

## THE EARLY SKELETAL ORGANISM *CLOUDINA*: NEW OCCURRENCES FROM OMAN AND POSSIBLY CHINA

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**ABSTRACT.** Cloudinids are a distinctive group of calcareous tubes, known from the Vendian and possibly the Lower Cambrian of a number of Gondwana localities, including Namibia, Brazil, and Spain. Here we report new occurrences of *Cloudina* cf. *hartmannae* from the subsurface Ara Formation of Oman in biohermal (stromatolitic and calcareous algal dominated) sediments deposited close to the Precambrian-Cambrian Boundary. This occurrence extends the biogeographical range of *Cloudina* and provides support for the notion that the tube walls were lightly mineralized. In addition, cloudinid-like tubes are reported from the Gaojiashan Formation which is close to the Precambrian-Cambrian boundary in Shaanxi Province, China.

### INTRODUCTION

Of all the events that punctuate earth history, none is so remarkable to paleontologists as the sudden appearance of skeletal parts in strata close to the Precambrian-Cambrian boundary (Brasier, 1979; Conway Morris, 1987, 1989). Biostratigraphic correction and geochronological acuity are both still too imprecise to constrain either the exact sequence in which skeletal groups appear or the rate at which skeletal acquisition proceeded. Two points, however, seem clear: (A) The rise of skeletal parts in the earliest Cambrian was not geologically instantaneous, although the principal episode of skeletogenesis may have occupied less than 10 my. (B) Skeletogenesis appears to have been polyphyletic: not only were the metazoans that developed hard-parts in many cases unrelated, but the prokaryotic cyanobacteria also developed an ability to secrete carbonate skeletons at about the same time (Riding, 1982, but see Pratt, 1984, for an alternative proposal that calcification is a diagenetic process).

If a precise order of skeletal acquisition is not yet clear, some generalities seem to be emerging. Trilobites and echinoderms, for example, appear to be somewhat later entrants, although in neither case is their first appearance likely to represent their actual time of origination. This is not only because of sampling imperfections in the fossil record. Exoskeletons of some early trilobites appear to have been lightly mineralized and flexible, suggesting that their appearance is as much the breaching of a taphonomic threshold as it is of any evolutionary event *ab initio*. Trace fossils that were probably produced by arthropods appear earlier in the Cambrian than body fossils (Narbonne and Myrow, 1988; Crimes, 1989). It seems likely that some may have been produced by

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trilobites. Similarly for echinoderms, possible ancestors have been identified in strata as old as the late Vendian, in Ediacaran sandstones of South Australia (Gehling, 1987). So far as can be ascertained these small discoidal animals lacked skeletal parts.

In terms of skeletogenesis, the earliest occurrences of preserved skeletal parts are of critical interest. Such findings will hopefully cast light on whether skeletogenesis typically was manifested first as granules or spicules of a biomineral embedded in an organic matrix, which were subsequently welded into more robust units—with a correspondingly enhanced preservation potential (Lowenstam and Margulis, 1980). Furthermore, were the first biominerals of a particular type, and if so, which type; and is there any evidence that different biominerals arose in an identifiable sequence (Brasier, 1986)?

It is in this context that the tubicolous genus *Cloudina* is regarded with special significance (type species *C. hartmannae*, note Glaessner's, 1976, nomenclatural correction to *hartmannae* is etymologically correct but invalid under I.C.Z.N. regulations, see also Hahn and Pflug, 1985, p.422). It was first reported from carbonate units of the Kuibis and Schwarzrand Subgroups of the Nama succession in central Namibia (fig. 1), which are some hundreds of meters in thickness (Germs, 1972; see

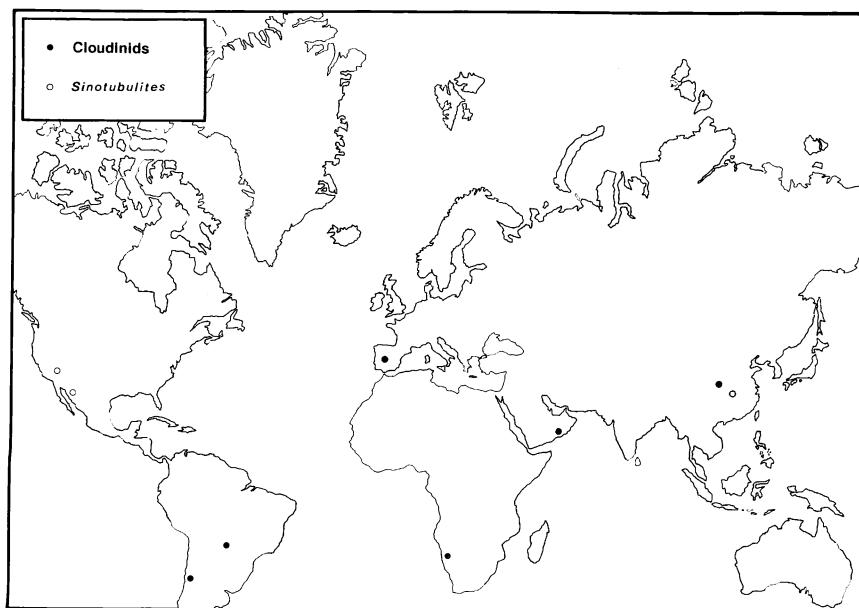


Fig. 1. Distribution of cloudinids and *Sinotubulites* on map of the present world. See text for details of the localities; not shown is a possible occurrence in Antarctica (see Yochelson and Stump, 1977).

also Glaessner, 1984). These units have also received wide attention because clastics interbedded with the carbonates have yielded soft-bodied faunas with Ediacaran affinities. The importance of this co-occurrence is that Ediacaran faunas elsewhere consist only of soft-bodied animals and precede the appearance of hard skeletal parts by millions of years.

#### CLLOUDINA FROM THE NAMA GROUP—PROBLEMS WITH DATING

In his initial description of the Nama Group assemblage Germs (1972) suggested that *Cloudina* might be assigned to the Cribricyathea, a somewhat enigmatic group of calcareous organisms from the Lower Cambrian of the Altai-Sayan region, USSR. This proposal was accepted by Glaessner (1976), who proposed further that the cribricyatheans (including *Cloudina*) be compared closely to the serpulid polychaetes (Annelida). In contrast, Hahn and Pflug (1985) were skeptical of a relationship between *Cloudina* and cribricyatheans, a view with which we concur.

Since the original description of *Cloudina* (Germs, 1972), the Namibian occurrences have been the object of renewed study and comment by various investigators (for example, Yochelson and Herrera, 1974, pl. 1, figs. 1–3, pl. 2, figs 1–3; Glaessner, 1976, pl. 1, fig. 2, pl. 2, figs 1–6, 1984, fig. 2.12; Hahn and Pflug, 1985, pl. 2, fig. 5; Grant, 1989, 1990). They have been cited by those interested in the age of the sequence (Germs and Crimes, 1982; Germs, Knoll, and Vidal, 1986), in its paleobiogeography (McMenamin, 1982; Piper, 1987), or in such wider problems as the onset of biomineralization (Lowenstam and Margulis, 1980).

Although there is a consensus that most of the Nama sequence, including the occurrences of *Cloudina*, belongs in the late Precambrian (Vendian) the precise age remains uncertain. Apart from some remains of calcified algae (Grant and Knoll, 1987) and *Cloudina*, no other skeletal fossils have been reported. The soft-bodied faunas are clearly of Ediacaran aspect and share some taxa with other localities, notably the enigmatic foliate organism *Pteridinium*, and medusoids similar to *Tirasi-ana* (Glaessner, 1984, p. 75, 77). More questionable are the possible metameric metazoan *Spriggina* (Germs, 1973) and the abundance of bag-like ernietids (see Glaessner, 1979; Jenkins, Plummer, and Moriarty, 1981). Evidence in support of an Ediacaran age also comes from organic-walled microfossils. These show a corrosion that, although characteristic for this interval, remains of uncertain significance (Germs, Knoll, and Vidal, 1986). The data from trace fossils are not so precise for biostratigraphic purposes, although the appearance of *Phycodes pedum* near the top of the Nama sections (Crimes and Germs, 1982) seems to indicate a Cambrian age (see Narbonne and Myrow, 1988). However, Crimes and Germs (1982) did not exclude the possibility that, on the basis of these trace fossils, the Precambrian-Cambrian boundary lay stratigraphically lower, within the Schwarzrand Subgroup. Tubular

structures have also been described from the Kuibis Subgroup by Hegenberger (1987), but he makes clear that these are pseudofossils.

Other stratigraphic methods have potential for dating the Nama succession. Kroner and others (1980), for instance, presented paleomagnetic evidence to suggest that the Kuibis and Schwarzrand Subgroups are of late Precambrian age, while the overlying Fish River Subgroup, containing the trace fossil *Phycodes pedum* is Cambrian. Chemostratigraphic methods, such as the correlation of carbon and sulfur isotope age curves across the Precambrian-Cambrian boundary (see Conway Morris, 1987; Tucker, 1989) may also prove to be useful. Kaufman and others (1986) have presented some preliminary  $\delta^{13}\text{C}$  data for the Kuibis and Schwarzrand Subgroups and noted similarity to other late Proterozoic sequences.

#### OTHER OCCURRENCES OF *CLOUDINA*

A number of other tubicolous fossils have also been assigned to or compared with *Cloudina* (fig. 1). The Fuentes Formation, from a locality adjacent to Puerto del Rey in central Spain, has yielded abundant specimens of *Cloudina* (Palacios, 1989). The age of this unit, which underlies the Pusa Formation, appears to be reliably dated as late Vendian (see also Brasier, Perejon, and San Jose, 1979). Cloudinids are also reported from at least two localities in South America. Tubes of Early Cambrian age from the Sierra de Villicum, Argentina, were identified as *Cloudina? borrelloii* by Yochelson and Herrera (1974). This material was subsequently reassigned to *Acuticloudina borrelloii* by Hahn and Pflug (1985). Although the latter authors retained *Acuticloudina* in the Cloudinidae, the structure of the tubes as illustrated by Yochelson and Herrera (1974) suggests that these Argentinian fossils may not be closely related to *Cloudina*, a point also suggested by Yochelson (1977, p. 451).

Fossils from near Corumba in southwest Brazil which had been assigned to the algae (*Aulophycus lucianoii*) by Beurlen and Sommer (1957) were reclassified as the cloudinid *Cloudina waldei* by Hahn and Pflug (1985). Zaine and Fairchild (1987; see also Fairchild, 1978; Fairchild and Sundaram, 1981) concurred with this proposal but retained the original specific name, referring to *C. lucianoii*. However, as the I.C.Z.N. regulations are not applicable to plants dealt with under the Botanical Code, it seems that erection of the species *C. waldei* by Hahn and Pflug (1985) is justified. The Tamengo Formation in which these calcareous tubes occur is dated as late Vendian (Fairchild, 1978; Hahn and others, 1982; Hahn and Pflug, 1985; Zaine and Fairchild, 1987), although the evidence seems to be slender and a Lower Cambrian age is conceivable.

Lower Cambrian sediments exposed on the Taylor Nunatak, adjacent to the Shackleton Glacier in Antarctica, have yielded tubes that Yochelson and Stump (1977) referred to as ?*Cloudina* but compared to *Acuticloudina borrelloii*.

In late Precambrian sections from the Yangtze Gorges in Hubei, China calcareous tubes (*Sinotubulites baimatuoensis*) have been reported from dolomites of the Dengying Formation (Chen, Chen, and Qian, 1981). The material is not well preserved, and although compared with *Cloudina* (Chen and others, 1981), there seems little justification for such a comparison (but see Grant, 1990). It seems likely, however, that these fossils are approximately correlative with the Namibian occurrences, especially as rare Ediacaran forms are also known from the Hubei sections (Sun, 1986). The Chinese occurrences of *Sinotubulites* were discussed by McMenamin (1985), who reported further examples (*S. cienegensis*) from the La Cienega Formation of northwest Mexico and the Deep Spring Formation of Nevada. To these records of Vendian calcareous tubes and possible related forms from the Lower Cambrian, now may be added a new occurrence of *Cloudina* from a Precambrian-Cambrian boundary sequence in the subsurface of Oman.

#### THE OCCURRENCE OF *CLOUDINA* IN OMAN

The specimens of *Cloudina* found in Oman come from the Ara Formation, the uppermost stratigraphic unit of the Huqf Group (Mattes and Conway Morris, 1990; see also Clarke, 1988). The Ara Formation is widely distributed in the subsurface of the South Oman Salt Basin (fig. 2), which is one of a series of basins that formed on the edge of the Arabian Shield in late Proterozoic times. The sedimentary sequence consists of cyclic alternations of carbonates, siliciclastics, and evaporites (fig. 3), the cyclicity having been controlled by changes in sealevel. High organic productivity and anoxia at the time of deposition, combined with suitable reservoir characteristics in the carbonates, make the Ara Formation an important hydrocarbon source and trap in southern and central Oman (see also Raynaud, Lugardon, and Lacrampe-Couloume, 1989). The Ara Formation is not exposed at the surface, and correlations with the Precambrian-Cambrian sequence in outcrop (Gorin, Racz, and Walter, 1982) are not entirely clear.

Facies analysis of the Ara Formation has revealed a complex paleogeography, with sedimentary facies ranging from coastal plain through shallow platform to a deeper water basin being represented. The dominant organo-sedimentary component is cryptalgal laminites and thrombolites. *Cloudina* occurs in biohermal algal mounds which were probably only a few meters in height; these formed linear belts that separated areas of restricted platform or lagoonal sedimentation in which finely laminated stromatolites were abundant from an open platform with higher energy conditions.

The age of this occurrence is not well constrained, although the close similarity between the Omani *Cloudina*, *C. hartmannae* from the Kuibis and Schwarzrand Subgroups of Namibia, and *Cloudina* sp. from Spain suggest that the Ara Formation examples are also of latest Precambrian age. Independent evidence for the precise age of this formation, however, is elusive. Firm paleontological evidence is provided by Lower

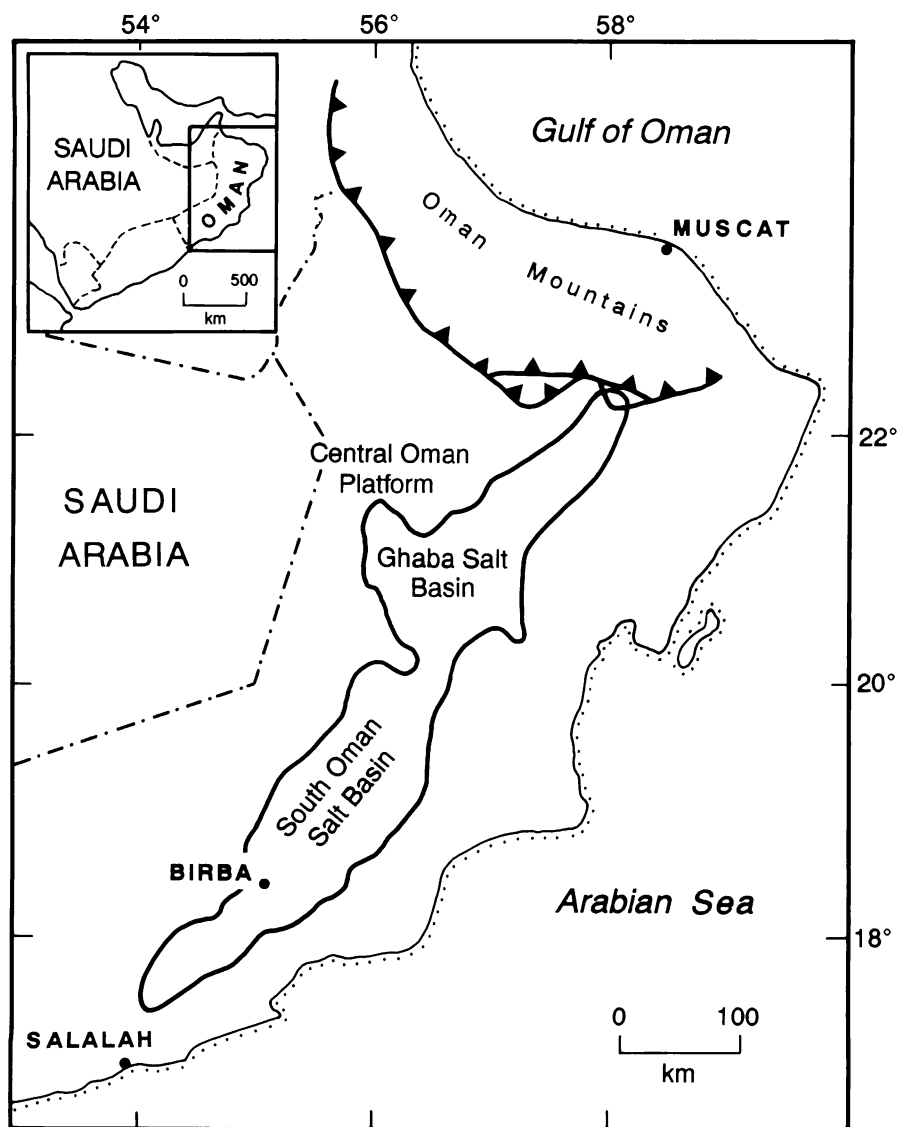


Fig. 2. Locality map of southeast Arabia, showing the location of the principal salt basins in Oman and the Birba borehole. Redrawn and simplified from Mattes and Conway Morris (1990, fig. 1).

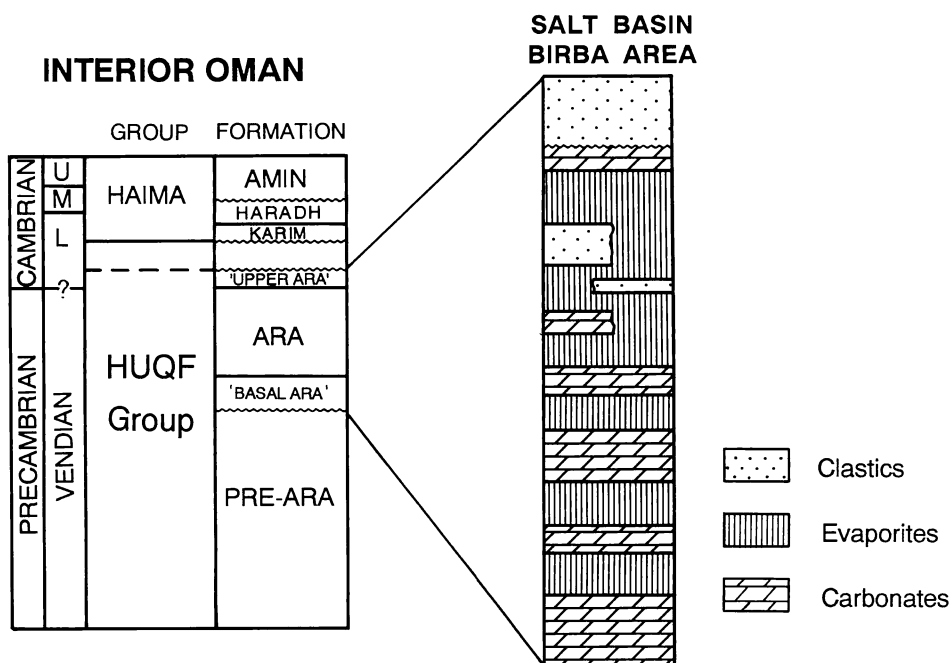


Fig. 3. Stratigraphic scheme for the Precambrian-Cambrian Boundary sequence in the interior of South Oman (including Birba) and the internal "sequence" stratigraphy of the Ara Formation of the Birba area. Redrawn from parts of figures 4 and 6 in Mattes and Conway Morris (1990).

Cambrian trilobites in the overlying Haima Group (fig. 3) (Mattes and Conway Morris, 1990) and in correlative units elsewhere in the Middle East. The recognition of the calcified alga *Angulocellularia* (Mattes and Conway Morris, 1990, fig. 7c), which is one of a number of cyanobacteria that developed the ability to calcify at about the time of the Precambrian-Cambrian boundary, is also significant. To date *Angulocellularia* has been recorded only from the Lower Cambrian (Tommotian) of Siberia and Mongolia (Riding and Voronova, 1982, 1984).

Isotope data also support a latest Precambrian-earliest Cambrian age for the Ara Formation (Mattes and Conway Morris, 1990). In particular, very heavy  $\delta^{34}\text{S}$  values recorded in sulfates within the Ara sequence (fig. 3) might correspond to the major  $\delta^{34}\text{S}$  excursion, referred to as the Yudomski event, that Holser (1977; see also Conway Morris, 1987) recognized as an important marker for the latest Precambrian. In addition, radiometric determinations on intracrystalline clays extracted from the Ara carbonates indicate an age of  $550 \pm 10$  Ma (Mattes and Conway Morris, 1990). This would place it close to the generally accepted date for the Precambrian-Cambrian boundary (see Conway Morris, 1988).

## SYSTEMATIC DESCRIPTION

Phylum, Class, Order: Uncertain

Family: Cloudinidae Hahn and Pflug, 1985

Genus: *Cloudina* Germs, 1972*Cloudina cf hartmannae*

*Occurrence.*—From the Birba North-1 borehole (fig. 2), at a subsurface depth of about 4500 m in the Ara Formation (fig. 3), Sultanate of Oman.

*Preservation.*—The matrix in which the tubes occur is dolomitized, with an extensive initial porosity infilled with diagenetic anhydrite cement (fig. 4). In the samples available for this study the matrix shows few relict features, although poorly preserved clumps of a calcareous alga (*Angulocellularia*) are abundant. Possible stromatolitic structures are also present.

The walls of the fossil tubes (see also Mattes and Conway Morris 1990, fig. 7b) are not well preserved but appear to be formed of very finely crystalline dolomite (fig. 4.18). These are believed to be a direct replacement of the original calcium carbonate. The dark color of the thin walls is apparently due to this fine-grained texture and to the presence of inclusions, including kerogen and fluid inclusions. A notable feature, especially of the inner walls in some specimens (fig. 4.5, 9, 14, 17, 18) is an irregular folding discordant with respect to adjacent walls. In the absence of any evidence for either tectonic deformation or displacive diagenetic crystal growth, this distortion is tentatively ascribed to the combined effects of very thin walls and a high organic content. It remains to be explained why deformation of adjacent walls is often discordant. One suggestion is that the degree of calcification was variable, while an alternative possibility is that the diagenetic dissolution affected some layers more than others. Epitaxial overgrowth of the walls by radially arranged dolomite is common, and the spaces between the walls are often filled by a coarser grained dolomite spar or by anhydrite.

*Description.*—The material is available only in the form of petrographic and polished sections taken from core samples. Tubes occur scattered throughout the matrix (see also Mattes and Conway Morris, 1990, fig. 11d), probably in life position; they are occasionally concentrated, presumably by sedimentation, along bedding planes (fig 4.6). In contrast to the observations of Germs (1972), no unequivocal examples of epizoid attachment have been noted.

In transverse cross section (size range about 1–4 mm) the tubes typically consist of a series of eccentrically located and spaced walls around a central cavity (fig. 4.7–18). Moreover, their eccentric arrangement typically involves all the walls, so that they converge toward one side of the tube (fig. 4.7, 11, 12, 16). In some tubes the walls are more or less concentric to one another, but more often they describe incomplete arcs (fig. 4.13, 15). This latter feature is enhanced by a slight obliquity of the sections but is caused principally by an irregular arrangement of the



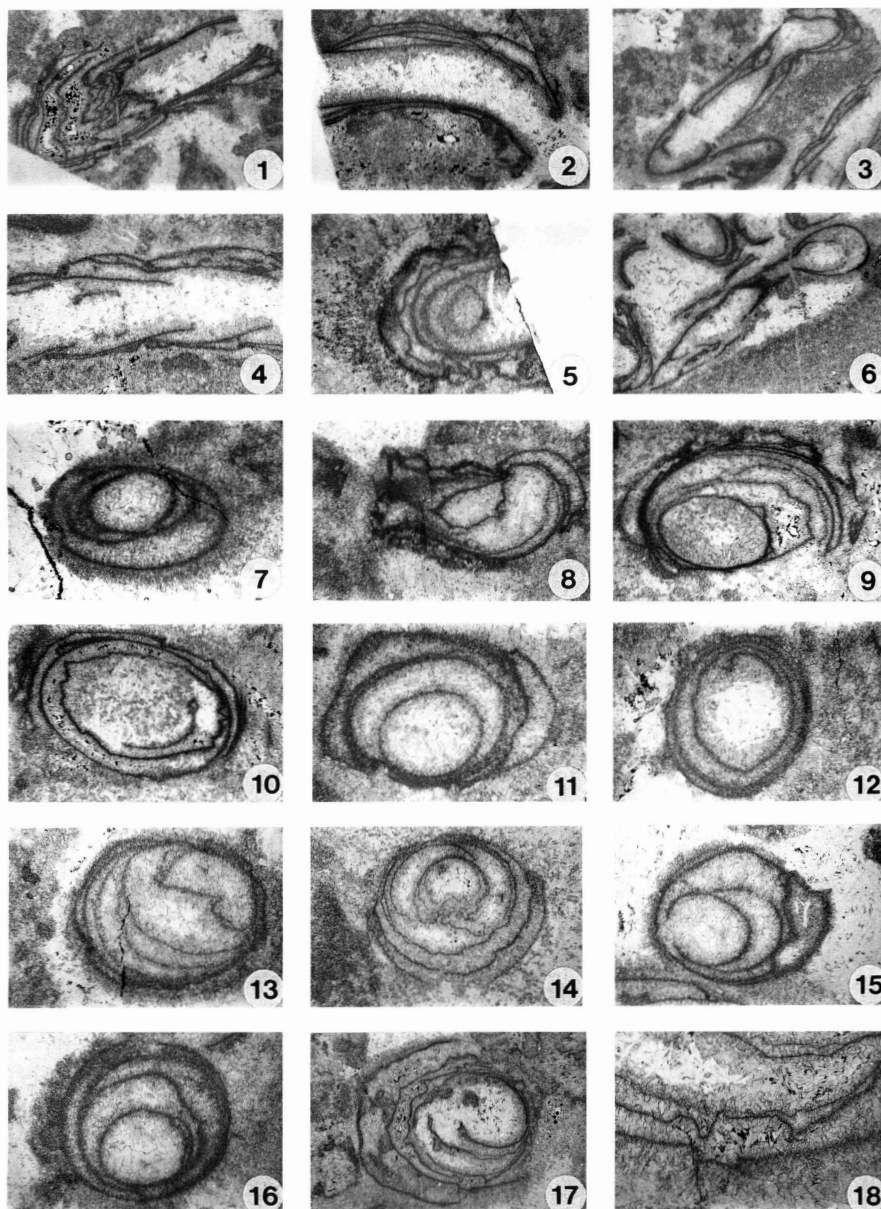


Fig. 4. Representative examples of *Cloudina* cf. *hartmannae* from the Ara Formation, subsurface of Oman. (1 to 6) oblique and longitudinal sections; (7 to 18) transverse and sub-oblique sections. (1) SM X.21483,  $\times 6.3$ ; (2) SM X.21484,  $\times 8.7$ ; (3) SM X.21485,  $\times 6.1$ ; (4) SM X.21486,  $\times 11.8$ ; (5) SM X.21487,  $\times 10.6$ ; (6) SM X.21488,  $\times 6.2$ ; (7) SM X.21489,  $\times 23.0$ ; (8) SM X.21490,  $\times 12.2$ ; (9) SM X.21491  $\times 11.5$ ; (10) SM X.21492,  $\times 10.4$ ; (11) SM X.21493,  $\times 18.2$ ; (12) SM X.21494,  $\times 15.3$ ; (13) SM X.21495,  $\times 14.8$ ; (14) SM X.21496,  $\times 10.7$ ; (15) SM X.21497,  $\times 14.4$ ; (16) SM X.21498,  $\times 15.0$ ; (17) SM X.21499,  $\times 6.0$ ; (18) SM X.21500,  $\times 20.3$ . SM: Sedgwick Museum, Department of Earth Sciences, University of Cambridge, United Kingdom.

walls. In more oblique and longitudinal sections (fig. 4.1–6), which may show a gentle curvature, the walls are seen to form a crude cone-in-cone structure. In detail the courses of the wall are often irregular, comprising walls of varying length and insertion at different angles. In many cases the arrangement is complex (for example fig. 4.2,3).

*Significance.*—This report of *Cloudina* from Oman significantly extends the geographic range of this genus. Its close similarity to the example from Namibia, South America, and Spain suggests that migration around the margins of Gondwana occurred. McMenamin (1982) drew attention to the possible restriction of cloudinids to Gondwana. More particularly Donovan (1987) reviewed the distribution of Ediacaran faunas in an attempt to reconcile biogeographic distributions with various paleocontinental reconstructions proffered for the late Precambrian. Although Donovan (1987) did not include *Cloudina* in his taxonomic list (but see Piper, 1987, p. 250–251) the distribution of this genus accords with the consistent contiguity of the South American, African, and Arabian cratons. The reconstruction prepared by Piper (1987) has the additional virtue of placing the occurrences of *Cloudina* on a broadly similar paleolatitude. Many of the other reconstructions result in the spread of *Cloudina* over a much wider latitudinal range. The position of Spain in this continental assemblage seems not to have received attention, but the occurrence of *Cloudina* in central Spain (Palacios, 1989) argues for proximity to Gondwana and especially to the Arabian craton.

Unfortunately, the occurrence in Oman does little to constrain more precisely the stratigraphic range of *Cloudina*; evidence that this genus is a diagnostic marker of Vendian sediments has to be offset against its coincidence occurring with calcified algae in Oman, which elsewhere have been considered to be diagnostic of the Tommotian (Riding and Voronova, 1982, 1984).

#### CLLOUDINA-LIKE MATERIAL FROM SHAANXI, CHINA

Precambrian-Cambrian boundary sections in China are widespread around the Yangtze Platform, including localities in Yunnan (especially Meishucun, the Chinese candidate for Boundary Stratotype), Sichuan, Shaanxi, and Hubei (Yangtze Gorges) provinces. The stratigraphic succession at all these localities is broadly similar, with a thick Precambrian sequence dominated by dolomite, a thin, basal Cambrian phosphatic interval (richly fossiliferous with small skeletal fossils) overlain by predominantly siliciclastic units in which the first trilobites appear (Xing and others, 1984). The Precambrian dolomites, which for the most part are placed in the Dengying Formation, are largely devoid of metazoan remains. Rare specimens of a pennatulacean-like Ediacaran animal (*Paracharnia*) are known from the Shibantan Member exposed in the Yangtze Gorges, while *Sinotubulites* are locally abundant in this member and the overlying Baimatuo Member. Their poor preservation largely precludes detailed comparisons with *Cloudina* (see also Grant, 1990).

During an investigation of the Precambrian-Cambrian boundary sections near Kuanchuanpu, Shaanxi province (see Conway Morris and Chen, 1989) tubular fossils were collected from the top of the Dengying Formation, which is also referred to in this region as the Gaojiashan Formation. This unit underlies the Kuanchuanpu Formation in which skeletal fossils appear in abundance. The specimens occur in the uppermost dolomites, which are well exposed in a stream section about 300 m to the west of the hamlet of Xuanjiangping and about 2.8 km south of the village of Kuanchuanpu (Conway Morris and Chen, 1989, fig. 3).

The best preserved specimen (fig. 5) is about 7.5 mm in length. It has thin walls of inclined lamellae which typically show minor wrinkles and corrugations. The lamellae are subparallel and occasionally the intervening areas are traversed by intervening walls. The tube expands distally and has a convex termination, but presumably this is due to the section being oblique. In petrographic thin section apparently equivalent tubes are seen to be more or less circular with short external spinose extensions but without clear evidence of the inclined lamellae.

#### DISCUSSION

The faunal relationships of *Cloudina* continue to remain enigmatic. Previous suggestions have fallen broadly into two camps, which are not mutually exclusive. Firstly, many workers (for example Germs, 1972; Zaine and Fairchild, 1987) have been struck by similarities to the cribricyatheans, a relatively poorly known group of calcareous organisms largely confined to the Altai-Sayan region in the Soviet Union. Although the cribricyatheans have been compared with the archaeocyathids, Hill (1972) prefers to regard them as unrelated and of problematic status. A second school of thought portrays *Cloudina* as an early representative of the polychaete annelids, with particular comparisons being drawn to the serpulids that secrete a calcareous tube in which the lamellae are laid down at an inclined angle to the axis.

There seems, however, to be little evidence to support either of these viewpoints. Although *Cloudina* does resemble in morphology certain cribricyatheans, such as *Vologdinophyllum*, most representatives of the cribricyatheans are considerably smaller and have a porous inner wall that has no counterpart in *Cloudina* (Hahn and Pflug, 1985). Similarly, comparisons between the calcareous walls of serpulid polychaetes (for example, Wrigley, 1950; Schmidt, 1951; Hedley, 1958; Zibrowius and ten Hove, 1987) and the structure of *Cloudina* suggest that there is little to suggest these early Phanerozoic tubes should be referred to the annelids.

In passing, it is worth noting that a number of tubicolous organisms from the Paleozoic also show certain, presumably convergent, similarities to *Cloudina*. One such example is *Trypanopora* from the Devonian (Givetian) of northeast France (Mistiaen and Poncet, 1983; see also Pel and Lejeune, 1971). These vermiform tubes are associated with stromatolites and have a complex system of thin, internal dissepiment-like

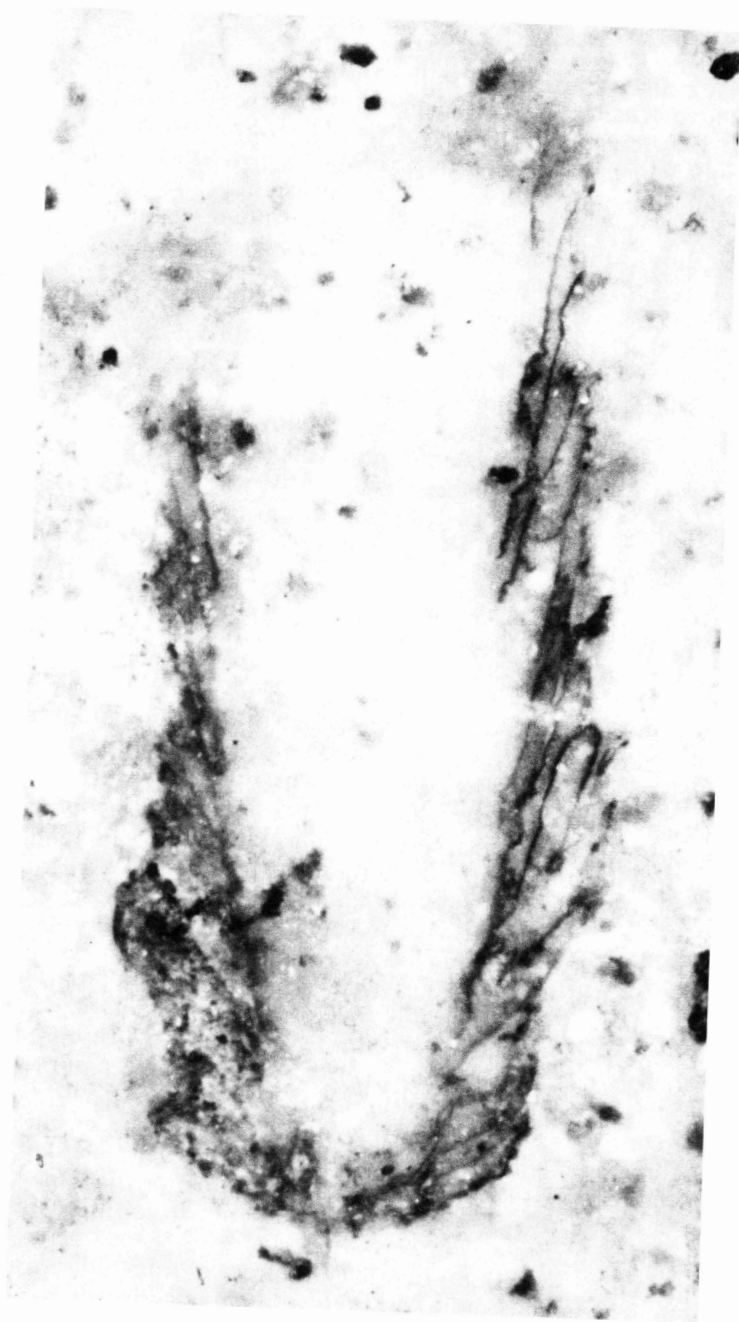


Fig. 5. Cloudinid-like tube from the Gaojiashan Formation, Kuanchuanpu, Shaanxi, China. IGAS-BC-88-30206,  $\times 20.0$  IGAS: Institute of Geological Sciences, Academia Sinica, Beijing, China.

walls more or less parallel to the tube axes. Although it has sometimes been regarded as a tabulate coral, Mistiaen and Poncet (1983) suggest the tube was built by a worm. Another example is *Torquaysalpinx sokolovi*, also of the Givetian age, recorded from Devon (Plusquellec, 1968). Its tube walls are poorly preserved but appear to be formed of obliquely inclined lamellae, while the interiors of the tubes are transversely divided by occasional septa. Unlike the abovementioned forms, *Torquaysalpinx* forms an intimate symbiotic association with tabulate corals.

#### CONCLUSION

*Cloudina* is emerging as a distinctive element of the latest Proterozoic faunas, although it is still uncertain whether this genus ranges into the Lower Cambrian. Many problems remain unsolved. What are the affinities of this organism, indeed is a place in the Metazoa beyond dispute? Should a metaphyte relationship be reconsidered? How did the organism build its tube wall, and are similarities with other tubicolous taxa in younger rocks ones of convergence only? Finally, was *Cloudina* restricted to the late Proterozoic Gondwana, and can it throw more light on the problems of understanding the earliest stages of metazoan biogeography?

When answered these and other questions will help to explain the appearance of biomineralizers close to the Precambrian-Cambrian boundary and their ecological significance. The documentation of the material from Oman and related fossil tubes from South China are broadly consistent with *Cloudina* being restricted biostratigraphically to a limited time interval. It suggests that this genus may be used to test further paleogeographical reconstructions, especially as they pertain to circum-Gondwana sites.

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