewed in one direction (See Figure 9). Assuming that the skewness is not a taphonomic result (e.g. the result of gravity after the death of the organism), then the skewness is due to the effect of gravity on the shell during growth or is the result of a choice on the part of *Cloudina* to grow in a certain direction. Perfectly concentric nested shells (Figure 9A) indicate that there is little, if any, lateral influence of gravity on shell formation and thus indicates that the life-position is vertical. A skewed distribution of the shells (Figure 9B) indicates that gravity was a factor in shell formation, in which case the organism could be horizontal, curving at that point, or, at the very least, non-vertical; were the skewness due to the organism's preferred growth mode, it would indicate a curve (as seen in specimen B in Figure 2). Seeing both skewed and concentric patterns in the same specimen implies that it is curved, though the reconstructions made in this study do not exhibit such a morphology.

The possibility that *Cloudina* was not actually on the reef is more difficult to determine. Were *Cloudina* to be located off-reef, the most probable location would be on seaweeds surrounding the reef. Seaweeds are present in microbial reef environments today in large numbers, and, given that calcified seaweeds have also been found in beds with *Cloudina* (Grant

et al., 1991), it would not be unreasonable to assume that seaweeds were abundant in Ediacaran microbial reef environments. Evidence from the "test tube" rings is not definitive in this case, especially since the orientation of the shell when on seaweeds is uncertain. Like modern worms that position themselves on seaweeds, *Cloudina* could have attached its entire shell to the length of the seaweed (R. Bambach, pers. comm.) or it could have attached its bottom to the seaweed and dangled off; determining between the two is difficult, if not impossible. The orientation of the seaweeds with respect to gravity is also unknown, but it is possible to imagine a situation in which, due to the way that the seaweed floats in the water, the "test tube" rings were skewed on one specimen and concentric on another. If we assume that *Cloudina*, as one of the first organisms to form a shell, is also a relatively simple organism and thus unable to fully control its direction of growth, then having various orientations on seaweeds with respect to gravity would explain the variety observed in the skewness of the "test tube" rings.

Placing *Cloudina* onto seaweeds (or, at the very least, off of the reef) would also provide the most reasonable explanation for the fossil distributions that have been observed. Were *Cloudina* attached to seaweeds, the lack of fossils actually found on the reef is easily explained—it never lived there. Even if the seaweeds were directly above the reef, currents could pull shells that had fallen from the seaweeds onto the debris flow. This would be fully consistent with the lack of fossils on or in the actual reef.

The findings of Bengtson and Zhao (1992) and Hua et al. (2003) do not contradict a refutation of Seilacher's (1999) theory and are consistent with an organism whose length was the entire shell. Were *Cloudina*'s body evenly distributed through the shell (as would be expected if the cause of shell-lengthening was based on increased length), the distribution of bore-holes should be random (or, at the very least, not preferentially located towards the top). If *Cloudina*

were actually infaunal or if the way the predators approached *Cloudina* was by first arriving at the top and boring in at the first opportunity, then a preferential location of the bore-holes towards the top would be expected. Most bore-holes observed by Bengtson and Zhao (1992) and Hua et al. (2003) are not close to the top of the organism (at least not those pictured in the figures). The specimen in Figure 3, for example, has its bore-hole in the middle of the shell, and of the ten specimens in the Hua et al. (2003) paper, only one of them is pictured with a hole near the top of the organism (this specimen also has a hole near the bottom). This indicates that the attacks by the predators were unsuccessful; that *Cloudina* had protective measures that covered the entrance; that *Cloudina* was able to retract into the shell in times of danger; that *Cloudina* was distributed rather evenly throughout the shell, resulting in no need for predators to target a specific vertical location on the shell; or some combination of these.

PHYLOGENY

Given that Grant's (1990) suggestion that *Cloudina* had a cnidarian-like grade of organization was based on his conclusion that the "test tubes" had bottoms, this new reconstruction implies that it is far less likely that *Cloudina* is a stem group cnidarian, even though there is evidence for budding (Figure 3). While there is still no definitive evidence, this proposed reconstruction is more favorable to annelid and pogonophoran worms than previous reconstructions have been. Serpulid worms (phylum Annelida), for example, form a straight, non-segmented tube adhering to a solid object and, when they reach the adult stage, they add a second shell layer to the tube (Wrigley, 1950). Pogonophoran worms also form contiguous, non-segmented shells in marine environments. All three groups, like *Cloudina*, are suspension feeders. Despite the new morphology proposed in this paper, the evidence in support of either a stem group cnidarian or annelid / pogonophoran classification is still unconvincing. More work

will need to be done before any preliminary affinity can be taken seriously. Any new interpretation will need to be based on 3D reconstructions such as presented in this paper and not on thin section analysis alone.

Conclusions

If we subscribe to the maxim "form follows function," then in order to infer any function for a paleontological organism we must first fully understand its form. For small, shelly fossils from the Ediacaran, serial sectioning followed by a 3D reconstruction is currently the most accurate way to recreate the 3D structure and provides much more information than could be gained either from thin sections or from phosphatized specimens. Though time-intensive, applying this method to *Cloudina* yields a reconstruction significantly different from the up-until-now accepted reconstruction and requires a reexamination of current thought about *Cloudina* paleoecology and phylogeny.

Acknowledgments

References

Bengtson, S., and S. Conway Morris. 1992. Early radiation of biomineralizing phyla. In Lipps, J. H., and P. W. Signor (Eds.), Origin and Early Evolution of the Metazoa. Plenum Press, New York, pp. 447-481.

Bengtson, S., and Y. Zhao. 1992. Predatorial borings in late Precambrian mineralized exoskeletons. *Science* 257:367-369.

Conway Morris, S. 1993. The fossil record and the early evolution of the Metazoa. *Nature* 361:219-225.

Conway Morris, S., B. W. Mattes, and C. Menge. 1990. The early skeletal organism *Cloudina*: new occurrences from Oman and possibly China. *American Journal of Science* 290-A:245-260.

Gaucher, C. 2000. Sedimentology, palaeontology and stratigraphy of the Arroyo del Soldado Group (Vendian to Cambrian, Uruguay). *Beringeria (Würzburger geowissenschaftliche Mitteilungen)* 26:1-120.

Geiger, B. 1993. Three-dimensional modeling of human organs and its application to diagnosis and surgical planning. Ph.D. Thesis. Ecole des Mines, Paris.

Germs, G. J. B. 1972. New shelly fossils from Nama Group, South West Africa. *American Journal of Science* 272:752-761.

Germs, G. J. B. 1974. The Nama Group in South West Africa and its relationship to the Pan African Geosyncline. *Journal of Geology* 82:301-317.

Germs, G. J. B. 1983. Implications of a sedimentary facies and depositional environmental analysis of the Nama Group in South West Africa / Namibia. In R.M. Miller, ed. Evolution of the Damara Orogen. The Geological Society of South Africa, Special Publication 11:89-114.

Glaessner, M. F. 1976. Early Phanerozoic annelid worms and their geological and biological significance. *Journal of the Geological Society, London* 132:259-275.

Grant, S. W. F. 1990. Shell structure and distribution of *Cloudina*, a potential index fossil for the terminal Proterozoic. *American Journal of Science* 290-A:261-294.

Grant, S. W. F., A. H. Knoll, and G. J. B. Germs. 1991. Probable calcified metaphytes in the latest Proterozoic Nama Group, Namibia: origin, diagenesis, and implications. *Journal of Paleontology* 65:1-18.

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

Grotzinger, J. P., W. A. Watters, and A. H. Knoll. 2000. Calcified metazoans in thrombolite-stromatolite reefs of the terminal Proterozoic Nama Group, Namibia. *Paleobiology* 26:334-359.

Hagadorn, J. W., and B. Waggoner. 2000. Ediacaran fossils from the southwestern Great Basin, United States. *Journal of Paleontology* 74:349-359.

Hahn, G., and H. D. Pflug. 1985. Die Cloudinidae n. fam., Kalk-Röhren aus dem Vendium und Unter-Kambrium. *Senckenbergiana lethaea* 65:413-431.

Hofmann, H. J., and E. W. Mountjoy. 2001. *Namacalathus-Cloudina* assemblage in Neoproterozoic Miette Group (Byng Formation), British Columbia: Canada's oldest shelly fossils. *Geology* 29:1091-1094.

Hua, H., B. R. Pratt, and L.-Y. Zhang. 2003. Borings in *Cloudina* shells: complex predator-prey dynamics in the terminal Neoproterozoic. *Palaios* 18:454-459.

Knoll, A. H., M. R. Walter, G. M. Narbonne, and N. Christie-Blick. 2004. The Ediacaran Period: a new addition to the geologic time scale. *Lethaia*, in press.

Martin, H. 1965. The Precambrian geology of South West Africa and Namaqualand. Rustica, Wynberg, South Africa.

Seilacher, A. 1999. Biomat-related lifestyles in the Precambrian. *Palaios* 14:86-93.

Seilacher, A., D. Grazhdankin, and A. Legouta. 2003. Ediacaran biota: the dawn of animal life in the shadow of giant protists. *Paleontological Research* 7:43-54.

Watters, W. A. 2000. Digital reconstruction of fossil morphologies, Nama Group, Namibia. M. S. thesis. Massachusetts Institute of Technology, Cambridge.

Watters, W. A., and J. P. Grotzinger. 2001. Digital reconstruction of calcified early metazoans, terminal proterozoic Nama Group, Namibia. *Paleobiology* 27:159-171.

Wrigley, A. 1950. The differences between the calcareous tubes of Vermetids and of Serpulids. *Journal of Conchology* 90:118-121.
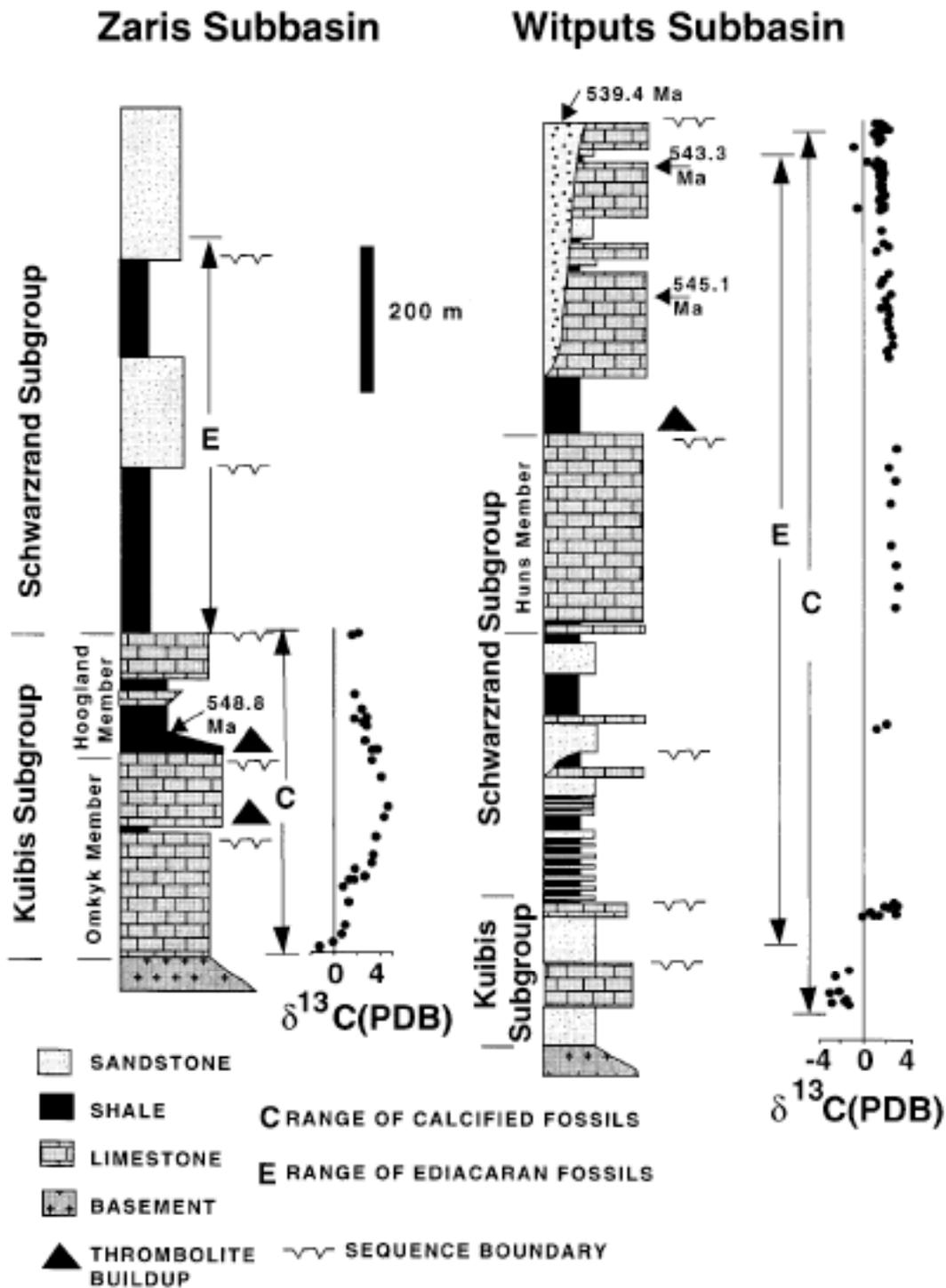
Figure 1: "Generalized stratigraphy of the Nama Group for the Zaris (north) and Witputs (south) subbasins, showing major lithostratigraphic, chemostratigraphic, biostratigraphic, and sequence stratigraphic attributes. Note the positions of thrombolite reef complexes above sequence boundaries." [Source: Grotzinger et al., 2000]
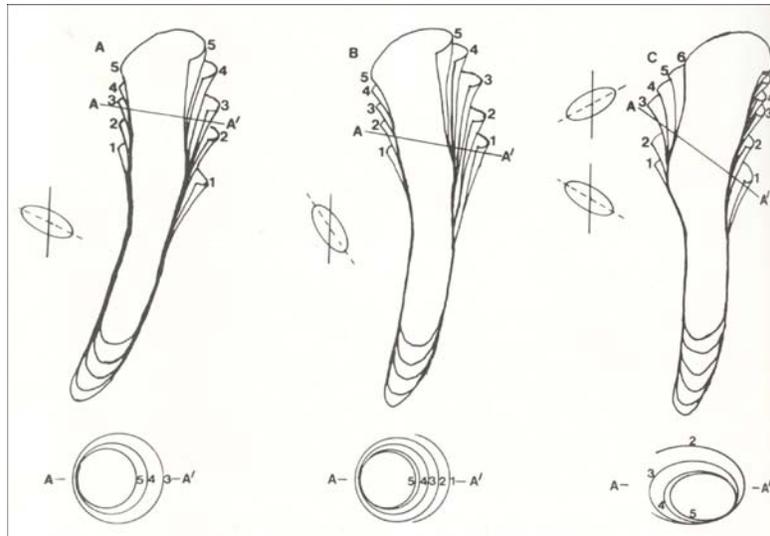
Figure 2: Reconstruction of *Cloudina* from Grant (1990). Note the "test tube" structure with each "test tube" having its own bottom. Also note the eccentricity of the shells in the lower portion of the figure. [Source: Grant (1990), Figure 9]

Figure 3: Budding structure in *Cloudina* as observed by Hua et al. (2003). Predatory bore-hole indicated by white arrow. Scale bar = 150μm. [Source: Hua et al. (2003), Figure 3E]
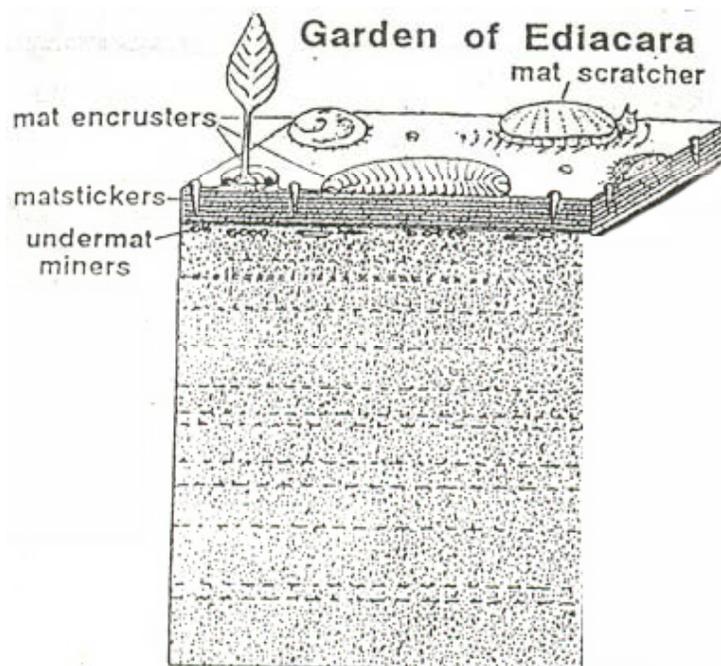
Figure 4: Seilacher (1999) reconstruction of life environment of *Cloudina* ("matstickers") and other organisms in the "Garden of Ediacara." [Source: Seilacher (1999), Figure 1]
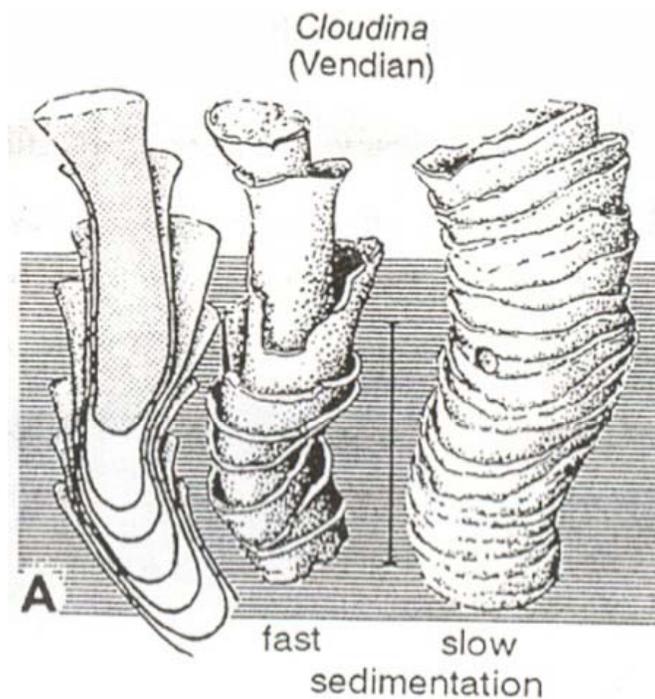

Figure 5: Seilacher (1999) reconstruction of *Cloudina* paleoecology. Under the Seilacher hypothesis, *Cloudina* is a "mat sticker" whose growth rate—and thus shape—depends on the sedimentation rate. [Source: Seilacher (1999), Figure 9A]

Figure 6A: Complete 3D serial reconstruction of two specimens, identified by arrows. Note the apparent lack of flanges and shape of the shell, as well as the apparent shared wall (which could be taphonomic) between the two specimens. There is also a good amount of noise due to the other structures in the rock around these fossils. More explanation is in the text.

Figure 6B: Cross section of specimens seen in Figure 6A. The slanted line running through all of the specimens in this image is interpreted to be a fracture filled with calcite. Note the length of the specimen on the left and how it appears that there is only one contiguous shell for that individual, with a single flange (arrow). The specimen on the right displays a complex wall structure, but no flanges or shells within shells. Some of the interactions between walls could be due to taphonomic influences. The wall structure of the specimen on the right could indicate that the organism secreted a shell wall as it decreased in size later in life, or it could indicate that the rock ends before the "test tube" structure can be seen.

Figure 7A: Complete 3D image of specimen 3. Part of the view is obscured by neighboring specimens. No flanges or shell segmentation is visible in this view of the specimen. Please see text for more information.

Figure 7B: Cross section of reconstruction in Figure 7A. Note the lack of "test tube" bottoms, the variable width of the walls, and the way they interact with one another. A possible flange is visible on the upper right (arrow). See text for explanation of V-shaped hole in wall of reconstruction.

Figure 8: Side view from original specimen of reconstruction in Figure 7. See text for explanation.
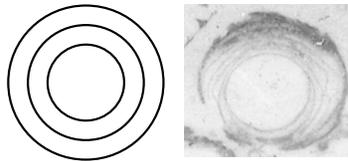

Figure 9A: Concentric shell schematic indicating little influence from gravity with example from rock used in analysis. The example shown is that of the specimen to the right in Figure 6.
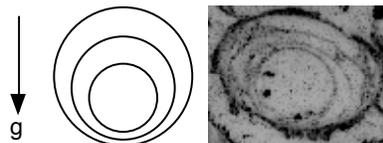

Figure 9B: Skewed shell schematic indicating large possible gravity influence with example from rock used in analysis.