Cloudinid

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The **Cloudinids**, an early metazoan family containing the genus *Cloudina*, lived in the late Ediacaran period and became extinct at the base of the Cambrian. They formed millimetre-scale conical fossils consisting of calcareous cones nested within one another; the appearance of the organism itself remains unknown. The name *Cloudina* honors the 20th-century geologist and paleontologist Preston Cloud.^[1]

Cloudinids had a wide geographic range, reflected in the present distribution of localities in which their fossils are found, and are an abundant component of some deposits. They never appear in the same layers as soft-bodied Ediacaran biota, but the fact that some sequences contain Cloudinids and Ediacaran biota in alternating layers suggests that these groups had different environmental preferences. It has been suggested that Cloudinids lived embedded in microbial mats, growing new cones to avoid being buried by silt. However no specimens have been found embedded in mats, and their mode of life is still an unresolved question.

The classification of the Cloudinids has proved difficult: they were initially regarded as polychaete worms, and then as coral-like cnidarians on the basis of what look like buds on some specimens. Current scientific opinion is divided between classifying them as polychaetes and regarding it as unsafe to classify them as members of any broader grouping.

Cloudinids are important in the history of animal evolution for two reasons. They are among the earliest and most abundant of the small shelly fossils with mineralized skeletons, and therefore feature in the debate about why such skeletons first appeared in the Late Ediacaran. The most widely-supported answer is that their shells are a defense against predators, as some *Cloudina* specimens from China bear the marks of multiple attacks, which suggests they survived at least a few of them. The holes made by predators are approximately proportional to the size of the *Cloudina* specimens, and *Sinotubulites* fossils, which are often found in the same beds, have so far shown no such holes. These two points suggest that predators attacked in a selective manner, and the evolutionary arms race which this indicates is commonly cited as a cause of the Cambrian explosion of animal diversity and complexity.

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Morphology



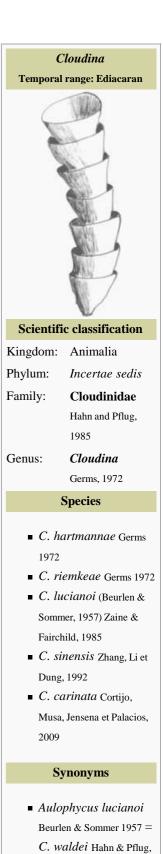
Cutaway diagram of *Cloudina* showing "living space" within the shell.

Cloudina varies in size from a diameter of 0.3 to 6.5 mm, and 8 to 150 mm in length.^[1] Fossils consist of a series of stacked vase-like calcite tubes, whose original mineral composition is unknown.^[2] Each cone traps a significant pore space beneath it, and stacks eccentrically in the one below. This results in a ridged external appearance. The overall tube is curved or sinuous, and occasionally branches. The tube walls are 8 to 50 micrometers thick, usually lying in the range 10 to 25 μ m.^[3] Although it used to be thought that the tubes had test-tube like bases,^[1] detailed three-dimensional reconstruction has shown that the tubes had an open base.^[4] There is evidence that the tube was flexible.^[5]

Classification

Cloudina was originally classified in 1972 as a member of the Cribricyathea, a class known from the Early Cambrian.^[1] Glaessner (1976) accepted this classification and also proposed that Cloudina was similar to the annelid worms, particularly serpulid polychaetes.^[6] However, Hahn & Pflug (1985) and Conway Morris *et al.* (1990) doubted both Germs' and

Glaessner's suggested relationships, and were unwilling to classify it to anything more than its own family, Cloudinidae.^{[7][8]} Some specimens of *Cloudina hartmannae* display budding,^[1] which implies asexual reproduction.^[9] On this basis Grant (1990) classified *Cloudina* as a coral-like cnidarian.^[3] Since the tubes had an open base, creating a single living space rather than a series of separate chambers, *Cloudina* is more likely to be a stem group polychaete worm,^[4] in other words an



1985 = *C. lucianoi*

Zaine & Fairchild, 1985



Specimen showing budding structure, and predatory boring (arrow).

evolutionary "aunt" or "cousin" of more recent polychaetes. This interpretation is reinforced by the even distribution of boreholes made by predators.^{[10][11]} However, as with so many Ediacaran life forms, there is great debate surrounding its position in the tree of life, and classification between the kingdom and family level may be unwise.^{[3][8][12]}

Ecology

Cloudina is usually found in association with microbial stromatolites, which are limited to shallow water; their isotopic composition^[13] suggests that water temperatures were relatively cool. They have also been found in normal sea-floor sediments, suggesting that they were not only restricted to dwelling on microbial mounds.^[14] On the other hand *Cloudina* has never been found in the same layers as the soft-bodied Ediacara biota, but *Cloudina* and Ediacara biota have been found in alternating layers. This suggests that the two groups of organisms had different environmental preferences.^[4]

In many *Cloudina* specimens the ridges formed by the cones are of varying width, which suggests the organisms grew at a variable rate. Adolf Seilacher suggests that they adhered to microbial mats, and that the growth phases represented the organism keeping pace with sedimentation—growing through new material deposited on it that would otherwise bury it. Kinks in the developing tube are easily explained by the mat falling slightly from the horizontal.^[15] Because of its small size, *Cloudina* would be expected to be found *in situ* in the microbial mat, especially if, as Seilacher suggests, sedimentation built up around it during its lifetime. But all the many specimens discovered to date have only been found having been washed out of their places of growth. A further argument against Seilacher's hypothesis is that the predatory borings found in many specimens are not concentrated at what would be the top end, as one would expect if the animal was mainly buried. An

alternative is that the organism dwelt on seaweeds,^[4] but until a specimen unquestionably *in situ* is discovered, its mode of life remains open to debate.

The tubes often appear to form colonies, although they are sometimes found in more isolated situations. The frequent appearance of large and sometimes single-species colonies has be attributed to the lack of significant predation.^[1] On the other hand, in some locations up to 20% of *Cloudina* fossils contain predatory borings ranging from 15 to 400 μ m in diameter.^{[10][11]} The boreholes are rather evenly distributed along the tube length, and some tubes had been bored multiple times—hence the organism could survive attacks, since predators do not attack empty shells. This may indicate that the animal could vary its position in the tube in response to predation, or that it occupied the full length—but not the full width— of the tube. The even distribution is perhaps difficult to reconcile with an infaunal lifestyle, mainly buried in a microbial mat, and adds weight to Miller's suggestion that the animal lived on seaweeds or in a reef environment. If modern-day molluscs are a suitable analogy, the size distribution of the borings suggests that the predator was similar in size to *Cloudina*.^[5]

Fossil locations

Cloudina occurred in calcium carbonate rich areas of stromatolite reefs. It is found in association with *Namacalathus*, which like *Cloudina* was "weakly skeletal" and solitary, and *Namapoikia*, which was "robustly skeletal" and formed sheets on open surfaces.^[16]

First found in the Nama Formation in Namibia,^[1] *Cloudina* has also been reported in Oman,^[8] China's Dengying Formation,^{[8][11]} Canada,^[17] Uruguay,^{[18][19]} Argentina,^[20] Antarctica,^[21] Brazil,^[22] Nevada,^[23] central Spain, northwest Mexico and California,^[3] in west and south Siberia. The *Cloudina* fossils found in association with late Precambrian-Early Cambrian anabaritids SSF and tubular agglutinated skeletal fossils *Platysolenites* and *Spirosolenites* in Siberia.^{[24][25]}

Paleontological importance

Although not the first small shelly fossil to be found, *Cloudina* is one of the earliest and most abundant.^[26] The evolution of external shells in the Late Ediacaran is thought to be a defence against predators, marking the start of an evolutionary arms race.^{[26][27]} While predatory borings are common in *Cloudina* specimens, no such borings have been found in *Sinotubulites*, a similar shelly fossil sometimes found in the same beds. In addition, the diameters of borings in *Cloudina* are proportional to the sizes of specimens, which suggests that predators were selective about the size of their prey. These two indications that predators attacked selectively suggest the possibility of speciation in response to predation, which is often postulated as a potential cause of the rapid diversification of animals in the Early Cambrian.^[11]

See also

List of Ediacaran genera

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