Inconsistencies in proposed annelid affinities of early biomineralized organism *Cloudina* (Ediacaran): structural and ontogenetic evidences

Olev Vinn [1]

Michał Zatoń [2]

Abstract: *Cloudina*, an important Ediacaran index fossil, is considered as one of the earliest biomineralizing organisms. Its biological affinities have not been fully resolved and phylogenetic links with both annelids and cnidarians have traditionally been suggested. Differences in tube morphology, ultrastructure and biomineralization suggest that *Cloudina* is not closely related to any recent skeletal annelid (*e.g.*, serpulids, sabellids and cirratulids) and their skeletons are not homologous. The way of asexual reproduction in *Cloudina* resembles more that of cnidarians. The presence of a closed tube origin (base) in *Cloudina* is also compatible with the hypothesis of an animal of cnidarian grade.

Key Words: *Cloudina*; Annelida; Serpulidae; Cnidaria; Ediacaran; biomineralization.

Citation: Vinn O. & Zatoń M. (2012).- Inconsistencies in proposed annelid affinities of early biomineralized organism *Cloudina* (Ediacaran): structural and ontogenetic evidences.- Carnets de Géologie [Notebooks on Geology], Brest, Article 2012/03 (**CG2012_A03**), p. 39-47.

Résumé : *Incohérences dans les affinités supposées de l'organisme primitif biominéralisé* Cloudina *(Ediacaran) avec les annélides : preuves relevant de la structure et du développement ontogénétique*.- *Cloudina*, un important fossile édiacarien, est considéré comme l'un des premiers organismes biomineralisés. Ses affinités biologiques n'ont pas encore été entièrement élucidées : des relations phylogénétiques avec les annélides et les cnidaires sont habituellement envisagées. Des différences dans la morphologie, l'ultrastructure et la biominéralisation du tube suggèrent que *Cloudina* ne puisse être étroitement apparentée à aucun squelette d'annélides actuelles, qu'il s'agisse de serpulidés, de sabellidés ou de cirratulidés ; leurs squelettes ne sont pas homologues. Le mode de reproduction asexuée de *Cloudina* ressemble davantage à celui des cnidaires. De plus, la configuration fermée de la partie initiale (proximale) du tube chez *Cloudina* est compatible avec l'hypothèse d'un animal de la catégorie des cnidaires.

Mots-Clefs : *Cloudina* ; Annelida ; Serpulidae ; Cnidaria ; Édiacarien ; biominéralisation.

1. Introduction

Cloudina is a tube-building metazoan organism of problematic affinities that widely occurs in deposits of the terminal Neoproterozoic Ediacaran Period (Grant, 1990), between 549 ± 1 Ma and 542 ± 1 Ma (Grotzinger *et al.*, 1995; Amthor *et al.*, 2003). Two distinct species are recognized, *C. hartmannae* Germs, 1972, and *C. carinata* Cortijo *et al.*, 2010, while rest of species could be junior synonyms of *C. hartmannae* (Cortijo *et al.*, 2010). It is significant for being among the precursors of biologically controlled mineralization and being an important Ediacaran index fossil (Hua *et al.*, 2005).

The geochemical data suggest that *Cloudina* formed originally aragonitic skeleton (Callow & Brasier, 2005), however, relatively little is known about the biology of *Cloudina*. There is a record of drilling predation upon *Cloudina* (Bengtson & Yue, 1992; Hua *et al.*, 2003). Followed from the location of predatory drill holes, *Cloudina* organism was presumably able to protect its shell nearest to the aperture and its soft body may have been located in the upper, growing portion of the tube (Hua *et al.*, 2003).

According to traditional point of view, *Cloudina* was closely related to annelids and especially to serpulids (Germs, 1972; Glaessner, 1976). However, Hahn & Pflug (1985) and Conway Morris *et al.* (1990) did not support Germ's and Glaessner's proposed relationships, and classified *Cloudina* just in its own family, Cloudinidae. The occurrence of dichotomous branching in *C. hartmannae*, which implies asexual reproduction led Grant (1990) to classify *Cloudina* as a coral-like cnidarian. Recently, dichotomous branching has also been found in *C. carinata* Cortijo *et al.*, 2010, from the Ediacaran of Spain (Cortijo *et al.*, 2010). In contrary, as a result of their thorough review on biology of *Cloudina*, Hua *et al.* (2005) found that *Cloudina*'s morphology, skeletogenesis, and asexual reproduction are broadly similar to modern

---

[1] *Department of Geology, University of Tartu, Ravila 14A, EE-50411 Tartu (Estonia)*
Olev.Vinn@ut.ee

[2] *Faculty of Earth Sciences, University of Silesia, Będzińska 60, PL-41-200 Sosnowiec (Poland)*
mzaton@us.edu.pl

Manuscript online since March 12, 2012
[Editor: Christian Emig]

serpulid annelids, indicating possible phylogenetic relationships or morphological convergence. They also concluded that traditional hypothesis of *Cloudina*'s annelid affinities remains plausible.

The earliest definitive annelids with biomineral skeletons (calcitic) were machaeridians in the Early Ordovician, which had a body covered with the calcareous plates (VINTHER *et al.*, 2008), but they did not build calcareous tubes. The earliest hitherto known calcareous annelid tubeworms are serpulids (Serpulidae) and their definitive representatives are known from the Triassic (VINN *et al.*, 2008c, 2008a; VINN & MUTVEI, 2009). The calcareous tubes also occur in sabellid (Sabellidae) and cirratulid (Cirratulidae) polychaetes, since the Early Jurassic (JÄGER, 2004; VINN *et al.*, 2008a) and the Oligocene respectively (FISCHER *et al.*, 2000; VINN, 2009). Recent discoveries on the skeletal structures and biomineralization of calcareous polychaetes (WEEDON, 1994; VINN, 2005, 2007, 2008, 2009; VINN *et al.*, 2008c, 2008a, 2008b, 2008d, 2009; SANFILIPPO, 2009; VINN & MUTVEI, 2009; TANUR *et al.*, 2010) allows us for the first time to make a complete comparison with the skeletal structures and skeletogenesis of problematic tubicolous fossils such as *Cloudina*.

The aims of this paper are:

1. to compare the skeletal structures and skeletogenesis of *Cloudina* with those of the calcareous polychaete tubeworms (*e.g.*, serpulids, sabellids and cirratulids) in order to test its annelid affinities, and
2. to discuss the zoological affinities of *Cloudina*.

2. Results and Discussion

Cloudina hartmannae tube has a closed origin (HUA *et al.*, 2003, 2005: fig. 1B): Fig. 1. *C. hartmannae* (HUA *et al.*, 2003, 2005: fig. 1A-B) and *C. carinata* (CORTIJO *et al.*, 2010: figs. 4-6) tubes do not have flattened attachment surfaces. The diameter of *C. hartmannae* shell could increase relatively rapidly after dichotomous branching (HUA *et al.*, 2003: fig. 3E, 2005: fig. 1P): Fig. 2. The tube diameter of both daughter tubes could be about equal and smaller than the diameter of parent tube (HUA *et al.*, 2005: fig. 1K-L, 2007: fig. 6.5) in *C. hartmannae* (Figs. 2 - 3) and different in *C. carinata* (CORTIJO *et al.*, 2010: fig. 8). The shape of *C. hartmannae* tube cross section changes during dichotomous branching from circular (parent tube) to semi-circular, both daughter tubes (HUA *et al.*, 2005: fig. 1L): Fig. 3. Growth lamellae of *C. hartmannae* tube are long and straight in longitudinal section - it lacks chevron shaped growth lamellae - (HUA *et al.*, 2005: fig. 1C): Fig. 4. Tube wall has a microgranular homogeneous ultrastructure (FENG *et al.*, 2003; HUA *et al.*, 2003: fig. 3O, 2005: fig. 1H): Fig. 5a.

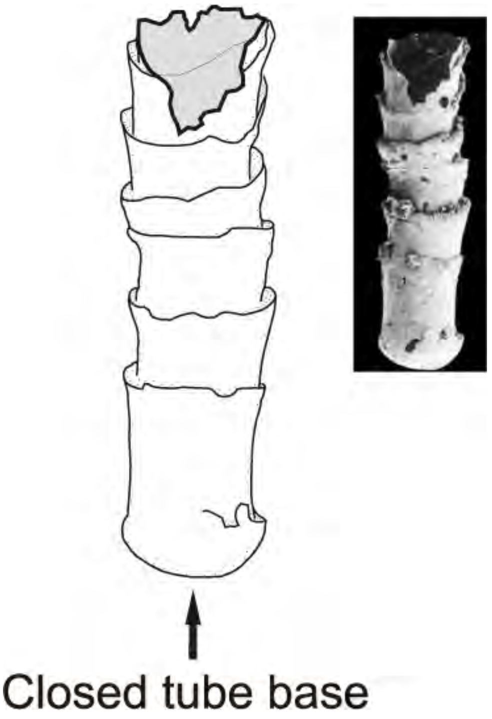

Figure 1: *Cloudina hartmannae* from Dengying Formation, closed bulbous basal end (SEM photo reprinted by permission of publisher from HUA *et al.* (2005: fig. 1A).

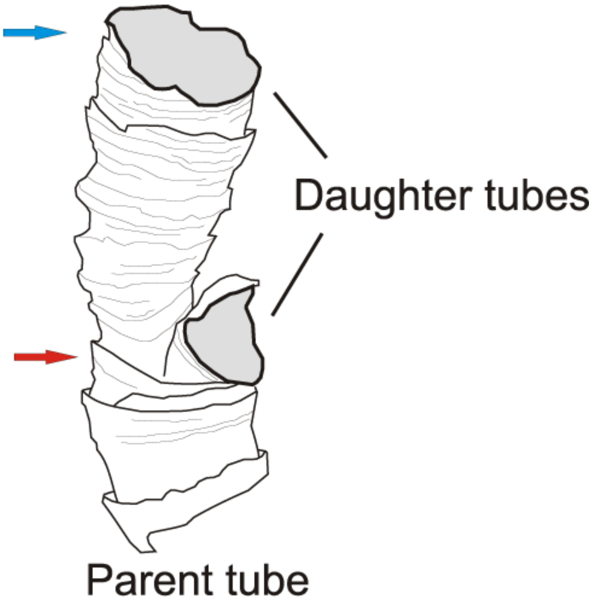

Figure 2: *Cloudina hartmannae* from Dengying Formation, dichotomous branching, showing rapid increase of daughter tubes diameter (arrows), drawn after HUA *et al.* (2003: fig. 3E).

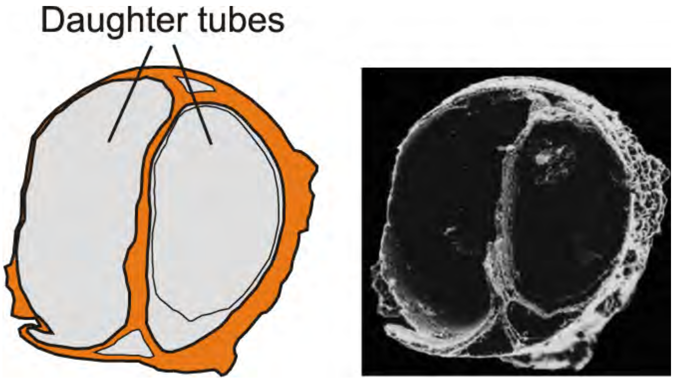

Figure 3: Cross section of daughter tubes within the parent tube, note the semicircular cross section of daughter tubes (SEM photo reprinted by permission of publisher from HUA *et al*. (2005: fig. 1L).

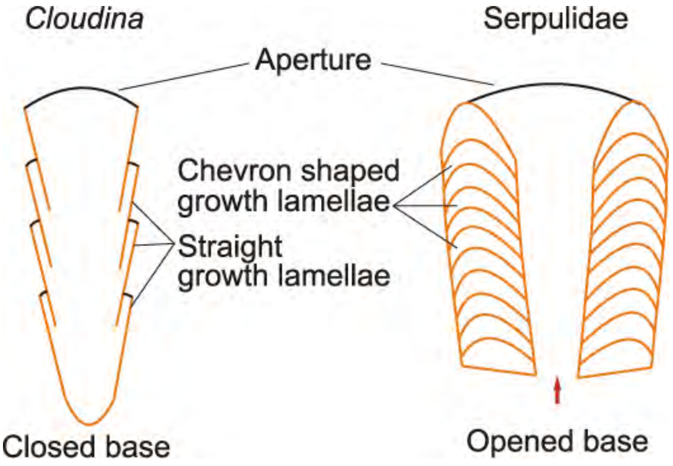

Figure 4: Schematic line drawings of *Cloudina* and serpulid tubes, showing morphology of growth lamellae and tube base.

a. Discussion of characters

Cloudina has a tubicolous shell that somewhat resembles tubes of calcareous polychaete annelids (*e.g.*, serpulids, sabellids and cirratulids) in its probably calcareous original composition, smooth tube lumen and presence of peristome-like structures on the shells external surface (Figs. 1 - 2). *Cloudina* (Fig. 2) also resembles some serpulids (Fig. 6) and calcareous Cirratulidae (FISHER *et al.*, 2000) by its occurrence of asexual reproduction (PERNET, 2001; ten HOVE & KUPRIYANOVA, 2009). HUA *et al.* (2005) found that there are following differences between *Cloudina* and serpulids: a) serpulid tube walls are thicker and solid, and they do not consist of nested funnels; b) the dichotomous branches of serpulids are not as deeply nested within the parent tube as in *Cloudina*. In addition, we found several other important differences between the calcareous polychaete tubes and *Cloudina*:

1) **Ultrastructure** - Annelids do not have microgranular tube ultrastructure. Their primitive tube ultrastructure is either spherulitic – sabellids - (VINN *et al.*, 2008a), spherulitic prismatic – sabellids and cirratulids - (VINN *et al.*, 2008a; VINN, 2009) or composed of irregularly oriented elongate prisms - serpulids - (VINN *et al.*, 2008c, 2008b). The presence of microgranular tube structure in serpulids is an artifact of sample natural breakage surface. Unpolished and not etched samples of serpulids with irregularly oriented prismatic structure seem to be composed of homogeneous fine granules under SEM (O. VINN, pers. obs.). The tube ultrastructure of asexually reproducing *Salmacina* and *Filograna*, compared to *Cloudina* by HUA *et al.* (2005), is not fine microgranular, but composed of irregularly oriented elongate prisms in a homogeneous matrix (see VINN *et al.*, 2008b): Fig. 5b. However, ultrastructure of organic-rich tabulae (= transverse cross walls) inside the *Serpula vermicularis* tube is indeed similar to that of *Cloudina*, but they are formed in a different process than the tube wall (VINN *et al.*, 2008b). However, the original structure of *Cloudina* may have not been microgranular, as different phosphatized calcareous skeletons and organic substrates could show this kind of fabric.

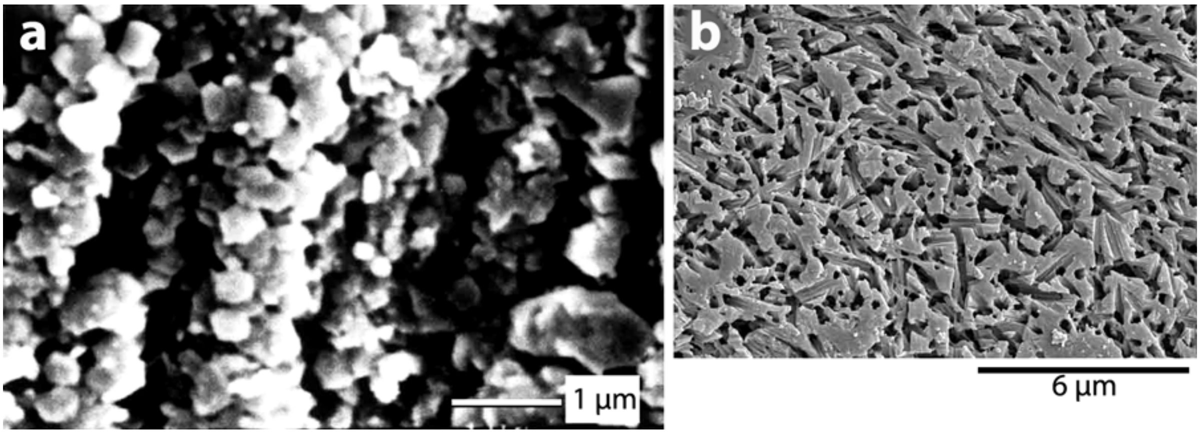

Figure 5: **a.-** Microgranular ultrastructure of *Cloudina sinensis*, Gaojiashan Member of Dengying formation, Ningqiang, Shaanxi, China (after FENG *et al*., 2003: fig. 1b). **b.-** Irregularly oriented prismatic structure in cross section in *Salmacina incrustans*, ZMA V.Pol.3814, Costa Brava, Spain.

2) **Biomineralization** - Hua *et al.* (2005) found that *Cloudina* tubes do not show radial fibrous microstructure or palisade orientation of crystals, crystal nucleation and growth on a sheeted organic or inorganic substrate did not play a significant role in *Cloudina* skeletogenesis. They concluded that crystals were probably precipitated by skeleton-secreting organs and mixed with an organic matrix, what is similar to serpulids (Hedley, 1958; Neff, 1971; Nott & Parker, 1975). However, standard granular secretion model of serpulids (Hedley, 1958; Neff, 1971) has recently been cast in doubt by the discovery of complex oriented tube structure in *Pomatoceros americanus* (Vinn *et al.*, 2009) on which the model of serpulid secretion was based. Several other discoveries on the skeletal ultrastructures in serpulids contradict the traditional point of view on their biomineralization (Vinn *et al.*, 2008a, 2008b, 2008d). New evidence on the skeletal structures of serpulids suggests that serpulids were organic matrix-mediated biomineralizers similar to that of molluscs (Vinn *et al.*, 2008a, 2008b, 2008d, 2009; Tanur *et al.*, 2010). The biomineralization of sabellids (Fig. 7) and cirratulids produces oriented prismatic structures, perpendicular to organic sheets, which cannot be achieved in a granular secretion process, as well (Vinn *et al.*, 2008a; Vinn, 2009).

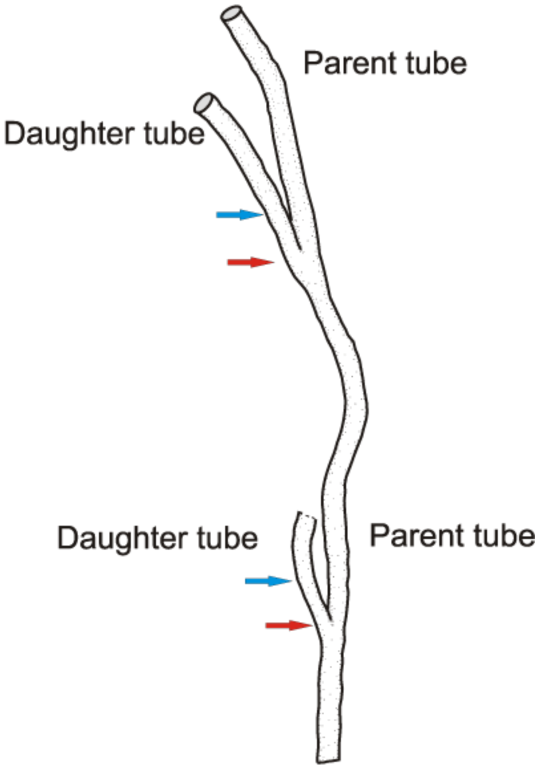

Figure 6: *Salmacina amphidentata* (Serpulidae), Indian River Lagoon in the vicinity of Fort Pierce Inlet, Florida. Detail of an aggregation showing periodic branching of the tubes. Note that diameter of the daughter tubes increases very slowly after branching (arrows). Drawn after Pernet (2001: p. 110, fig. 1B).

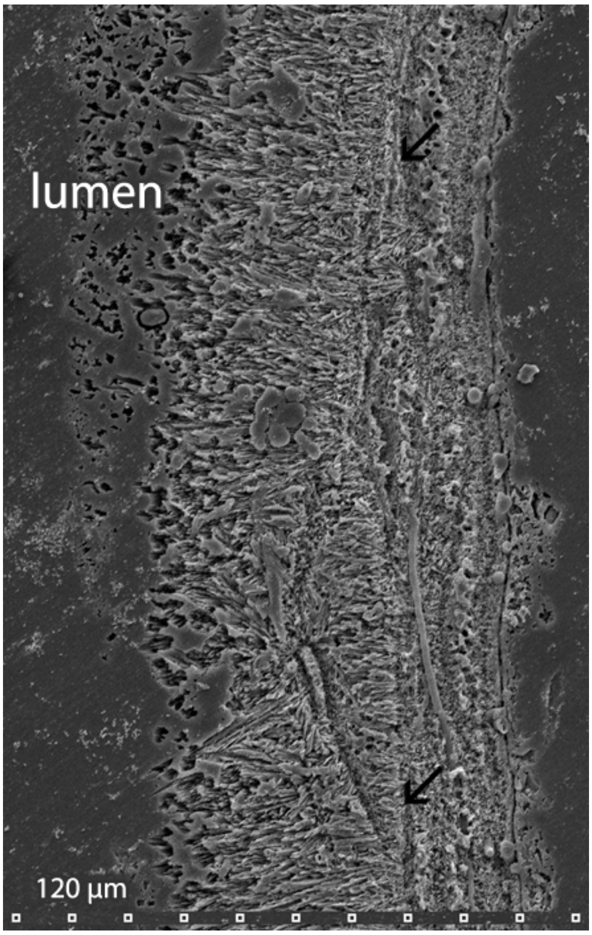

Figure 7: *Glomerula piloseta* (Sabellidae), Recent, Lizard Island, Australia, polished and etched longitudinal section, showing aragonitic spherulitic prismatic structure. Arrows point to long subparallel to tube walls growth lamellae.

3) **Morphology of growth lamellae** - Growth lamellae are much longer than in serpulids (Weedon, 1994; Sanfilippo, 1996; Vinn & Furrer, 2008) in the longitudinal section, resembling those of tubicolous molluscs such as vermetid gastropods or scaphopods. Unlike the straight growth lamellae of *Cloudina*, most of serpulids have chevron shaped growth lamellae (Weedon, 1994; Vinn & Furrer, 2008): Fig. 8. Thus, tube formation in *Cloudina* should have been different from that of anterior accretion of serpulid tubes. However, growth lamellae of sabellids - *Glomerula* - (Fig. 7) and cirratulids can be much longer in longitudinal section than in serpulids and thus resemble more those of *Cloudina*. The growth lamellae of *Yangtzitubus* (Ediacaran) are slightly similar to those of *Cloudina* (Liu *et al.*, 2009).

4) **Morphology of tube origin** - Embryonic serpulid tubes are opened at both ends (ten Hove & van den Hurk, 1993; Taylor & Vinn, 2006): Figs. 4 & 9, in contrast to closed tube origin of *C. hartmannae* (Hua *et al.*, 2003, 2005): Figs. 1 & 4. In *C. carinata* tube origin is reported to be open, but this was based on a fragmentary material, which may not represent complete tubes (Cortijo *et al.*, 2010). Serpulid

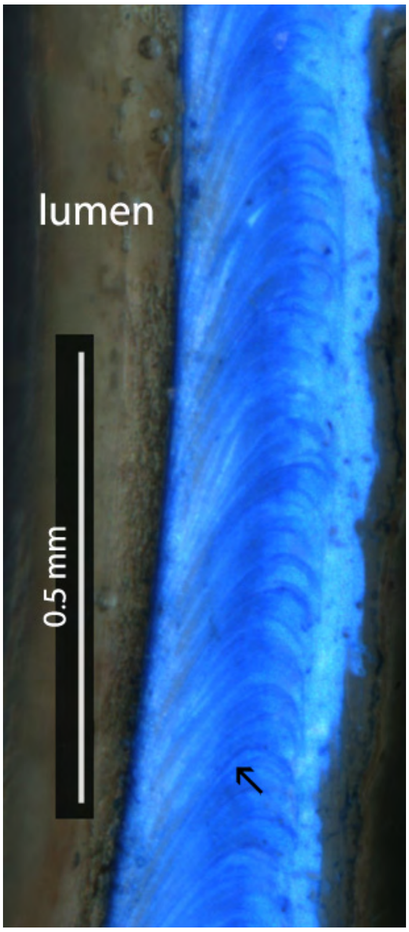

Figure 8: *Pomatoceros triqueter* (Serpulidae), Recent, Tjärnö, Sweden, polished section treated with MUTVEI solution, showing chevron shaped growth lamellae.

tubes are often closed off by the tabulae (see SANFILIPPO, 2009, and references therein). Similarly, tubes of *Glomerula* (Sabellidae) have presumably an open origin because of similar tube formation. It is likely that also calcareous cirratulid tubes are not closed at their origin. Thus, the beginning of tube formation in *Cloudina* should fundamentally differ from that of serpulids and probably also from the other calcareous polychaetes.

5) **Shape of tube cross section** – Semicircular cross section of daughter tubes lumen inside the parent tube in *Cloudina* (Fig. 3) differs from that of circular lumen cross section of serpulid and sabellid tubes. Tubes with semicircular cross section occur in *Yangtzitubus semiteres* LIU *et al.* (2009) from the Ediacaran (Doushantuo Formation) of southern China (LIU *et al.*, 2009), but differently from *Cloudina*, their tubes are never circular in cross section. A semicircular cross section is also known in *Conotubus* ZHANG & LIN *in* ZHANG (1986) from the Dengying Formation (Ediacaran) of southern China (HUA *et al.*, 2007; LIU *et al.*, 2009).

6) **Expansion of the tube** - Rapid increase of tube diameter after dichotomous branching in *Cloudina* (Fig. 2) is different from that of slow increase in serpulids (see PERNET, 2001: figs. 1B & 4A): Fig. 6. *Cloudina* could have a tube divergence angle about 30° that is not possible in case of serpulid or any other calcareous polychaete tubes (personal obs. O. VINN). Such a rapid increase in diameter of tube, probably reflecting the increase of soft body volu-

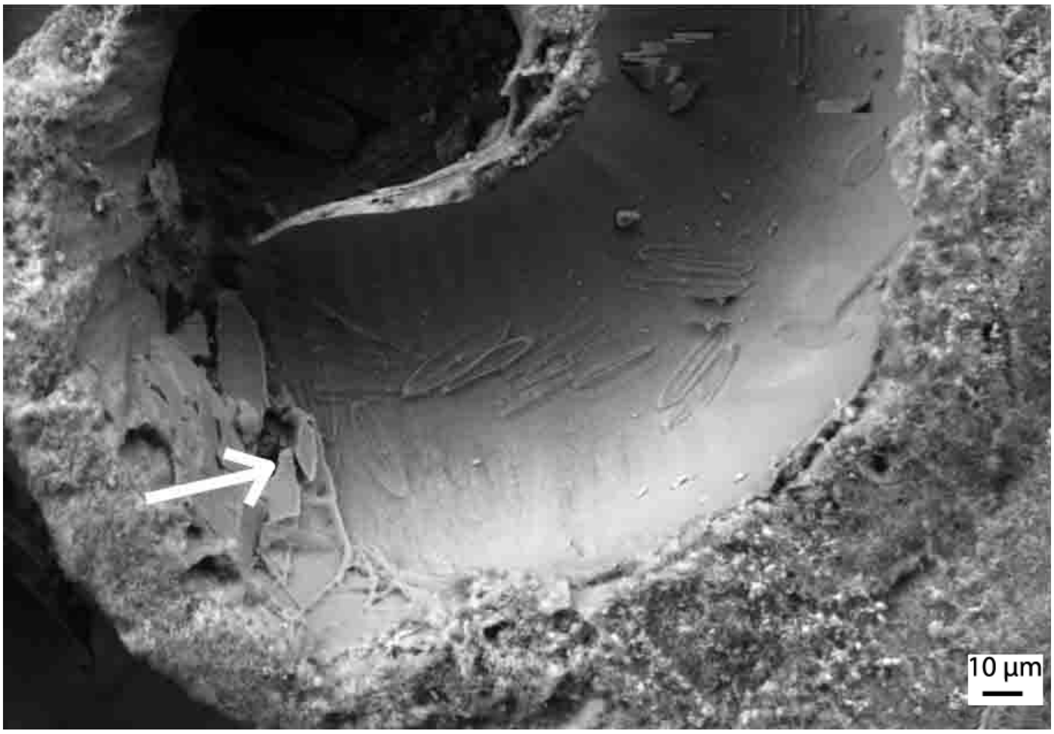

Figure 9: Serpulid *Spirorbis spirorbis*, substrate cemented side, showing an open tube apex (arrow), Recent, North Sea.

me would have prevented the deep retraction of soft body into the tube possibly in all calcareous polychaete tubeworms. Rapid increase of tube diameter after dichotomous branching in *Cloudina* somewhat resembles *Ramitubus increscens* (Liu *et al.*, 2008: pl. 1, fig. 6) interpreted as cnidarian (Chen *et al.*, 2002; Liu *et al.*, 2008) or alternatively as algae (Bengtson, 2005).

7) **Change of tube diameter** - Diameter of both daughter tubes is smaller than that of parent tube (before branching) after the dichotomous branching in *Cloudina* (Hua *et al.*, 2005: fig. 1K-L, 2007: fig. 6.5). It is different from that of serpulids where parent tube diameter does not decrease after budding (Pernet, 2001: fig. 4A). Similarly to *Cloudina* tube diameter of both daughter tubes is smaller than the parent one in *Ramitubus increscens* (Liu *et al.*, 2008: pl. 1, fig. 6).

8) **Attachment surfaces** - A lack of flattened attachment surfaces in *Cloudina* tube differs from that of tubes of calcareous polychaetes. Almost all known calcareous polychaetes begin their growth cemented to the substrate with the exception of serpulid *Ditrupa* (ten Hove & Smith, 1990). However, the tube of *Ditrupa* is opened from both ends and it has chevron shaped growth lamellae, two layered tube with outer layer having an oriented ultrastructure (Vinn *et al.*, 2008d). Phylogenetically, *Ditrupa* is among the most derived serpulids and does not represent the plesiomorphic condition for serpulids (ten Hove, 2008, personal comm.). The plesiomorphic serpulids were all substrate cemented at least in the beginning of their growth.

b. Affinities of *Cloudina*

Only tubicolous shell, smooth lumen and presence of peristomes in *Cloudina* are unequivocally similar to that of serpulids (Table 1). Zhuravlev *et al.* (2011) found some similarity between sabellid tubes constructed of thin organic films and aragonitic layers. However, there are strong differences between *Cloudina* and other calcareous polychaetes (*e.g.*, sabellids and cirratulids). *Cloudina* differs from serpulids in the tube ultrastructure, proposed type of biomineralization, closed tube origin (base), semicircular cross section of daughter tubes, rapid increase of the tube diameter after dichotomous branching, change of tube diameter, and lack of attachment surfaces. These differences in tube morphology, ultrastructure and biomineralization indicate that *Cloudina* is not closely related to any recent skeletal annelid (*e.g.*, serpulids, sabellids and cirratulids) and their skeletons are not homologous (Table 1). However, taking into account that annelids are a very diverse group of invertebrates and biomineralization can appear and disappear several times within the phyla (Taylor, 2008) it is impossible to entirely rule out the annelids as potential close relatives to *Cloudina*.

Characters	*Cloudina*	Calcareous polychaetes (Serpulidae, Sabellidae, Cirratulidae)	Cnidaria
Tubicolous shell	x	x	x
Smooth lumen	x	x	x
Peristomes	x	x	x
Asexual reproduction	x	x	x
Granular microstructure	x	-	x
Closed tube base	x	-	x
Semicircular tube cross section	x	-	x
Rapid increase of the tube diameter	x	-	x
Diameter of daughter tubes about equal	x	-	x
Attachment surfaces lacking	x	-	x

Table 1: Comparison of *Cloudina* characters with calcareous polychaetes and Cnidaria.
[x : character present; - : character absent]

The following characters are easiest to understand if one assumes a cnidarian affinity for *Cloudina* (Table 1):

a) Diameter of shell can increase relatively rapidly after dichotomous branching;
b) Diameter of both daughter tubes is about equal and diameter of each daughter tube is smaller than the diameter of parent tube during the dichotomous branching;
c) Shape of tube cross section changes during dichotomous branching from circular (parent tube) to semi-oval (both daughter tubes).

Thus, the way of asexual reproduction in *Cloudina* resembles closely that of cnidarians, especially anthozoans. ZHURAVLEV *et al.* (2011) found that pattern of asexual reproduction of *Cloudina* that has been observed by HUA *et al.* (2005: fig. 1K-R) matches well to intercalar budding of cnidarians but not to serpulid budding with a bud tube development at the surface of the parental one but not inside it (PERNET, 2001). The closed tube origin of *Cloudina* is also compatible with the hypothesis of an animal of cnidarian grade. There is a coral with conical shell (*Cothonion*) known from the Early Cambrian of Australia and North Greenland (PEEL, 2011). It shares some characters with the *Cloudina*, such as conical shape, closed base and fast increase of the diameter.

Alternatively, ZHURAVLEV *et al.* (2011) found that the presence of both 'hemispherical basal end' and tabulae could favour a microconchid lophophorate affiliation for *Cloudina*. However, microconchids are evolutionarily derived encrusting tentaculitoid tubeworms, that appeared first in the Late Ordovician (VINN, 2010), and so not the best candidates among tentaculitoids for comparison with *Cloudina*. The earliest known tentaculitoids were cornulitids, that presumably appeared in the Middle Ordovician (VINN & MUTVEI, 2009). If tentaculitoid tubeworms are indeed the stem group phoronids as proposed by TAYLOR *et al.* (2010), they may well have been present at least as early as in the Early Cambrian. However, early tentaculitoids probably had a plesiomorphic substrate cemented life mode (VINN & MUTVEI, 2009) that differs from life mode of unattached *Cloudina*. In addition, skeletal ultrastructures of tentaculitoids are much more advanced than that of *Cloudina*.

In contrast, the simple ultrastructure in *Cloudina* (FENG *et al.*, 2003; HUA *et al.*, 2005) does not give many clues for comparison with any particular invertebrate phylum as they all could have had such a plesiomorphic condition in the Ediacaran. In addition to *Cloudina*, tubes could branch in a few other Ediacaran tubicolous fossils (LIU *et al.*, 2009). These are *Ramitubus*, *Yangtzitubus* and *Waltheria* GAUCHER et SPRECHMANN, 1999. *Yangtzitubus* has also slightly similar wall structure, and it lacks cross walls (LIU *et al.*, 2009). Thus, among the non-biomineralizing tubicolous fossils of Ediacaran, *Yangtzitubus* could phylogenetically be most closely linked to *Cloudina*.

c. Paleobiology of *Cloudina*

HUA *et al*. (2003) found that predatory borings in *Cloudina* are located at relatively uniform distance from the shell apertures that points to either control by the life orientation of the shells, such as the position of the sediment surface, or, more likely, an avoidance response by the predator to protective measures located near the aperture.They hypothesized that absence of boreholes further from the aperture implicates one or more of the following:

1. the older part of the shell was typically embedded in the substrate;
2. the predator responded to a sensory trigger by drilling nearer to the aperture than the apex; or
3. the predator was programmed to know that soft tissues were located in the upper, growing portion of the tube.

Cloudina is envisioned here as an animal that is not capable for much moving back and forwards in its tube, or not moving at all, because of the fast increase of tube diameter after the dichotomous branching. The *Cloudina* animal was probably also entirely attached to the tube wall with its soft body surface and it changed shape of its soft body cross section from circular before the asexual reproduction to semicircular after the asexual reproduction. Presumably, *Cloudina* was not retracting into the tube in asexual reproduction, but it was divided by lateral fission into two daughter animals which thereafter laterally secreted new tube walls around their soft body inside the parent tube (*e.g.*, almost equal split of a cylindrical funnel into two half-cylinders in *C. hartmannae*).

3. Conclusions

1. *Cloudina* does not share affinities with any extant calcareous tubicolous annelids.
2. *Cloudina* characters are easier to understand if one assumes its cnidarian affinity.

Acknowledgements

We are grateful to the Paleontological Society for a SEPKOSKI Grant, to Estonian Science Foundation for grant ETF9064 and to the Estonian Ministry of Education and Science for the target project SF0180051s08. We thank Brian PRATT and an anonymous reviewer for constructive reviews.

Bibliographic references

AMTHOR J.E., GROTZINGER J.P., SCHRÖDER S., BOWRING S.A., RAMEZANI J., MARTIN M.W. & MATTER A. (2003).- Extinction of *Cloudina* and *Namacalathus* at the Precambrian-Cambrian boundary in Oman.- *Geology*, Boulder, vol.

31, p. 431-434.

Bengtson S. (2005).- Mineralized skeletons and early animal evolution. *In*: Briggs D.E.G. (ed.), Evolving form and function: fossils and development.- Yale Peabody Museum Publications, New Haven, CT, p. 101-124.

Bengtson S. & Yue Z. (1992).- Predatorial borings in late Precambrian mineralized exoskeletons.- *Science*, Washington, vol. 257, p. 367-369.

Callow R. & Brasier M. (2005).- A closer examination of biomineralization in the late Precambrian.- The Palaeontological Association 49th Annual Meeting 18th-21st December 2005, University of Oxford, Abstracts, p. 37-38.

Chen J.-Y., Oliveri P., Gao F., Dornbos S.Q., Li C.-W., Bottjer D.J. & Davidson E.H. (2002).- Precambrian animal life: probable developmental and adult cnidarian forms from Southwest China.- *Developmental Biology*, Amsterdam, vol. 248, p. 182-196.

Conway Morris S., Mattes B.W. & Chen M. (1990).- The early skeletal organism *Cloudina*: New occurrences from Oman and possibly China.- *American Journal of Science*, New Haven, vol. 290-A, p. 245-260.

Cortijo I., Martí Mus M., Jensen S. & Palacios T. (2010).- A new species of *Cloudina* from the terminal Edicaran of Spain.- *Precambrian Research*, Amsterdam, vol. 176, p. 1-10.

Feng W., Chen Z. & Sun W. (2003).- Diversification of skeletal microstructures of organisms through the interval from the latest Precambrian to the Early Cambrian.- *Science in China*, Beijing, (Series D), vol. 46, p. 977-985.

Fischer R., Pernet B. & Reitner J. (2000).- Organomineralization of cirratulid annelid tubes - fossil and recent examples.- *Facies*, Erlangen, vol. 42, p. 35-50.

Gaucher C. & Sprechmann P. (1999).- Upper Vendian skeletal fauna of the Arroyo del Soldado Group, Uruguay.- *Beringeria*, Würzburg, vol. 23, p. 55-91.

Germs J.G.B. (1972).- New shelly fossils from the Nama Group, South West Africa.- *American Journal of Science*, New Haven, vol. 272, p. 752-761.

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

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

Grotzinger J.P., Bowring S.A., Saylor B.Z. & Kaufman A.J. (1995).- Biostratigraphic and geochronologic constraints on early animal evolution.- *Science*, Washington, vol. 270, p. 598-604.

Hahn G. & Pflug H.D. (1985).- Die Cloudinidae n. fam., Kalk-Röhren aus dem Vendium und Unter-Kambrium.- *Senckenbergiana Lethaia*, Frankfurt, vol. 65, p. 413-431.

Hedley R.H. (1958).- Tube formation by *Pomatoceros triqueter* (Polychaeta).- *Journal of the Marine Biological Association of the United Kingdom*, Plymouth, vol. 37, p. 315-322.

Hove H.A. ten & Hurk P. van den (1993).- A review of Recent and fossil serpulid 'reefs'; actuopalaeontology and 'Upper Malm' serpulid limestones in NW Germany.- *Geologie en Mijnbouw*, Utrecht, vol. 72, p. 23-67.

Hove H.A. ten & Kupriyanova E.K. (2009).- Taxonomy of Serpulidae (Annelida, Polychaeta): the state of affairs.- *Zootaxa*, Auckland, vol. 2036, p. 1-126.

Hove H.A. ten & Smith R.S. (1990).- A redescription of *Ditrupa gracillima* Grube, 1878 (Polychaeta, Serpulidae) from the Indo-Pacific, with a discussion of the genus.- *Records of the Australian Museum*, Sydney, vol. 42, p. 101-118.

Hua H., Chen Z. & Yuan X. (2007).- The advent of mineralized skeletons in Neoproterozoic Metazoa— new fossil evidence from the Gaojiashan Fauna.- *Geological Journal*, Malden, vol. 42, p. 263-279.

Hua H., Chen Z., Yuan X., Zhang L. & Xiao S. (2005).- Skeletogenesis and asexual reproduction in the earliest biomineralizing animal *Cloudina*.- *Geology*, Boulder, vol. 33, p. 277-280.

Hua H., Pratt B.R. & Zhang L. (2003).- Borings in *Cloudina* shells: Complex predator-prey dynamics in the terminal Neoproterozoic.- *Palaios*, Tulsa, vol. 18, p. 454-459.

Jäger M. (2004).- Serpulidae und Spirorbidae (Polychaeta sedentaria) aus Campan und Maastricht von Norddeutschland, den Niederlanden, Belgien und angrenzenden Gebieten.- *Geologisches Jahrbuch*, Stuttgart, vol. A157, p. 121-249.

Liu P., Xiao S., Yin C., Tang F. & Gao L. (2009).- Silicified tubular microfossils from the upper Doushantuo Formation (Ediacaran) in the Yangtze Gorges area, South China.- *Journal of Paleontology*, Tulsa, vol. 83, p. 630-633.

Liu P., Xiao S., Yin C., Zhou C., Gao L. & Tang F. (2008).- Systematic description and phylogenetic affinity of tubular microfossils from the Ediacaran Doushantuo Formation at Weng'an, South China.- *Palaeontology*, London, vol. 51, p. 339-366.

Neff J.M. (1971).- Ultrastructural studies of the secretion of calcium carbonate by the serpulid polychaete worm, *Pomatoceros caeruleus*.- *Zeitschrift für Zellforschung*, New York, vol. 120, p. 160-186.

Nott J.A. & Parker K.R. (1975).- Calcium accumulation and secretion in the serpulid polychaete *Spirorbis spirorbis* L. at settlement.- *Journal of the Marine Biological Association of the United Kingdom*, Plymouth, vol. 55, p. 911-923.

Peel J.S. (2011).- The coral *Cothonion* from the lower Cambrian of North Greenland.- *Alche-*

ringa, Abingdon, vol. 35, p. 405-411.

PERNET B. (2001).- Escape hatches for the clonal offspring of serpulid polychaetes.- *Biological Bulletin*, Woods Hole, vol. 200, p. 107-117.

SANFILIPPO R. (1996).- Micromorphology, microstructure and functional morphology of the *Josephella marenzelleri* (Polychaeta Serpulidae) tube. In: Cerchi A, (ed.), Autoecology of selected fossil organisms: achievements and problems.- *Bolletino della Società Paleontologica Italiana*, Special Volume, Modena, vol. 3, p. 205-211.

SANFILIPPO R. (2009).- Systematics and life habit in *Serpula israelitica* AMOUREUX, 1977 (Polychaeta Serpulidae) from the Mediterranean with remarks on other soft-bottom serpulids.- *Journal of Natural History*, London, vol. 43, p. 2009-2025.

TANUR A.E., GUNARI N., SULLAN R.M.A., KAVANAGH C.J. & WALKER G.C. (2010).- Insights into the composition, morphology, and formation of the calcareous shell of the serpulid *Hydroides dianthus*.- *Journal of structural Biology*, San Diego, vol. 169, p. 145-160.

TAYLOR P.D. (2008).- Seawater chemistry, biomineralization and the fossil record of calcareous organisms. *In*: OKADA H., MAWATARI S.F., SUZUKI N. & GAUTAM P. (ed.), Origin and evolution of natural diversity.- Proceedings of International Symposium "The origin and evolution of natural diversity", 1-5 October 2007, Sapporo, 21st Century COE for Neo-Science of Natural History, Hokkaido University, p. 21-29.

TAYLOR P.D. & VINN O. (2006).- Convergent morphology in small spiral worm tubes ('*Spirorbis*') and its palaeoenvironmental implications.- *Journal of the Geological Society*, London, vol. 163, p. 225-228.

TAYLOR P.D., VINN O. & WILSON M.A. (2010).- Evolution of biomineralization in "lophophorates".- *Special Papers in Palaeontology*, London, vol. 84, p. 317-333.

VINN O. (2005).- A new cornulitid genus from the Silurian of Gotland, Sweden.- *GFF*, Stockholm, vol. 127, p. 205-210.

VINN O. (2007).- Taxonomic implications and fossilization of tube ultrastructure of some Cenozoic serpulids (Annelida, Polychaeta) from Europe.- *Neues Jahrbuch für Geologie und Paläontologie*, Stuttgart, vol. 244, p. 115-128.

VINN O. (2008).- Tube ultrastructure of the fossil genus *Rotularia* DEFRANCE, 1827 (Polychaeta, Serpulidae).- *Journal of Paleontology*, Tulsa, vol. 82, p. 206-212.

VINN O. (2009).- The ultrastructure of calcareous cirratulid (Polychaeta, Annelida) tubes.- *Estonian Journal of Earth Sciences*, Tallinn, vol. 58, p. 153-156.

VINN O. (2010).- Adaptive strategies in the evolution of encrusting tentaculitoid tubeworms.- *Palæogeography, Palæoclimatology, Palæoecology*, Amsterdam, vol. 292, p. 211-221.

VINN O. & FURRER H. (2008).- Tube structure and ultrastructure of serpulids from the Jurassic of France and Switzerland, its evolutionary implications.- *Neues Jahrbuch für Geologie und Paläontologie*, Stuttgart, vol. 250, p. 129-135.

VINN O., HOVE H.A. ten & MUTVEI H. (2008a).- On the tube ultrastructure and origin of calcification in sabellids (Annelida, Polychaeta).- *Palaeontology*, London, vol. 51, p. 295-301.

VINN O., HOVE H.A. ten, MUTVEI H. & KIRSIMÄE K. (2008b).- Ultrastructure and mineral composition of serpulid tubes (Polychaeta, Annelida).- *Zoological Journal of the Linnean Society*, London, vol. 154, p. 633-650.

VINN O., JÄGER M. & KIRSIMÄE K. (2008c).- Microscopic evidence of serpulid affinities of the problematic fossil tube "*Serpula*" *etalensis* from the Lower Jurassic of Germany.- *Lethaia*, Oslo, vol. 41, p. 417-421.

VINN O., KIRSIMÄE K. & HOVE H.A. ten (2009).- Tube ultrastructure of *Pomatoceros americanus* (Polychaeta, Serpulidae): implications for the tube formation of serpulids.- *Estonian Journal of Earth Sciences*, Tallinn, vol. 58, p. 148-152.

VINN O. & MUTVEI H. (2009).- Calcareous tubeworms of the Phanerozoic.- *Estonian Journal of Earth Sciences*, Tallinn, vol. 58, p. 286-296.

VINN O., MUTVEI H., HOVE H.A. ten & KIRSIMÄE K. (2008d).- Unique Mg-calcite skeletal ultrastructure in the tube of the serpulid polychaete *Ditrupa*.- *Neues Jahrbuch für Geologie und Paläontologie*, Stuttgart, vol. 248, p. 79-89.

VINTHER J., VAN ROY P. & BRIGGS D.E.G. (2008).- Machaeridians are Palaeozoic armoured annelids.- *Nature*, London, vol. 451, p. 185-188.

WEEDON M.J. (1994).- Tube microstructure of recent and Jurassic serpulid polychaetes and the question of the Palaeozoic 'spirorbids'.- *Acta Palaeontologica Polonica*, Warsaw, vol. 39, p. 1-15.

ZHANG L. (1986).- Preliminary study of the Gaojiashan biota from the latest Sinian in Ningqiang County, Shaanxi.- *Bulletin of the Xi'an Institute of Geological Sciences*, Xian, vol. 13, p. 67-88.

ZHURAVLEV A.Yu., LIÑÁN E., GÁMEZ VINTANED J.A., DEBRENNE F. & FEDOROV A.B. (2011, online first).- New finds of skeletal fossils in the terminal Neoproterozoic of the Siberian Platform and Spain.- *Acta Palaeontologica Polonica*, Warsaw. DOI: 10.4202/app.2010.0074.