

## SHELL STRUCTURE AND DISTRIBUTION OF *CLOUDINA*, A POTENTIAL INDEX FOSSIL FOR THE TERMINAL PROTEROZOIC

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**ABSTRACT.** *Cloudina*-bearing biosparites and biomicrites in the lower part of the Nama Group, Namibia, contain a wide morphological diversity of shell fragments that can all be attributed to the two named species *C. hartmannae* and *C. riemkeae*. The curved to sinuous tubular shells of *Cloudina* were multi-layered. Each shell layer was 8 to 50  $\mu\text{m}$  thick and in the form of a slightly flaring tube with one end open and the other closed. Growth appears to have been periodic with successive shell layers forming within older layers. Each added layer was slightly elevated from the previous layer at the proximal end and was asymmetrically placed within the older layer so that only a portion of the new shell layer was fused to the previous layer. This type of growth left a relatively large unmineralized area between the shell layers which was often partially or fully occluded by early marine cements. The thin shell layers exhibit both plastic and brittle deformation and were likely formed of a rigid  $\text{CaCO}_3$ -impregnated organic-rich material. Often the shell layers are preferentially dolomitized suggesting an original mineralogy of high-magnesian calcite. Both species in the Nama Group formed thickets, or perhaps bioherms, and this sedentary and gregarious habit suggests that *Cloudina* was probably a filter-feeding metazoan of at least a cnidarian grade of organization.

The unusual shell structure of *Cloudina* gives rise to a characteristic suite of taphonomic and diagenetic features that can be used to identify *Cloudina*-bearing deposits within the Nama Group and in other terminal Proterozoic deposits around the world. Species of *Cloudina* occur in limestones from Brazil, Spain, China, and Oman in sequences consistent with a latest Proterozoic age assignment. In addition, supposed lower Cambrian, pre-trilobitic, shelly fossils from northwest Mexico and the White-Inyo Mountains in California and Nevada, including *Sinotubulites*, *Nevadatubulus*, and *Wyattia*, are all either closely related to or con-generic with *Cloudina*. Hence, it is probable that these outcrops are latest Proterozoic in age, and that *Cloudina* or *Cloudina*-like organisms were widely distributed at that time. It is possible, moreover, to suggest that metazoan biomineralization occurred on a global scale by the latest Proterozoic, at the same time that evidence for complex multicellularity and locomotion in animals appears in siliciclastic "Ediacaran" rocks in the form of body and trace fossils.

### INTRODUCTION

The shelly fossil *Cloudina* was first described from the late Proterozoic Nama Group, Namibia, by Germs (1972a,b) in limestones interbedded with siliciclastic rocks containing the remains of Ediacaran body fossils (Gürich, 1933; Germs, 1972a, 1973; Pflug 1970a,b, 1972a,b).

Subsequent to this discovery reports of *Cloudina* from Brazil (Zaine and Fairchild, 1985, 1987; Hahn and Pflug, 1985) extended the geographic distribution of this genus in rocks also of likely terminal Proterozoic age. Additional occurrences of this genus have been reported from Argentina (Yochelson and Herrera, 1974) and Antarctica (Yochelson and Stump, 1977), but in both these cases the assignment to *Cloudina* was questionable. The only other report of a shelly genus from demonstrably late Proterozoic rocks had been *Sinotubulites* from China (Chen and Wang, 1977; Chen, Chen, and Qian, 1981). Thus, the occurrence of *Cloudina* in "Ediacaran" limestones has been considered as a geographically restricted anomaly that contradicted a global scale lower Cambrian origin and proliferation of a metazoan biomineralization.

In this paper, I argue that *Cloudina* was widely distributed in terminal Proterozoic carbonates. This contention follows from a new hypothesis concerning the shell structure of this genus determined from studies of *in situ* and redeposited remains of *Cloudina* from the Nama Group. Previous reports and descriptions of *Cloudina* indicated a more robust shell structure than is demonstrated here. Petrographic analysis reveals that *Cloudina* shells were in fact rather delicate, containing multiple thin layers with relatively large areas of unmineralized pore-space between the layers.

Taphonomic and diagenetic effects on the peculiar shell structure of *Cloudina* result in the preservation of diagnostic features, even in reworked shell deposits. These taphonomic and diagenetic characteristics can be observed in accumulations of tubular fossils known from other late Proterozoic and presumed lower Cambrian carbonates indicating that the organisms that secreted the shells were probably closely related to, or con-generic with, *Cloudina*. It is, therefore, possible to extend the geographic distribution of *Cloudina* to include deposits in Namibia, Brazil, central Spain, the Yangtze Gorges in China, northwest Mexico, the White Inyo region in California and Nevada, Oman, and, perhaps, Antarctica. In none of these deposits is *Cloudina* found associated with Cambrian shelly fossils, trace fossils or acritarchs, although reports of co-occurring Ediacaran body fossils as well as Vendian traces and acritarchs are not uncommon. It seems reasonable, therefore, to infer a latest Proterozoic (Ediacaran) age for deposits in which *Cloudina* is the only fossil present.

The widespread distribution of a terminal Proterozoic skeletalized metazoan, capable of producing significant quantities of bioclastic limestones, enhances our understanding of the early history of biomineralization in multicellular animals. It has been thought that the development of morphologically complex metazoans, evidenced by Ediacaran body and trace fossils, preceded the first appearance of biomineralization in animals—an event that has been informally used to demarcate the base of the Cambrian. A story of ecological replacement has been derived from this view in which a skeletalized lower Cambrian fauna may have

displaced the "soft-bodied" Ediacaran assemblage (McMenamin, 1986). There may be some truth in such speculation, but it is now clear that biomineralization in animals originated at least as early as the terminal Proterozoic. Thus at the resolution available to paleontologists, the developments of megascopic, multicellular complexity, biomineralization, and locomotion requiring fairly vigorous muscular activity appear to have been nearly synchronous in the Metazoa.

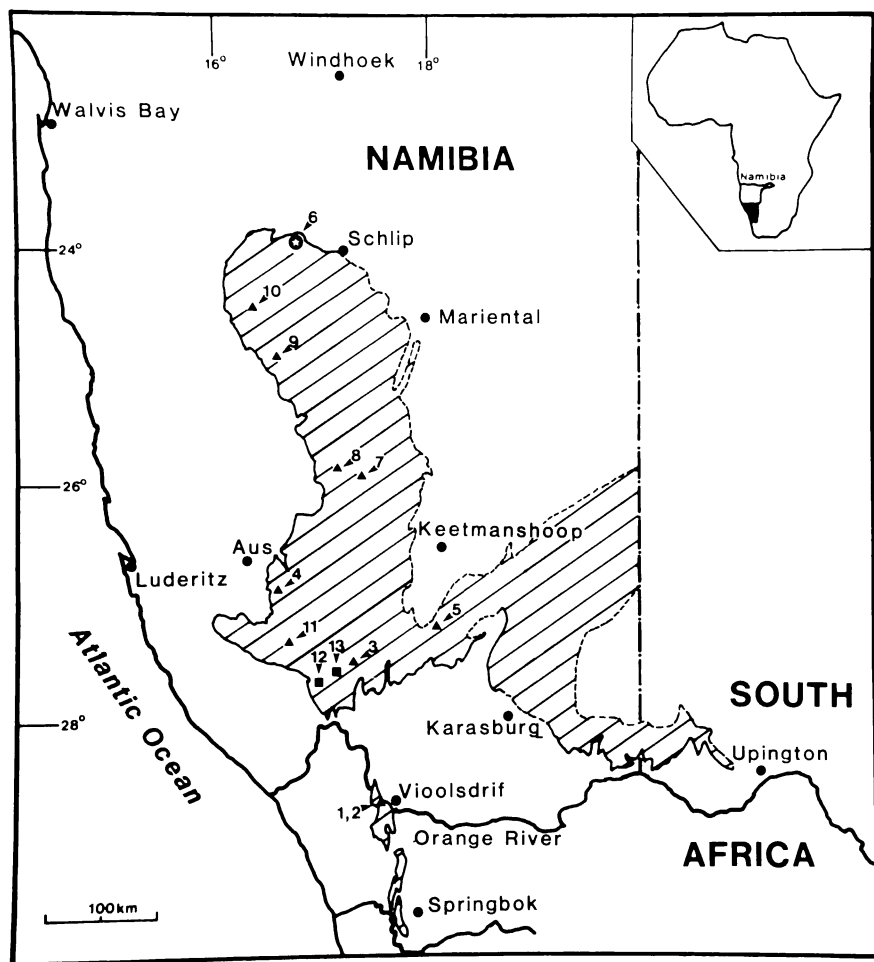


Fig. 1. Map of the Nama Group and the location of known bioclastic limestones: ●- in situ *Cloudina* thicket, ▲- *Cloudina* biosparites and biomicrites, ■- probable "phylloid alga." Descriptions of samples as well as their stratigraphic and geographic positions are given in the appendix.

## GEOLOGICAL SETTING AND AGE OF THE NAMA GROUP

The Nama Group covers an extensive area in southern and central Namibia and in adjoining areas of the northwestern Cape Province of South Africa (fig. 1). Nama sediments were deposited in both shallow marine and fluviatile environments on a stable continental platform that was only locally metamorphosed during Pan-African tectonism (Germis, 1972a, 1983; Kröner and others, 1980). The lower Nama Group, including the Kuibis and Schwarzrand Subgroups, contains sediments that largely derive from the Kalahari craton to the east, whereas the

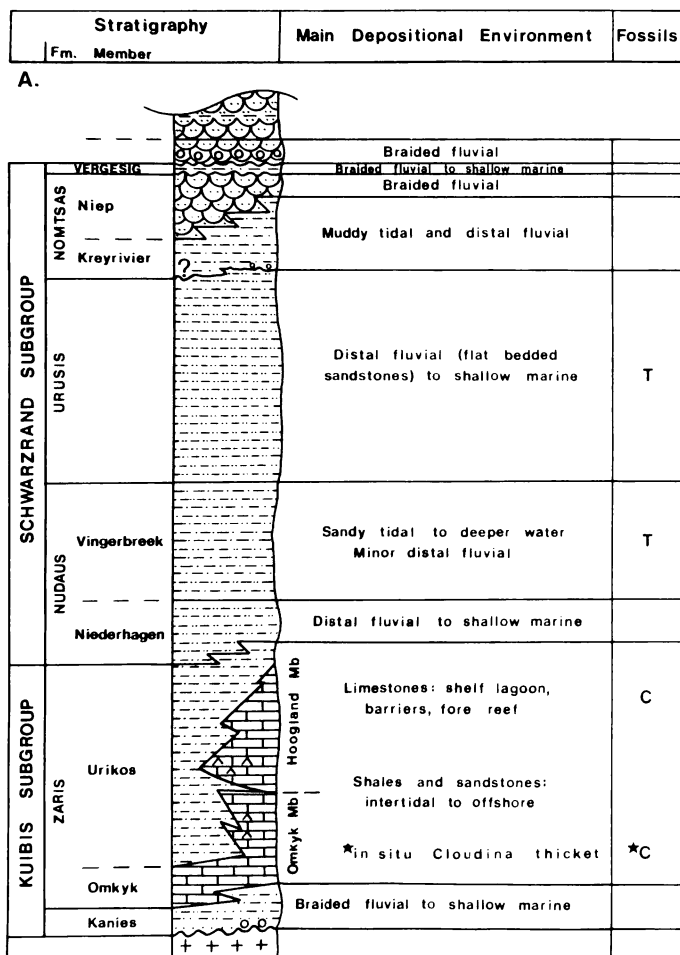



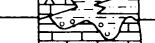
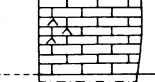
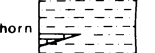


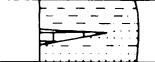

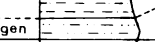


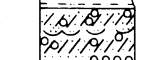




Fig. 2. Schematic stratigraphic sections of the Kuibis and Schwarzrand subgroups in the northern Zaris (A) and southern Wiputs sub-basin (B).

overlying Fish River Subgroup contains relatively immature, molasse-like deposits which resulted from the developing Damara orogeny to the north and west (Germs, 1983).

Lithologies in the Kuibis Subgroup vary according to distance from the Osis ridge, a structural high that divided the Nama basin into a

Stratigraphy		Main Depositional Environment	Fossils			
Fm.	Member					
B.						
SCHWARZRAND SUBGROUP	NOMTSAS		Braided fluvial			
			Braided fluvial	T		
			Muddy tidal carbonate platform in W	C(?), T		
			Sandy shallow marine in S			
	URUSIS	Spitskop		Carbonate platform, stromatolitic biostromes and bioherms in W	C(?)	
		Feldschuhorn		Muddy tidal and distal fluvial		
		Huns		Carbonate platform, stromatolitic biostromes and bioherms in W	C	
				Clastic tidal fluvial intercalations in E	M A	
		Nasep		Tidal Fluvial	M, T M, T	
		NUDAUS	Vingerbreek		Muddy tidal and distal fluvial	M
			Niederhagen		Sandy tidal some distal fluvial sediments	M
		ZARIS	Urikos		Inter-to shallow subtidal Shelf lagoon mainly subtidal	C
	KUIBIS SUBGROUP		Mooifontein		Inter-to shallow subtidal	M, T
		Kliphoek		Braided fluvial	M C	
DABIS			Mara		Carbonate platform in W Clastic inter-to shallow subtidal in E	
		Kanies		Braided fluvial		

Namibia (not to scale), showing the stratigraphic distribution of soft-bodied metazoan fossils (M), trace fossils (T), *Cloudina* (C), and a presumed phylloid alga (A). Modified from Germs, Knoll, and Vidal (1986).

northern Zaris and southern Wiputs sub-basin (Germs, 1972a, 1983). In the south, away from the ridge, Kuibis strata consist of two cycles with a basal sandstone, locally containing conglomerates, overlain by shales and limestones. In the deeper part of the northern basin shales and limestones predominate (fig. 2). Near the Osis ridge, oölitic, pisolitic, and stromatolitic facies occur in fairly thin sequences interbedded with fluviatile sediments. Stratigraphic thicknesses in the Kuibis Subgroup vary from a few tens of meters in the southeast and near the Osis ridge to as much as 800 m in the northwest (Germs, 1983; Germs, Knoll, and Vidal, 1986).

A conformable contact is generally found between the Schwarstrand and Kuibis Subgroups. There is a general decrease in maturity of the clastic sediments throughout the Schwarstrand. In the south, thick limestones with sandstone and shale intercalations occur; the carbonates become thinner and eventually grade into shales to the east and north (fig. 2). Unconformities are present in the sequence and are especially common in the eastern deposits (Germs, 1983).

Near the top of the Schwarstrand Subgroup the first red beds occur in the Nomtsas Formation, which shares many depositional characteristics with the feldspathic, fluviatile sandstones and siltstones of the Fish River Subgroup. No bedded carbonates are known from the Fish River. Stratigraphic thicknesses for this subgroup differ from the older sequences, with the thickest sections occurring in the south and east indicating a northern and western source related to the Damara Orogeny (Germs, 1983).

Biostratigraphical data from body fossils, organic-walled microfossils, and trace fossils place the lower part of the Nama Group in the uppermost Proterozoic and the overlying Fish River Subgroup in the Cambrian (Germs, 1972a, 1983; Germs, Knoll, and Vidal 1986; Crimes and Germs, 1982). It is noteworthy that both paleomagnetic and carbon isotopic data support this conclusion (Kröner and others, 1980; Kaufman and others, 1988, in press). The exact position of the Precambrian-Cambrian boundary for this area, however, has not been resolved. The reported occurrence of the trace fossil *Phycodes pedum* in the Nomtsas Formation (fig. 2) suggests that it may be Cambrian in age (Crimes and Germs, 1982). According to Kröner and others (1980), however, paleomagnetic data support a latest Proterozoic age for the Nomtsas Formation. Unfortunately, neither organic-walled microfossils (Germs, Knoll, and Vidal, 1986) nor carbon isotopic chemostratigraphy (Kaufman and others, in press) can be used to resolve the uncertain age of the Nomtsas. The presence of questionable remains of *Cloudina* in limestones of the lower Nomtsas Formation may suggest that, at least, part of the Nomtsas is latest Proterozoic in age, for this shelly genus can be found in Kuibis Subgroup limestones interbedded with siliciclastic rocks containing "soft-bodied" Ediacaran fossils.

Ediacaran body fossils are known from sandstones in the southern Wiputs sub-basin throughout the Kuibis Subgroup and up into the

Urusis Formation of the Schwarzrand Subgroup (Gürich, 1933; Pflug, 1970a,b, 1972a,b; Germs, 1972a,b, 1983; Jenkins, 1985). The local stratigraphic range of *Cloudina* overlaps with these body fossils, so that it is clear that this shelly genus should be considered an important component of the "Ediacaran" biota in the Nama Group. Germs (1983) reported the occurrence of *Cloudina* in the Mara Member limestone which underlies the body fossils found in the siliciclastic Kliphoek Member in the Kuibis Subgroup (fig. 2). Unfortunately, no *Cloudina*-bearing Mara samples were examined in this study. There is, however, one sample that contains redeposited *Cloudina* from the base of the Kliphoek Member, Dabis Formation at Hoogland in the southern sub-basin (fig. 1, loc. 4). This same member contains the most abundant and diverse assemblage of Ediacaran body fossils in the Nama Group including *Rangea*, *Pteridinium*, *Ernietta*, and probably *Beltanelliformis*; this latter-most genus, misidentified as the remains of a bivalved organism (Hahn and Pflug, 1988), is probably restricted to terminal Proterozoic deposits around the world (Narbonne and Hofmann, 1987). The undisputed Ediacaran body fossils *Rangea* and *Pteridinium* also occur in the Niederhagen Member of the Nudaus Formation in the central part of the basin near the Osis ridge. These remains, found in the lowermost siliciclastic deposit of the Schwarzrand Subgroup, overlie limestones of the Mooifontein Member that contain *Cloudina* (figs. 2 and 3; Germs, 1972a, and personal commun.). Other body fossils from higher up in the Schwarzrand Subgroup are also known, although the biostratigraphic signifi-

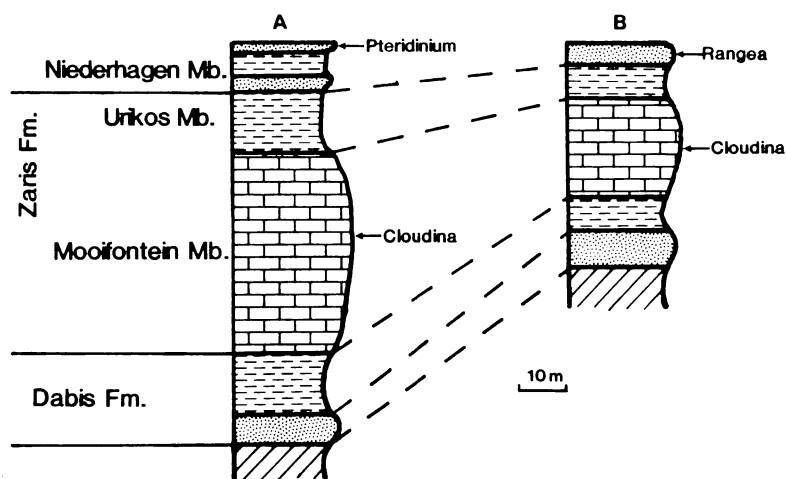


Fig. 3. Local stratigraphic sections from near the central part of the Nama basin with *Cloudina*-bearing limestones directly below Schwarzrand Subgroup siliciclastics containing biostratigraphically significant Ediacaran body fossils. (A) 25 km north of Helmeringhausen (25.7°, 16.9°), near locality 8 on figure 1; (B) Farm Chamis (26°, 16.9°), near locality 7 on figure 1.

cance of these remains is not as clear as for the other typical Ediacaran fossils. *Nasepia* from the Nasep Quartzite Member, Urusis Formation, is reported only from the Nama Group (Germs, 1972a, 1973), but this fossil does somewhat resemble *Chondroplon* from Ediacara (Wade, 1971). This latter genus may in fact represent a deformed *Dickinsonia* (Hofmann, 1988). Germs (1972a) also reports *Cyclomedusa* from even higher up in the Huns Limestone Member, Urusis Formation. As suggested by Glaessner (1984), it is possible that these medusoid remains are more appropriately classified as *Tirasiana*, which is also known to occur in Ediacaran biotas in the East European Platform (Palij, Posti, and Fedonkin, 1979) and in the Wernecke Mountains (Narbonne and Hofmann, 1987).

It is worth pointing out that the suggestion in Jenkins' (1985) appendix notes that the lower Nama Group in the northern Zaris sub-basin may be Cambrian, based on reported trace fossil occurrences (Crimes and Germs, 1982), while the southern Wiputs sub-basin is latest Proterozoic, owing to the presence of Ediacaran body fossils, is not convincing. Crimes and Germs (1982) reported trace fossils, thought to be indicative of Cambrian or younger deposits, in the Schwarzrand Subgroup north of the Osis ridge. The *Skolithos* they found in the Nasep Member, however, is not illustrated. Moreover, this ichnogenus may even extend into the Vendian in other parts of the world (Crimes, 1987). Additionally, the two specimens of *Chondrites* are questionably identified, and the *Diplocraterion* figured appears similar to the crossed meanders or curving, shallow burrows of a surface trace such as *Planolites*. Perhaps even more importantly, Jenkins' (1985) suggestion is not supported by detailed mapping of facies relationships in the Nama basin (Germs, 1972a, 1983).

Thus a latest Proterozoic age for the *Cloudina*-bearing deposits from the Nama Group can be demonstrated in several ways: (1) *Cloudina* is found in carbonates interbedded with siliciclastic deposits containing stratigraphically significant Ediacaran body fossils (Germs 1972a, 1983); (2) Vendian aspect organic-walled microfossils (Germs, Knoll, and Vidal, 1986) and trace fossils (Crimes and Germs, 1982; Crimes 1987) have been described from lower Nama Group deposits; (3) there are no known stratigraphically significant Cambrian shelly fossils, trace fossils, or organic-walled microfossils in the lower Nama Group, except for a reported occurrence of *Phycodes pedum* in the Nomtsas Formation above the last occurrence of *Cloudina*; and (4) paleomagnetic and carbon isotopic evidence is consistent with a terminal Proterozoic age for the lower Nama Group (Kröner and others, 1980; Kaufman and others, in press). It is noteworthy that other reported occurrences of *Cloudina* in Brazil (Zaine and Fairchild, 1985, 1987; Hahn and Pflug, 1985), Oman (Conway Morris; Mattes, and Chen, 1990) and the recently discovered, but not formally described, *Cloudina* from Spain (Liñán, Palacios, and Perejón, 1984; Palacios, 1989) are found in sequences considered as most likely latest Proterozoic in age. In addition, the following genera

that are probably either con-generic with, or closely related to, *Cloudina* — *Sinotubulites* from China, Mexico, and the White Inyo region of California and Nevada, *Nevadatubulus* and *Wyattia* both also from the White Inyos — derive from horizons that are consistent with a latest proterozoic age assignment.

Geochronological data from the Nama Group complement the biostratigraphy, suggesting that deposition of the entire Nama Group occurred between about 650 to 530 Ma ago. Rb-Sr whole rock dates on acidic volcanics that lie unconformably beneath basal Nama sediments in the Wiputs area indicate a maximum age of deposition at  $686 \pm 32$  Ma. A minimum age of deposition can be inferred to be between  $518 \pm 15$  and  $553 \pm 13$  Ma based on Rb-Sr whole rock dates from granitoid rocks of the Bremen Complex that intrude the Nama sediments (Allsopp and others, 1979). It should be noted that definite contact relationships have been determined only for the younger (518 Ma) intrusives, but Allsopp and others (1979) considered that the older part of the Bremen Complex probably post-dates Nama sedimentation as well. Furthermore, the fine mineral fraction ( $\leq 2 \mu\text{m}$ ) of Mulden Group shales from northern Namibia, considered to be in part correlative with the Nama Group, yielded a minimum age of about 535 Ma using the Rb-Sr and K-Ar methods (Kröner and Clauer, 1979). This presumed correlation is supported by Horstman (1987), who determined K-Ar dates on detrital muscovites and presumed authigenic ( $\leq 2 \mu\text{m}$  mineral fraction) minerals, bracketing the deposition of the Fish River Subgroup between 570 and 530 Ma. The same technique was applied to the lower Nama Group sediments, giving a time of deposition between 640 and 536 Ma.

#### SHELL STRUCTURE

The sinuous to curving tubular shells of *Cloudina* are 0.3 to 6.5 mm in maximum width and up to, at least, 3.5 cm long. A clear bimodal size distribution for *Cloudina* in the Nama Group led to the naming of two species (Germs, 1972a,b): *C. hartmannae* (tube diameters between 2.5–6.5 mm, fig. 4) and *C. riemkeae* (tube diameters between 0.3 to 1.3 mm, fig. 5). It is difficult to measure the length of individuals since the tubes curve out of the plane of any polished surface. Except for the size difference the shell structures of these two species appear to be nearly identical so that evidence from the two species will be used interchangeably in this discussion. Most of the known fossil deposits in Namibia (fig. 1) represent the remains of redeposited *Cloudina*, but there is one locality in the north, at Driedoornvlakte near Schlip, that appears to contain *in situ* remains (loc. 6, fig. 1). It is these deposits that will be discussed first as they reveal the most about the shell structure.

Germs (1972a,b) argued that biosparites from the top of the Omkyk Member limestone at Driedoornvlakte similar to those pictured in figure 6A represent biohermal deposits. It is not certain, however, whether the living structure had a significant relief so, rather than bioherms, these deposits could represent a nearly flat-lying thicket of *Cloudina*, not

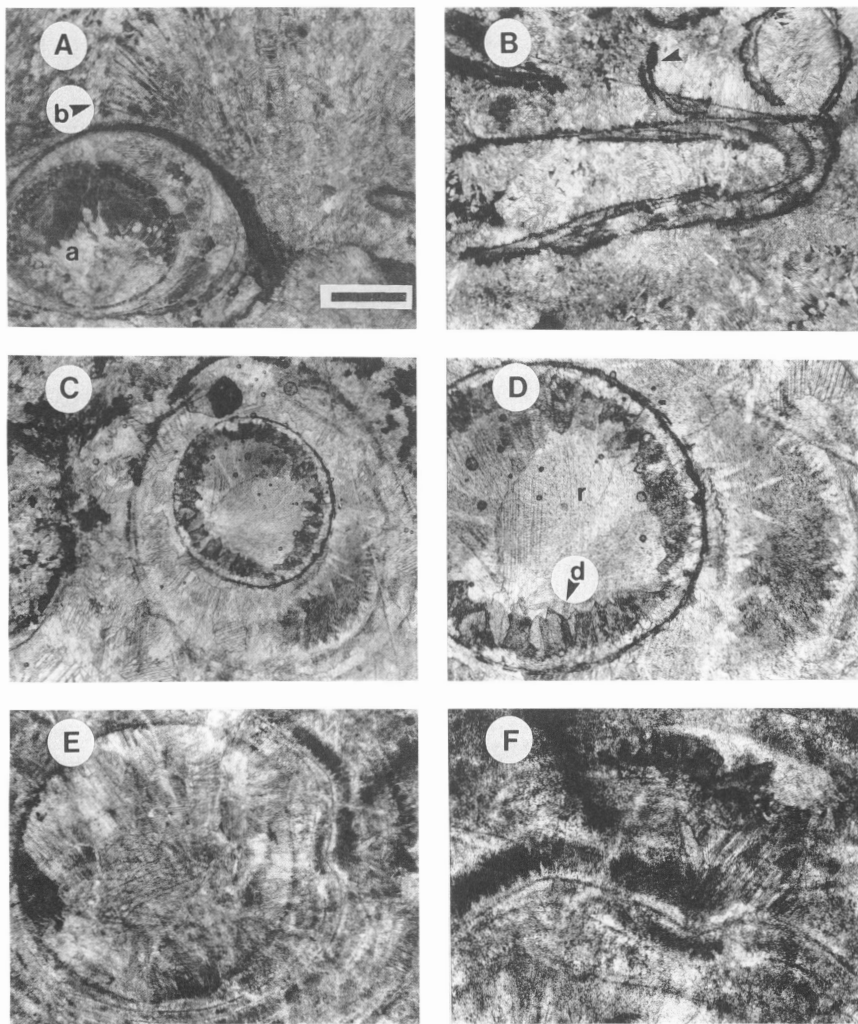


Fig. 4. *C. hartmannae* in thin section from the *in situ* thicket, Omkyk Member, Zaris Formation, Kuibis Subgroup on farm Driedoornvlakte near Schlip, Namibia (loc. 6, fig. 1), plane polarized light. (A) Note the ghosts after botryoidal aragonite within the central canal (a) and the large radiating fan (b) that grew outside the shell, slide HU 62337-b, scale bar = 1.6 mm. (B) The arrowed layer is bent back, exhibiting the plasticity commonly found in deformed shell layers, scale bar = 3.4 mm, slide HU 62338. (C and D) Transverse section of multiple-layered shell at different magnifications showing acicular ghosts after aragonite between shell layers, dolomite cements (d) rimming the central canal and radiaxial fibrous/fascicular optic calcite cement (r) filling the remaining space in the central canal, slide HU 62337-f, scale bar = 0.8 mm for (C) and = 0.4 mm for (D). (E and F) Thick section showing several shell layers each with a fibrous rind of calcitized aragonite, slide HU 62337-a-t, scale bar = 0.8 mm for (E) and = 0.4 mm for (F).

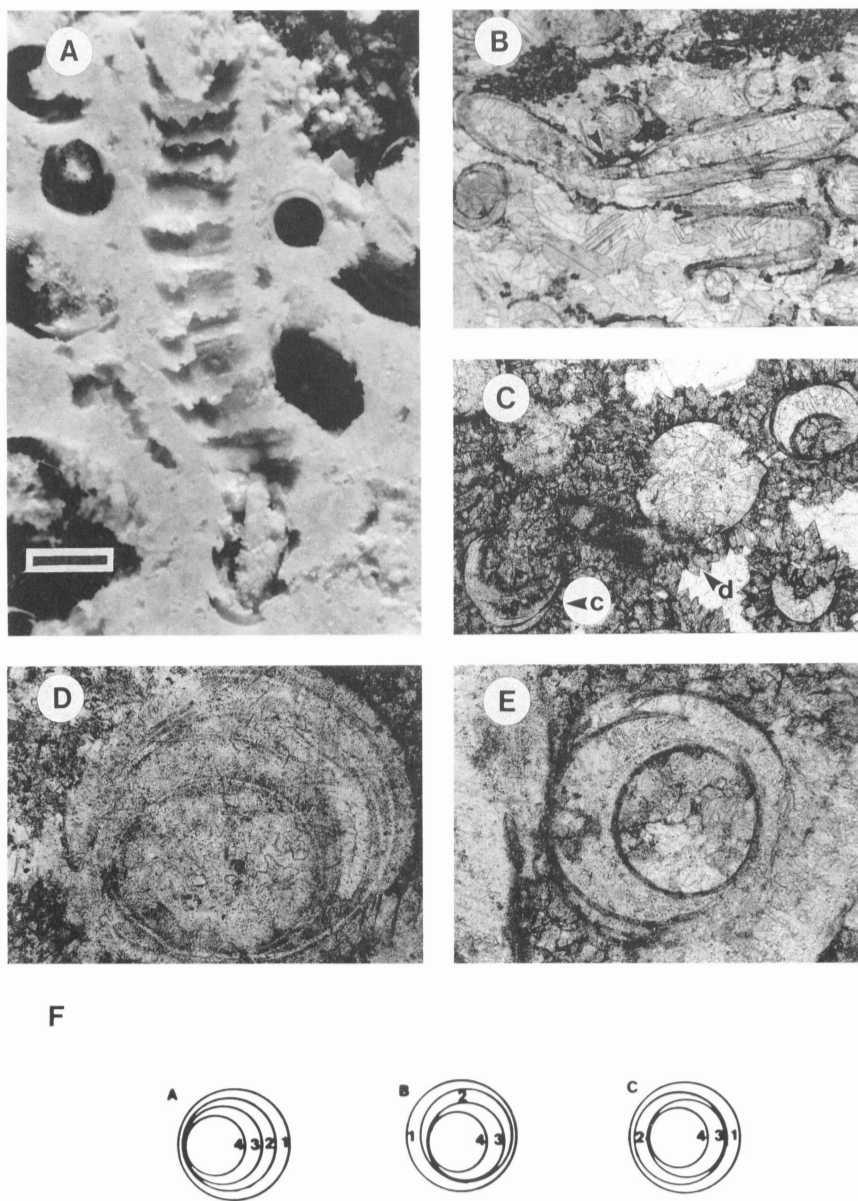


Fig. 5 *C. riemkeae* from the *in situ* thickset, Omkyk Member, Zaris Formation, Kuibis Subgroup on farm Driedoornvlakte near Schlip, Namibia (loc. 6, fig. 1). (A) Acid-etched longitudinal section showing "cone-in-cone" structure of partially dolomitized shell layers, sample HU 62341, scale bar = 0.6 mm. (B to E) Polished thin sections, plane polarized light. (B) Arrow points to broken shell layers exhibiting both brittle and plastic behavior, slide HU 62342-a, scale bar = 0.8 mm. (C) Transverse sections of partially dolomitized shells (the dark shell layers are dolomite) overgrown with dolomite (d). Note the ghost of a fibrous early cement precursor (c) between the shell layers in one of the specimens, slide HU 62341-p, scale bar = 0.5 mm. (D and E) Transverse sections showing eccentrically-nested shell layers: (D) from slide HU 62342-a, (E) from slide HU 62341-p, scale bar = 180  $\mu$ m for both. (F) schematic diagram of eccentrically-nested shell layers in transverse section. See text for further explanation.

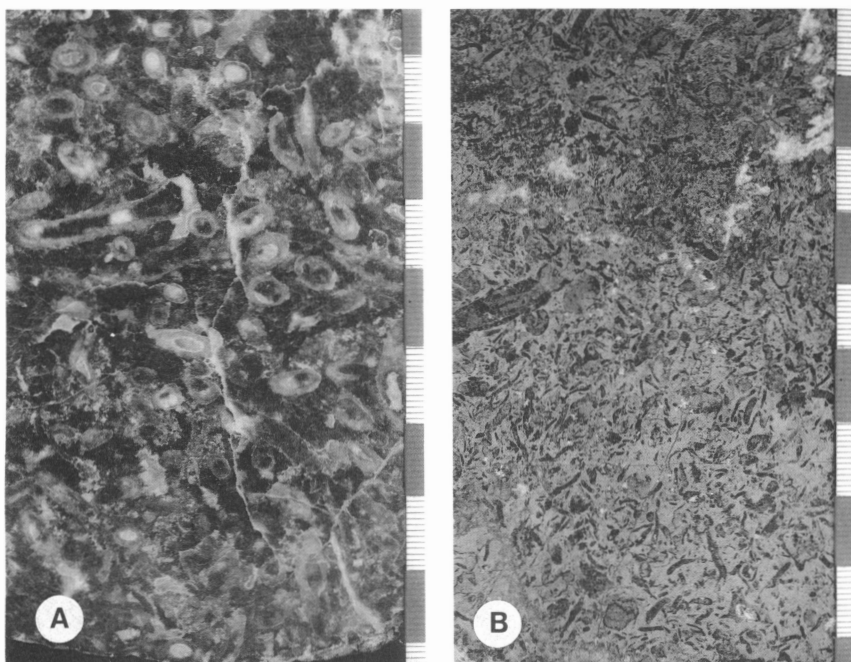


Fig. 6(A) Polished hand sample of *in situ* *C. hartmannae* thicket, sample HU 62337, Omkyk Member, Zaris Formation, Kuibis Subgroup from farm Driedoornvlakte near Schlip, Namibia (loc. 6, fig. 1). The dark area between the shells is predominantly calcitized botryoidal aragonite; scale in centimeters. (B) Weathered surface of reworked *Cloudina* biomicroite, sample HU 61813, Mooifontein Member, Zaris Formation, Kuibis Subgroup, 1 km east of Vioolsdrif, Namibia (loc. 1, fig. 1); scale in centimeters.

dissimilar to Paleozoic crinoid or bryozoan thickets. Distinguishing between these two kinds of *in situ* deposits requires more fieldwork, but there are sufficient reasons for dismissing the notion that these shell accumulations are coquinites. Current-sorted tubular fossils should exhibit a strong preferred orientation; the interpreted *in situ* deposits do not. In addition, the delicate nature of the *Cloudina* shell would not survive the current activity necessary to transport and concentrate objects of the size shown. The example of *Cloudina* shell hash shown in figure 6B can be contrasted with the *in situ* sample. That many of the reworked deposits are biomicroites suggests the current energies necessary to breakdown and erode the shells were not great.

In thin sections of the *in situ* material, calcitized aragonite cements, as well as dolomite and radiaxial fibrous/fascicular optic calcite cements (Kendall, 1985), can be seen filling space within the central canal of *Cloudina* and between the shells (fig. 4A, C, D). It is also possible to see the ghosts of cement crystals that grew into the pore-space that must have existed between shell laminae (fig. 4C–F). The preserved pseudo-hexagonal, square-ended and sometimes acicular habit of these

ghosts as well as their high Sr concentrations (up to 7000 ppm) indicate that the precursor mineral was aragonite (Sandberg 1984, 1985). Aragonite is unstable in meteoric (fresh water) fluids, so it is clear that these cements did not result from late diagenetic processes but formed very early, probably in marine fluids, and filled primary pore-space. Previous researchers assumed that the multi-layered structure of the shell was solid and the thin, usually dark, ghosts that appear as nested layers (figs. 4A–F, 5B–E) indicated the position of an organic-rich layer within an otherwise robust structure (Germs 1927a,b; Glaessner, 1976; Hahn and Pflug, 1985). The ghosts after a precursor aragonite cement demonstrate that there was pore-space between the laminae, hence the shell could not have been solid.

There are at least seven discrete layers preserved in the specimen of *C. hartmannae* pictured in figure 4E. Each layer is slightly off center and to the left in the photograph of the previous layer. Measurements on numerous shells indicate that individual layers are between 8 to 50  $\mu\text{m}$  thick, most measuring between 10 to 25  $\mu\text{m}$ . The variation in measured thickness probably results, in part, from dolomitization. However, many laminae that appear to be only one layer thick in fact contain two or more layers, also influencing lamina thickness. The composite nature of some parts of the shell is usually obfuscated by neomorphism, but distinct superimposed shell layers can be seen under cathodoluminescence (fig. 7A,B). In this close-up (fig. 4F) it can be seen that each layer is covered by a fibrous rind of aragonite cement since altered to calcite. This serves to emphasize once again that there was abundant pore-space between the layers of shell material. It is possible that inorganically precipitated early cements reinforced parts of the shell during the lifetime of the organism. The extent to which cementation affected the shell strength of living *Cloudina* is difficult to determine, but it may be that the inorganic precipitation of aragonite or high-magnesian calcite lent a robustness to the individual shells and, perhaps, the thicket or bioherm in general.

Some of the shell layers exhibit a plasticity that can be seen in figure 4B. It is, therefore, likely that the layers were originally formed of organic material impregnated with calcium carbonate. That the layers were entirely organic seems improbable, for there are examples of the brittle behavior expected of a mineralic substance, such as fractured shell layers (fig. 5B) and abundant shell hash associated with *Cloudina* coquinites (figs. 8A and C). Additionally, the shell layers are often preferentially dolomitized, allowing details of the shell structure to be revealed in acid etched samples (fig. 5A; Germs, 1972a,b). This diagenetic phenomenon is most easily explained by assuming that the original mineralogy of the shell was high-magnesian calcite and that during recrystallization this localized source of Mg caused dolomite to precipitate.

A schematic reconstruction of the shell structure of *Cloudina* in longitudinal section is illustrated in figure 9 and should be compared to

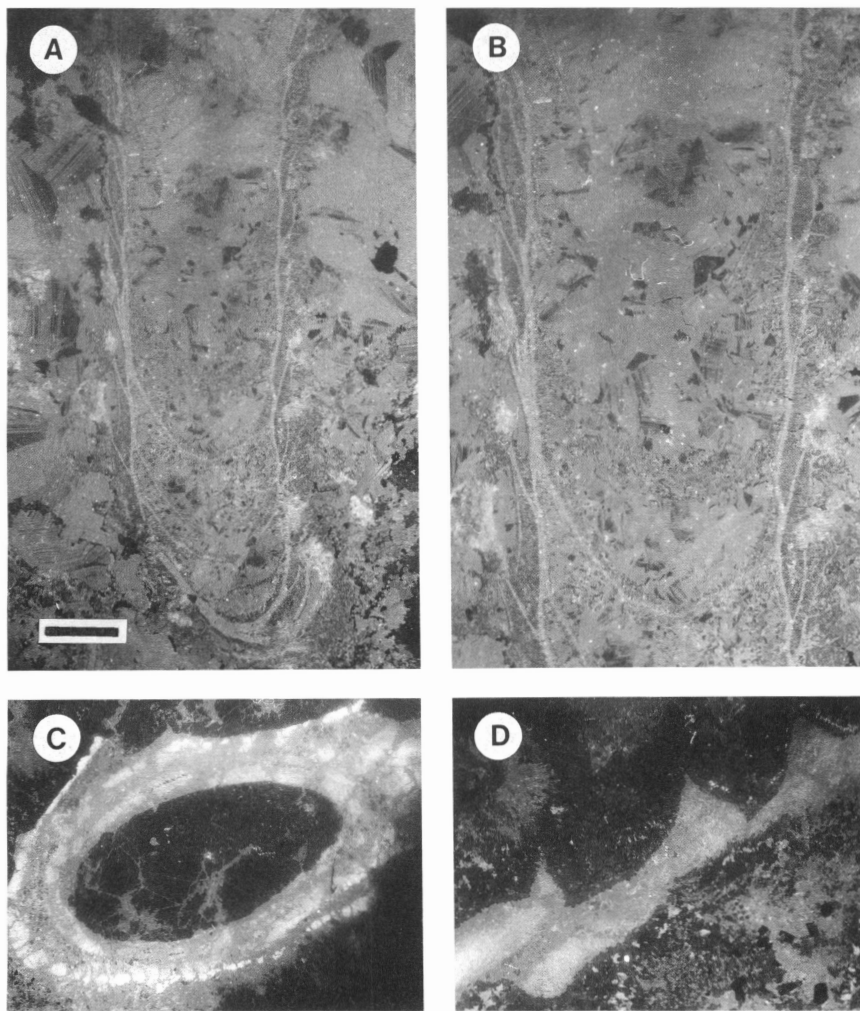


Fig. 7. Cathodoluminescence photomicrographs. (A and B) same specimen at different magnifications, *C. riemkeae*, slide HU 62342-b, Omkyk Member, Zaris Formation, Kuibis Subgroup (loc. 6, fig. 1). The slightly luminescent layers exhibit the characteristic shell structure illustrated in figure 9, each layer appears to be closed at the base, and successive shell layers are superimposed, scale bar = 0.4 mm for (A) and = 0.2 mm for (B), (C and D) *Cloudina* sp. from the Olistostroma del Membrillar, upper part of the Cijara Formation, central Spain, slide HU 62348-a-1 (sample courtesy A. Perejón). (C) Oblique transverse section showing traces of multiple layers, scale bar = 0.6 mm. (D) Shell fragment showing ridges that represent the calcitized outline of stacked shell layers that formed flanges, scale bar = 0.25 mm.

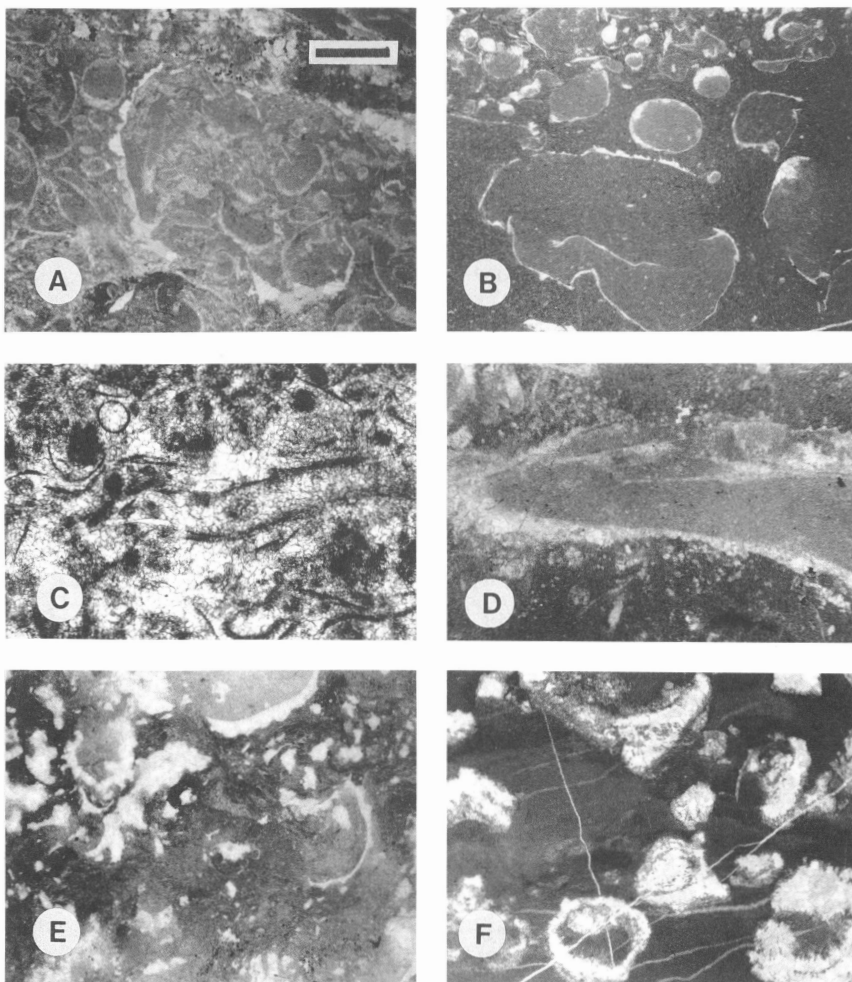


Fig. 8. Reworked *Cloudina* biomicrites and biosparites in thin and thick section, plane polarized light. (A) Note the co-occurrence of crescentic and circular shell fragments in cross section, scale bar = 3.4 mm, slide HU 61813-1, Mooifontein Member, Zaris Formation, Kuibis Subgroup (loc. 1, fig. 1). (B) Note the deformed fragment in the lower part of the photomicrograph indicating that the shelly material was flexible, scale bar = 3.4 mm, slide HU 61813-3-t, same stratigraphic position and locality as (A). (C) *C. riemkeae* biosparite, scale bar = 0.9 mm, slide HU 62343, Omkyk Member, Zaris Formation, Kuibis Subgroup at Driedoornvlakte (loc. 6, fig. 1). (D) Nearly complete specimen of transported *C. hartmannae* in micritic groundmass, note that the multiple shell layers can be calcitized to give the appearance of only an inner and outer wall, scale bar = 2.0 mm, slide HU 62345-t-2, Mooifontein Member, Zaris Formation, Kuibis Subgroup, from Zaris Pass, Namibia (loc. 9, fig. 1). (E) Apparent ornament on crescentic fragments. The unusual shape of these fragments probably results from the preservation of the irregular outlines of metastable cements that grew on shell layers. These layers with their cements were stripped off during postmortem transport and have since been calcitized to a clear spar, scale bar = 3.4 mm, slide HU 62344-b, Omkyk Member, Zaris Formation, Kuibis Subgroup, from near the *in situ* thickets (loc. 6, fig. 1). (F) *Cloudina?* biomicrite from the Nomtsas Formation, Schwarzrand Subgroup (loc. 11, fig. 1), slide HU 62346-t, scale bar = 1.5 mm.

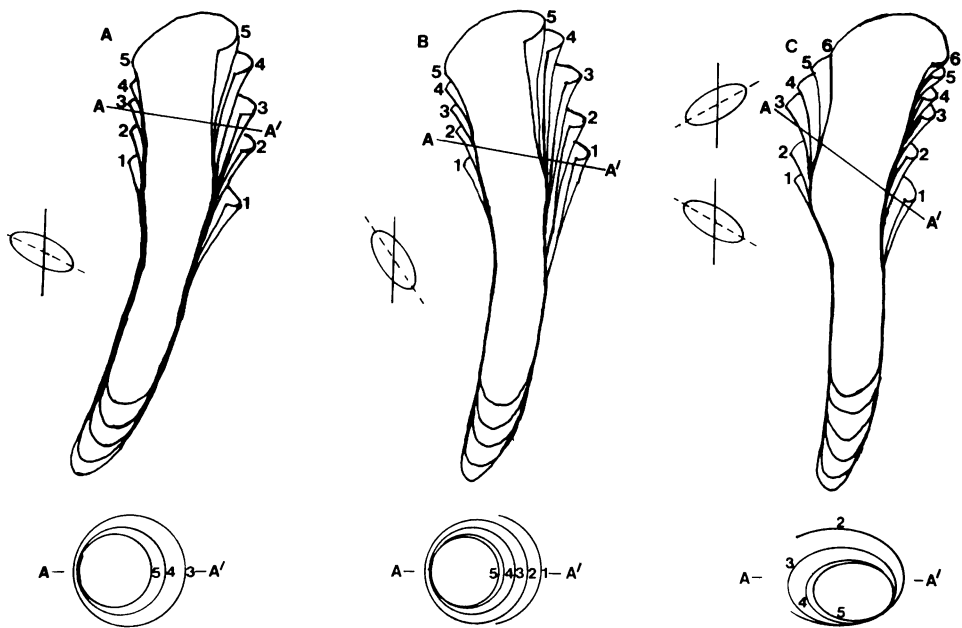


Fig. 9. Schematic reconstruction of the shell structure of *Cloudina*. See text for explanation.

the imperfectly preserved, acid-etched longitudinal section of *C. riemkeae* (fig. 5A). It is possible to describe these shells as having a cone-in-cone structure, though this is clearly an oversimplification. Each shell layer had the form of a slightly flaring tube with one end open and the other closed. Growth appears to have been periodic. The flanges of each new layer separate from the previous layer at different levels along the longitudinal axis. The ellipses shown to be at an oblique angle to the axis of growth and to the left of each longitudinal cross section (fig. 9) are meant to represent the plane wherein one layer separates from the previous. Quite simply, one side of each added shell layer remains in contact with the older layer along a greater distance of the tube than on the other side. The shell layers in figure 9 are numbered to make this feature obvious. If the line containing the maximum length of contact between two shell layers remains in the same place throughout growth (fig. 9A,B), then a curvature results along the length of the shell. If on the other hand the line containing the maximum length of contact between shell layers rotates throughout growth then a sinuous form results. The beginnings of a developing sinuosity can be seen in figure 9C, where the line of maximum contact is to the left between layers 1 and 2 and to the right between 4 and 5. This is why the two ellipses are shown to have rotated through 180 degrees.

A distinctive feature of transverse sections is that each new shell layer is placed eccentrically within the previous layer. Figure 5 shows cross sections that vary depending on whether the line containing the maximum length of contact along the axis of growth remains in the same place throughout growth (fig. 5D) or if it rotates with each new layer (fig. 5E). A graphical illustration of this is shown in figure 5F.

There are two controversial aspects of the shell structure that require further discussion. First, where two layers join did the organism secrete a new layer on top of the old or did it simply make use of the previous layer and save itself the trouble of depositing additional shell material (Germs, 1972a, b; Glaessner, 1976)? And second, was each successive tube closed at its base, or was only one basal layer formed (Germs, 1972a,b; Glaessner, 1976; Hahn and Pflug, 1985)? In some specimens, it appears that where two layers join, a second layer was deposited on top of the previous layer; thus shell material was deposited along the entire margin of each successive tube (fig. 7A,B). There is also evidence, using cathodoluminescence, that each layer had a closed base (fig. 7A,B).

Now that some basic features of the shell structure characteristic of *Cloudina* have been established, it is worth considering how such a shell would respond to current transport and diagenetic alteration. One might expect that erosion and transport would cause the outer flanges to be stripped off, leaving a smooth-walled, more robust central tubular structure denuded of its ornament. Indeed, biomicrites and coquinites in the Nama Group contain separated fragments of the relatively small central tubes and the larger flanges (fig. 8A–F). Particularly notable are incomplete rings or crescent-shaped skeletal fragments reflecting the eccentrically stacked “cone-in-cone” structure of the parent shell. Plastic deformation of the skeletal fragments is also commonly found in reworked *Cloudina* deposits (fig. 8B) and may be used as a diagnostic feature for identifying the reworked remains of this genus.

If the effects of early cementation and diagenetic recrystallization are superimposed, bizarre shapes such as those pictured in figure 8E can result. It is probable that the remarkable ornament on these crescentic structures represents the outlines of precursor metastable cements that grew on and between the shell layers before they were stripped off during transport. The shell and cement were later neomorphosed to a clear spar or dissolved and then replaced by diagenetic spar. Additionally, neomorphism or recrystallization of intact *Cloudina* shells can obliterate the multiple-layered structure of the shell, so that it appears that the shell was robust and contained only an inner and outer wall. This occurred fairly commonly in the *in situ* remains from the northern Nama basin.

In summary then, certain diagnostic characteristics facilitate the correct identification of *Cloudina*. These are: (1) a multi-layered tubular structure in which there was an abundance of pore-space between successive layers; (2) each layer is eccentrically placed within the former

layer: (3) longitudinal sections often exhibit a ridged appearance in thin section and in acid-etched specimens, and these ridges bear a superficial symmetry that belies the *en echelon*, off-center stacking of the successive layers: (4) bioclastic limestones derived from *Cloudina* exhibit a wide variation in fragment size and shape, with relatively small robust and tubular elements co-existing with larger ridged forms and crescentic fragments. These criteria have proved useful for identifying the remains of *Cloudina* in the Nama Group. Superficially dissimilar shelly remains (fig. 8) were thought to have been formed by organisms taxonomically distinct from *Cloudina* before this study was complete, but it is now clear that the unusual characteristics of the primary shell structure of this genus would be expected to give rise to such deposits. The stratigraphically highest shelly remains in the Nama Group, from the limestone in the lower Nomtsas Formation (fig. 8F), however, still can only questionably be assigned to *Cloudina*. Both circular and crescentic cross sections of what appears to be shell material are present (fig. 8F), but until better preserved, multiple-walled specimens are found, the identification of the Nomtsas material remains uncertain.

The above criteria, in addition to enhancing an understanding of the shelly remains within the Nama Group, can also be used to evaluate other late Proterozoic and supposedly lower Cambrian tubular fossils from around the world. It is possible to conclude from this re-evaluation that the known distribution of *Cloudina* is incomplete.

#### GLOBAL DISTRIBUTION OF *CLOUDINA*

In addition to Namibia, *Cloudina* has been reported from Brazil, Argentina, and Antarctica. The material from Argentina described by Yochelson and Herrera (1974) is probably not *Cloudina* but appears to be more closely related to the Cambrian genus *Salterella* (Fritz and Yochelson, 1988). The robust shell wall of *Cloudina*? *borrelloii*, obvious in plates 3 and 4 of Yochelson and Herrera (1974), appears solid, and a smooth inner and outer boundary is evident in longitudinal section that is quite distinct from the ridged expression of the multiple, nested shell layers seen in longitudinal sections of *Cloudina* (fig. 5A). Interestingly, the resemblance of *C.*? *borrelloii* to *Salterella* was noted by Yochelson and Herrera (1974), but they dismissed the similarity as superficial, for the Argentinean fossils lacked the diagnostic inner laminar deposits of *Salterella* (Fritz and Yochelson, 1988). Remains of *Salterella* from the lower Cambrian Forteau Formation, northwest Newfoundland commonly lack, or appear to lack, these inner deposits (personal observation). In the Newfoundland material, it is possible that the agglutinated inner core may have dropped out during current reworking or that these deposits consisted of calcareous material whose laminated features were obliterated or obfuscated during diagenesis. Such explanations may also apply to the Argentinean specimens.

The millimetric tubular fossils in the Tamengo Formation, Corumbá Group, Brazil, originally assigned to the algal taxon *Aulophycus*

*luciano* (Beurlen and Sommer, 1957), are undoubtedly *Cloudina* (Zaine and Fairchild, 1985, 1987; Hahn and Pflug, 1985). Published line drawings and microphotographs in Hahn and Pflug (1985) show eccentrically nested shell layers and a ridged outer wall. Crescentic fragments of shell material are also fairly common in the Brazilian material (fig. 10E). Often the shells are silicified, but despite this alteration it is possible to infer the existence of pore-space between the shell layers. The transverse section in figure 10E is filled with microquartz that contains small, clear circular areas which are probably ghosts of opal CT lepispheres (Maliva and Siever, 1988). Opal CT lepispheres are known to form as a pore-filling phase so that, as in the Namibian material, early cements suggest the former presence of pore-space between shell layers. It is probable that the sedimentary rocks containing these fossils are latest Proterozoic in age. This is supported by the similarity between the Namibian and Brazilian *Cloudina* and the occurrence in the Tamengo Formation of *Corumbella weneri* (Hahn and others, 1982), which resembles only Ediacaran body fossils. Moreover, *Bavlinella faveolata*, an organic-walled microfossil commonly found in late Proterozoic deposits (Vidal, 1976), has also been reported in the Tamengo Formation (Fairchild and Sundaram, 1981; Fairchild, 1984; Zaine and Fairchild, 1987).

Specimens referred to *Cloudina?* sp. were reported from the Shackleton Glacier area in Antarctica (Yochelson and Stump, 1977). The material is not well preserved, so that it seems best to maintain the questionable status of these fossils. The author has examined this material at the U. S. National Museum, and the strongest evidence for *Cloudina* affinities is the existence of a crescentic shell fragment pictured in Yochelson and Stump (1977, fig. 2C). Unfortunately the slides are covered, so that it was not possible to use cathodoluminescence or epifluorescence techniques to examine the material. The supposed trilobite fragment (Yochelson and Stump, 1977, fig. 2A) found associated with *Cloudina?* sp. is not convincing, so that the Cambrian age assigned by Yochelson and Stump (1977) is also not certain.

Tubular fossils I have examined from terminal Proterozoic deposits in central Spain are clearly *Cloudina* (Liñán, Palacios, and Perejón, 1984; Palacios, 1989). Though it is difficult to show the shell structure using transmitted light, the ridged outer wall (fig. 7D) and traces of the multi-layered shell (fig. 7C) are evident under cathodoluminescence. A well preserved specimen in transverse section, containing eccentrically nested shell layers is also evident in plate 16, figures 1 and 2 of Palacios (1989). Both Vendian aspect trace fossils and organic-walled microfossils support a late Proterozoic age for the *Cloudina*-bearing deposits in the central region of Spain (Palacios, 1983; Liñán, Palacios, and Perejón, 1984; Palacios, 1989).

Silicified tubular fossils from the Sinian Baimantuo Member, Dengying Formation, Eastern Yangtze Gorge area, Western Hubei, China, are also probably *Cloudina*. Chen and Wang (1977) originally described the material as *Cloudina?* sp., but a later publication assigned the fossils to

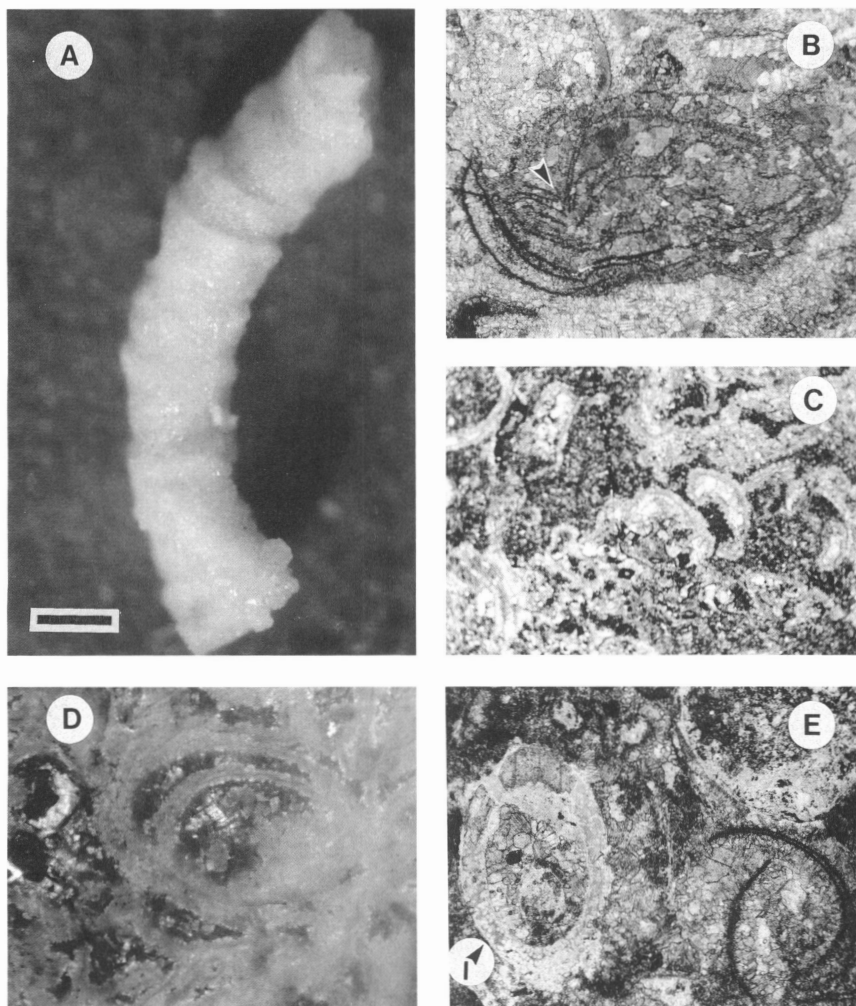


Fig. 10(A to C) Samples from *Nevadatubulus*-bearing limestones, lower Deep Spring Formation, White Inyo Mountains, eastern side of Mount Dunfee, just east of Gold Point, Nevada (samples courtesy P. Signor). (A) Holotype of *Nevadatubulus*, UCMP 37537, scale bar = 0.3 mm. (B) *Cloudina* sp. thin section of multiple-walled shell, arrow pointing to broken layers that exhibit both plastic and brittle behavior, slide UCMP 38570, scale bar = 0.7 mm, plane polarized light. (C) Shell hash from *Nevadatubulus*-bearing deposits containing numerous crescent-shaped fragments, slide UCMP 38571, scale bar = 2.0 mm, plane polarized light. (D) Thick section of *Wyattia*-bearing sample, uppermost Reed Dolomite, White Inyo Mountains, Schulman Grove, California. Note the eccentrically-nested layers in the transverse section, slide HU 60840-1, scale bar = 1.2 mm, plane polarized light. (E) Thin section of *Cloudina*-bearing sample from the Tamengo Formation, Corumbá Group, Brazil, note the crescentic fragments in the bottom right. A transverse section contains small clear circular ghosts that are probably after opal C-T lepispheres (l) which were likely the pore-filling precursor to the microquartz now present, scale bar = 0.6 mm, slide HU 62349.

*Sinotubulites baimatuoensis* (Chen, Chen, and Qian, 1981). The silicified specimens were etched out using a dilute acid solution and three co-occurring morphs of this species were described: (1) large tubes 4 to 5 mm in diameter, the outer wall exhibiting circular ridges and the inner wall being smooth; (2) medium tubes 1.5 to 3 mm in diameter with variable type of external ornament, some with condensed uniform or regular ridges, others with high ridges that are much less condensed, and in these forms the ridges are not complete around the shell; and (3) small tubes 0.4 to 1 mm in diameter with a smooth exterior and interior surface to the shell. Chen, Chen, and Qian (1981) also noted that the central tube was often eccentrically located with respect to the outer shell margin. These features suggest that the Chinese material represents an accumulation of *Cloudina* shells that have suffered varying degrees of transport and erosion, the largest ridged forms being the least damaged. Successively smaller tubes have more outer flanges stripped off, and the smallest smooth-walled forms represent the remains of *Cloudina* completely denuded of external ornament. The incomplete rings or ridges on the medium sized tubes and the out-of-center position of the inner tube suggest that the shell layers were eccentrically stacked. A Sinian age has been maintained for these shelly fossils based on the presence of the Ediacaran fossil *Paracharnia* (Sun, 1986) and abundant *Vendotaenia* (Xing and others, 1984; Yin, 1985; Sun, 1986) in horizons just below those containing *Sinotubulites*. A characteristic and diverse assemblage of lower Cambrian early skeletal fossils also occurs in the Dengying Formation in beds overlying the *Sinotubulites*-bearing deposits (Xing and others, 1984), but these Cambrian fossils are never found associated with *Sinotubulites*. Conway Morris, Mattes, and Chen (1990) also report *Cloudina*-like material from the top of the Dengying Formation near Kuanchuanpu, Shaanxi province. More work needs to be done before the true affinities of these tubular fossils can be ascertained, but they do occur in a horizon that is likely latest Proterozoic in age.

The same features described in the Chinese material were noted by McMenamin (1985) in *Sinotubulites* from the La Ciénega Formation, Caborca region, northwestern Sonora, Mexico. Coquinities that contain both large elements with external ridges and smaller smooth-walled forms are described and interpreted as differentially abraded *Sinotubulites*. One specimen, misinterpreted as probable wave-invaginated circothecid hyolithids, shows the characteristic multiple-layered shell wall of *Cloudina* partially etched from the surrounding matrix (fig. 5.3, McMenamin, 1985). In thin section, it is furthermore evident that the layers are eccentrically nested (McMenamin, 1985, fig. 5.6; also, personal observation of author). The longitudinal striae or ribs thought to be characteristic of *Sinotubulites* are only found on some of the specimens from Mexico and probably represent folds that formed under compactional pressure. A lower Cambrian age has been suggested for the Mexican material, based on the presence of some poorly preserved shell

fragments assigned to Cambrian genera (McMenamin, Awramik, and Stewart, 1983; McMenamin, 1985). It is more likely that the deposits contain only *Cloudina* remains and that the La Ciénega Formation is latest Proterozoic in age.

A shelly fauna from the Deep Spring Formation in the White Inyo Mountains, on the east side of Mount Dunfee near Gold Point, Nevada described by Signor, Mount, and Onken (1987) also contains *Sinotubulites* along with *Nevadatubulus*, *Salanytheca*, and *Coleoloides*. Once again, it is probable that all these genera are different taphonomic and diagenetic types derived from *Cloudina* shells. *Salanytheca* and *Coleoloides* are very poorly preserved, but *Nevadatubulus* bears some characteristic features of *Cloudina*. Three dimensional specimens, freed by acid digestion (Signor, Mount, and Onken, 1987, fig. 4.1–4.14), appear to be internal casts of *Cloudina* that are between 0.5 to 1.2 mm in diameter; a similar size range has been reported for *C. riemkeae* from the Nama Group. The holotype for *Nevadatubulus dunfee* is reproduced in figure 10A, and it is easy to see that if the acid-etched *C. riemkeae* in figure 5A formed a mold then the cast would look very similar to the holotype of *N. dunfee*. My own investigations of thin sections and hand samples of fossiliferous samples from the Mount Dunfee locality (kindly provided by P. Signor) lend further support for *Cloudina* affinities. In some thin sections brittle and plastic deformation of multi-layered shells is evident (fig. 10B), as well as accumulations of crescentic shell fragments (fig. 10C). The *Cloudina* sp. (fig. 10B) pictured is about 3.5 mm in maximum dimension and comparable in size to *C. hartmannae* from the Nama Group, but larger than the size range recorded for *Nevadatubulus*. *Sinotubulites*, the second most common fossil from the Mount Dunfee locality, however, was reported up to 3.3 mm in maximum diameter. Thus fossils with a size range, wall structure, and morphology similar to the two species of *Cloudina* from the Nama Group occur in the White Inyos. *Nevadatubulus* and *Sinotubulites* from this area are likely con-generic with *Cloudina*, the former comparable to *C. riemkeae* and the latter to *C. hartmannae*. It is even possible to suggest that *Wyattia* from the uppermost Reed Dolomite, also in the White Inyo region (Taylor, 1966), has a shell structure similar to that found in *Cloudina*. Though the material is extensively dolomitized, occasional transverse sections exhibit a suggestion of eccentrically-nested multiple layers (fig. 10D). Such transverse sections were noted by Taylor (1966) who described them as individuals with “U-shaped” internal structure. The individuals with the U-shaped internal structure were not referred to *Wyattia*, but it seems likely that they were constructed by the same organism due to their similar size and preservation. Whether *Wyattia* is con-generic with *Cloudina* is not clear, but it is likely that they at least had a similar shell structure. The ages of the upper Reed Dolomite and lower Deep Spring Formation are not certain. The pre-trilobitic shelly fossils from these horizons have been considered lower Cambrian (= Tommotian) (Signor and others, 1983; Mount, Gevirtzman, and Signor, 1983; Signor, Mount, and Onken, 1987). This

age assignment, however, was based on incorrect identifications of the fossil remains which are, in my view, dominantly *Cloudina*. It seems likely, therefore, that the "pre-trilobitic" fossils from the White Inyo region are latest Proterozoic in age.

*Cloudina* is also known from the Ara Formation, Huqf Group in Oman (Conway Morris, Mattes, and Chen, 1990). There is little to constrain the age of the Ara Formation (Gorin, Racz, and Walter, 1982; Conway Morris, Mattes, and Chen, 1990), other than the presence of *Cloudina*, so that a terminal Proterozoic age can be tentatively assigned. Conway Morris, Mattes, and Chen (1990) noted the presence of *Angulocellularia*, an algal form genus known from lower Cambrian deposits in Siberia and Mongolia (Riding and Voronova, 1982), and suggested that the age of the Ara may be Cambrian. *Angulocellularia* are solid clumps of micrite exhibiting a crude branching pattern thought to have been formed by calcifying cyanobacteria. It should be kept in mind, however, that this genus could have been formed by any number of microbes and that calcified cyanophytes have been reported from Vendian and earlier deposits (Bertrand-Sarfati, 1976; Riding and Voronova, 1984). Thus the biostratigraphical significance of the poorly preserved remains of *Angulocellularia* in the Ara Formation remains equivocal.

#### CONCLUSIONS

It is possible to conclude that *Cloudina* had a wide geographic distribution in the latest Proterozoic (fig. 11). The hatched area in figure 12 highlights *Cloudina*-bearing limestones. Undoubted Cambrian fossils

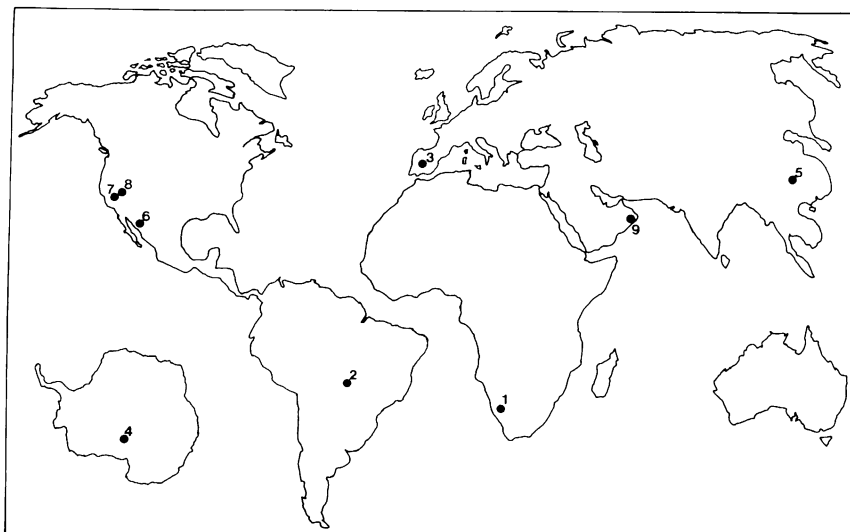


Fig. 11. Latest Proterozoic distribution of *Cloudina* and *Cloudina*-like fossils.

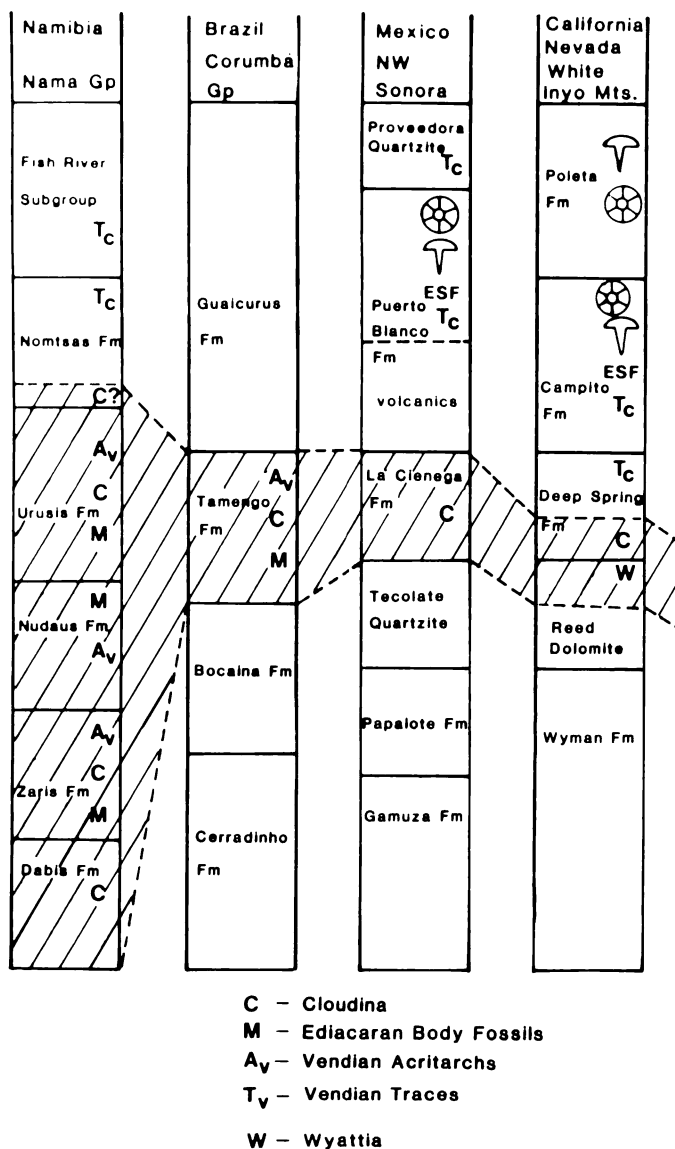


Fig. 12. Tentative correlation chart based on the occurrence of *Cloudina*. See text for references.

are only found above the horizons containing *Cloudina*, whereas *Cloudina* often occurs with Ediacaran fossils. Characteristic "pre-Ediacaran" acritarchs (Yin, 1985; Knoll and Butterfield, 1989; Zand and Walter, 1989) are only known from beds below *Cloudina*-bearing rocks. Thus

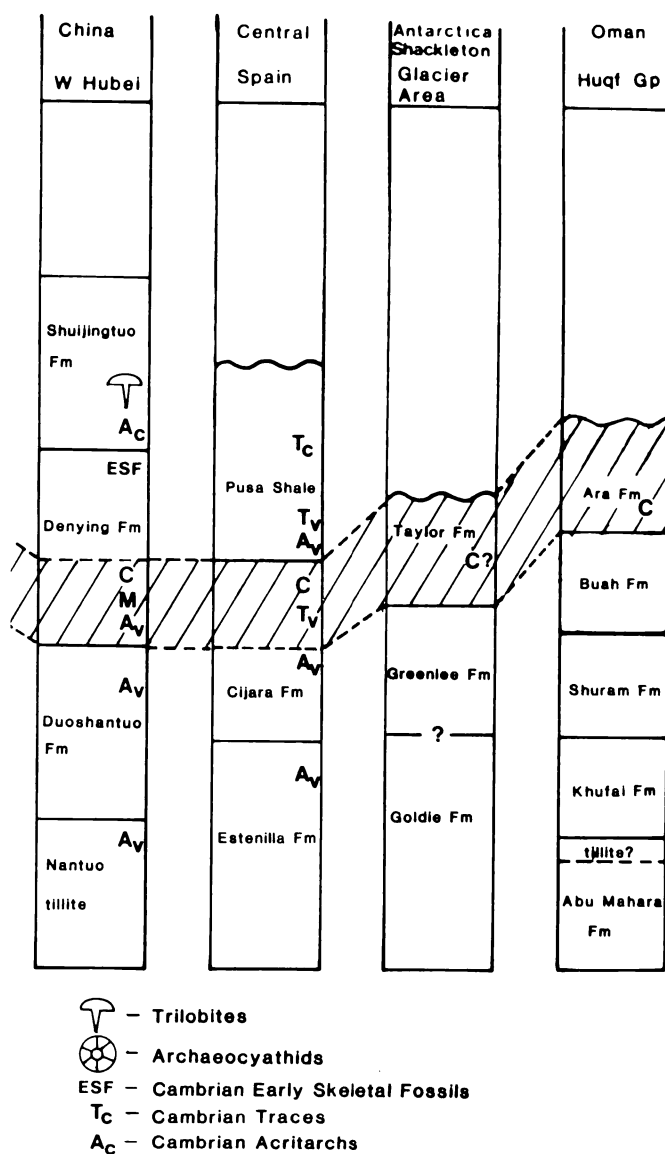


Fig. 12 (continued)

there is a fairly strong case to be made for considering *Cloudina* an index fossil for the late Vendian or Ediacaran.

If my interpretation of the shell structure is correct then it appears that the level of biological control over mineralization need only have

been minimal. This contrasts with the sophisticated mineralization systems known in many extant organisms and that also can be inferred for many of the more robust early Cambrian shells (Lowenstam and Weiner, 1989; Brasier, 1989). There appears to have been no specialized region or "lip" where shell growth took place, but rather calcium carbonate seems to have been periodically deposited in an organic matrix around much of the exterior of what was probably the basal part of the organism. Lowenstam and Margulis (1980) suggested that just such a primitive form of biomineralization may have preceded more intricate "organic-matrix-mediated" or "biologically controlled" mineralization systems (Lowenstam and Weiner, 1989). I do not know of any Cambrian or younger fossils that share features of the *Cloudina* shell structure so that it seems difficult to determine whether biomineralization in *Cloudina* represents an ancestral condition for more advanced systems or simply an evolutionary grade of organization that was not in a direct line to any of the sophisticated systems found today or in Phanerozoic rocks.

Given the global distribution of *Cloudina* it is clear that biomineralization in latest Proterozoic times was not simply a local phenomenon, though the significance of metazoan biomineralization as a calcium sink is uncertain. There was enough biologically precipitated carbonate to form fairly thick and locally widespread bioclastic limestone deposits (figs. 1, 6). The true taxonomic diversity of mineralizing organisms in the "Ediacaran" is also difficult to gauge. Some workers have suggested that calcareous spicules may have been formed by some of the large soft-bodied Ediacaran organisms. For example, the linear impressions on the interpreted axes and polyp leaves of *Charniodiscus* may indicate the former presence of spicules which occur in comparable tissues of living Pennatulacea (Glaessner and Wade, 1966; Jenkins and Gehling, 1978). The probability of preserving a micrite- or spicule-impregnated organic matrix is very low, and more effort to find disseminated spicules in Ediacaran and earlier limestones is needed. Besides such indirect evidence for biomineralization in animals, however, there appears to be but one late Proterozoic skeletalized genus—*Cloudina*. Further work may expand this apparently low diversity. In fact Grant, Knoll, and Germs (1987, in press) have described foliose crusts from the lower Nama Group which are apparently calcareous multicellular algae similar to the well known "phylloid algae" from the late Paleozoic (fig. 1). Moreover, Horodyski and Mankiewicz (1990) described possible calcified metaphytes from the top of the late Proterozoic Beck Spring Dolomite, southeastern California. It is possible, therefore, that biomineralization originated in the latest Proterozoic and in both metazoans and metaphytes. This contrasts with the more generally accepted view that skeletalization is a lower Cambrian novelty. In fact it appears more likely that development of complex multicellularity in animals, locomotion requiring fairly vigorous muscular activity, and biomineralization in metazoans and perhaps metaphytes as well, took place nearly synchronously in the latest Proterozoic.

SYSTEMATIC PALEONTOLOGY

The species level taxonomy that follows is concerned solely with the material from the Nama Group which received the greatest attention during this study. The two special *C. hartmannae* and *C. riemkeae*, mainly distinguished on the basis of size (Germs, 1972b), are maintained. The biomodal size distribution found in the Namibian material, however, may not exist for the numerous other *Cloudina* deposits from other parts of the world. Further study of these other remains may result in a reassessment of the two species of *Cloudina* recognized in the Nama Group. Pending future study, therefore, I will only synonymize at the genus level.

Phylum Uncertain

Class Uncertain

Order Uncertain

Family Uncertain

Genus *Cloudina* Germs 1972b

Figures 4 to 8, 10A to C, E

- 1957 *Aulophycus* Beurlen and Sommer, pages 31 to 33, plates 1 to 6.  
 ?1966 Individuals with a "U-shaped" (in transverse section) internal structure, Taylor, page 3, figure 3.  
 1972b *Cloudina* Germs, pages 753 to 757, plate 1, figures 1 to 13.  
 1976 *Cloudina* Glaessner, pages 265 to 268, plate 1, figure 2; plate 2, figures 1 to 6.  
 1977 *Cloudina*? Chen and Wang, pages 220 to 221, figure 1A and B.  
 ?1977 *Cloudina*? Yochelson and Stump, pages 872 to 875, figure 2A to D.  
 1981 *Sinotubulites* Chen, Chen and Qian, pages 119 to 120, plate 1, figures 1 and 2; plate 2, figures 1 to 6.  
 1985 *Cloudina* Zaine and Fairchild, page 130  
 1985 *Cloudina* Hahn and Pflug, pages 421 to 425, plate 1, figures 1 and 2; plate 2, figures 3 and 4.  
 1985 *Sinotubulites* McMenamin, pages 1416 to 1421, figures 3.2 to 3.6, 4.1, 4.2, 4.4 to 4.7, 5.2, 5.3, 5.5, 5.6.  
 1987 *Cloudina* Zaine and Fairchild, pages 804 to 807, figures 1 to 7.  
 1987 *Sinotubulites* Signor, Mount and Onken, pages 431 to 432, figure 5.1  
 1987 *Nevadatubulus* Signor, Mount and Onken, pages 428 to 429, figures 3, 4.1 to 4.14.  
 1989 tubular fossils, Palacios, page 63, plate 16, figures 1 to 4.  
 1990 *Cloudina* Conway Morris, Mattes, and Chen Menge, figure 2.  
*Type species.*—*Cloudina hartmannae* Germs, Kuibis and Schwarzrand Subgroups, Nama Group, Namibia.

*Emended diagnosis.*—Curved to sinuous tubular fossils, 0.3 to 6.5 mm in diameter and up to 3.5 cm in length. Shells with multiple thin, calcified organic-rich layers, originally probably high-magnesian calcite. Each layer 8 to 50  $\mu$ m thick in the form of a slightly flaring tube with one

end open and the other closed, terminal thin flanges developed at open end. New shell layers eccentrically deposited within previous layers.

*Remarks.*—An abundance of pore-space existed between terminal flanges that may have been, at least, partially occluded by early cements during the lifetime of the organism, but certainly cements formed between shell layers after the death of individuals. The free or weakly-cemented flanges were, in addition, easily abraded during post-mortem transport so that reworked *Cloudina* deposits are characterized by accumulations of smaller tubular elements occurring with larger ridged forms and crescentic shell fragments that represent the stripped-off flanges.

*Discussion.*—It is difficult to speculate about the biology of this organism since no soft parts are preserved. Periodic growth by internal accretion and the sinuous “test-tube” form of the organism are inconsistent with an algal origin. Affinities with sponges and archaeocyathids can be ruled out, for the shell layers are not porous. Both of the species from the Nama Group formed thickets or bioherms, and this gregarious and sedentary habit can be used to infer that *Cloudina* was probably a filter-feeding metazoan. Moreover, the organism that secreted these shells appears to have had to move up the tube between the deposition of successive shell layers implying a musculature and internal complexity consistent with a diploblastic or even triploblastic animal. Thus the *Cloudina* organism was probably a metazoan of at least a cnidarian grade of organization.

Glaessner (1976) proposed that *Cloudina* has affinities with the polychaete worms, but such a relationship is incompatible with the shell structure of *Cloudina* described herein. A relationship with the Cribriocyatha (Yankauskas, 1964, 1969, 1972; Germs, 1972a, b; Glaessner, 1976) is difficult to ascertain without having examined the material first hand, though some of the published microphotographs show a superficial similarity to *Cloudina*. Cribriocyathids do not appear to be congeneric with *Cloudina*, however, for their annulations seem more regular and to be made up of more robust shell layers than those associated with *Cloudina*.

*Geologic range and geographic distribution.*—Latest Proterozoic (“Ediacaran”)—Nama Group, Namibia (Germs, 1972b); Tamengo Formation, Corumbá Group, Brazil (Zaine and Fairchild, 1985, 1987; Hahn and Pflug, 1985); Olistostroma del Membrillar, upper part of the Cijara Formation, central Spain (Palacios, 1989); Baimantuo Member, Dengying Formation, eastern Yangtze Gorge, Western Hubei, China (Chen and Wang, 1977; Chen, Chen, and Qian, 1981); La Ciénega Formation, northwestern Sonora, Mexico (McMenamin, 1985); Deep Spring Formation, White Inyo Mountains, eastern California and Esmeralda County, Nevada (Signor, Mount, and Onken, 1987); ?Reed Dolomite, White Inyo Mountains, eastern California (Taylor, 1966); Ara Formation, Huqf Group, Oman (Conway Morris, Mattes, and Chen 1990); ?Taylor

Formation, Shackleton Glacier Area, Antarctica (Yochelson and Stump, 1977).

*Cloudina hartmannae* Germs, 1972b

Figures 4A to F, 6A, 8A, B, D, E

1972b *Cloudina hartmannae* Germs, pages 753 to 755, plate 1, figures 1 to 7.

1976 *Cloudina hartmannae* Glaessner, pages 266 to 268, plate 1, figure 2; plate 2, figures 1 to 6.

1985 *Cloudina hartmannae* Hahn and Pflug, page 422, plate 2, figure 5.

*Holotype*.—The specimen illustrated in plate 1, figure 1 of Germs (1972b) is the type for this species and is deposited in the South African Museum, Cape Town; S.A.M.K. 1071.

*Description*.—Curved to sinuous tubular fossils about 2.5 to 6.5 mm wide. Multiple-walled shell structure as described in the diagnosis for the genus. It is more common to find ghosts after early aragonite cements between the shell layers in this species (fig. 4D, F) than in *C. riemkeae*. Germs (1972b) reported that where two individuals grow together they share a common wall, but this does not find support in this study, nor were any cases of reproduction by budding observed.

*Occurrence*.—Found in limestones throughout the Kuibis and Schwarzrand Subgroups, Nama Group mostly as reworked remains, but also as an *in situ* *Cloudina* thicket in the Omkyk Member, Zaris Formation, Kuibis Subgroup on farm Driedoornvlakte near Schlip, Namibia.

*Cloudina riemkeae* Germs, 1972b

Figures 5A to E, 7A and B, 8C

1972B *Cloudina riemkeae* Germs, pages 755 to 757.

1976 *Cloudina riemkeae* Glaessner, page 266.

1985 *Cloudina riemkeae* Hahn and Pflug, pages 422 to 423.

*Holotype*.—The specimen illustrated in plate 1, figure 8 of Germs (1972b) is the type for this species and is deposited in the South African Museum, Cape Town: S.A.M.K. 1072

*Description*.—Curved to sinuous tubular fossils about 0.3 to 1.3 mm wide. Multiple-walled shell structure as described in the diagnosis for the genus. It is very rare to find ghosts after early cements in between shell layers within individual specimens (but see fig. 5C). This might be due to the more tightly-nested shell layers in this species that, unlike *C. hartmannae*, were more easily fully occluded by cements before meteoric diagenesis, or could simply be due to the vagaries of preservation following calcitization. Germs (1972b) reports two variations in the form of *C. riemkeae* which he calls  $\alpha$  and  $\beta$ . These appear to be similar specimens cut in different cross sectional planes,  $\beta$  being more tangential and farther from the longitudinal axis of growth.

*Occurrence*.—Found in limestones throughout the Kuibis and Schwarzrand Subgroups, Nama Group mostly as reworked remains, but also as an *in situ* *Cloudina* thicket in the Omkyk Mb., Zaris Formation., Kuibis Subgroup on farm Driedoornvlakte near Schlip, Namibia.

## REPOSITORY

All the specimens, except for the samples from the White Inyo Mountains, described or figured here are deposited in the Paleobotanical Laboratory, Botanical Museum, Harvard University (HU). The White Inyo material is deposited in the University of California Museum of Paleontology (UCMP) at the University of California, Berkeley.

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## APPENDIX

Number	Description	Stratigraphic Position	Locality
1	reworked <i>Cloudina</i>	Mo, Z, K	1km east of Vioolsdrif 28.7°, 17.6°
2	reworked <i>Cloudina</i>	H, U, Sw	Vioolsdrif West 28.8°, 17.7°
3	reworked <i>Coudina</i>	H, U, Sw	Uitsig 27.5°, 17.1°
4	reworked <i>Cloudina</i>	Kl, D, K	Hoogland 26.9°, 16.5°
5	reworked <i>Cloudina</i>	H? or Sp?, U, Sw	4km north of Hoolog 27.4°, 18°
6	<i>in situ</i> <i>Cloudina</i> 'thicket' and reworked <i>Cloudina</i>	O, Z, K Nu, Sw	Driedoornvlakte 23.9°, 16.7°
7	reworked <i>Cloudina</i>	Mo, Z, K	Mooifontein 25.9°, 17°
8	reworked <i>Cloudina</i>	Mo, Z, K	Helmeringhausen 25.8°, 16.8°
9	reworked <i>Cloudina</i>	Mo, Z, K	Zaris Pass 25°, 16.4°
10	reworked <i>Cloudina</i>	Ho, Z, K	Hauchabfontein 25.5°, 16.3°
11	reworked <i>Cloudina</i>	N, Sw	Swartkloofberg 27.4°, 16.5°

## APPENDIX (continued)

Number	Description	Stratigraphic Position	Locality
12	probable phylloid alga	H, U, Sw	Kolke 27.6°, 16.9°
13	probable phylloid alga	H, U, Sw	Arimas 27.5°, 17°

## Key for abbreviations

K—Kuibis Subgroup, Sw—Schwarzrand Subgroup

D—Dabis Formation, Z—Zaris Formation, Nu—Nudaus Formation, U—Urusis Formation, N—Nomtsas Formation

Kl—Kliphoek Member, Mo—Mooifontein Member, O—Omkyk Member, Ho—Hoogland Member, H—Huns Limestone Member, Sp—Spitskop Member.

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