

Ultrastructure and morphology of *Chuar* *circularis* (Walcott, 1899) Vidal and Ford (1985) from the Neoproterozoic Visingsö Group, Sweden

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Abstract

The organic-walled microfossil *Chuar* *circularis* [Walcott, C.D., 1899. Precambrian fossiliferous formations. Geol. Soc. Am. Bull. 10, 199–244] Vidal and Ford [Vidal, G., Ford, T.D., 1985. Microbiotas from the Late Proterozoic Chuar Group (Northern Arizona) and Uinta Mountain Group (Utah) and their chronostratigraphic implications. Precambrian Res. 28, 349–389] from the Visingsö Group in Sweden have been re-examined using reflected and transmitted light, scanning electron and (SEM) transmission electron (TEM) microscopy. Specimens extracted from the rock matrix and those in situ, compressed on the bedding planes, were both studied. Besides previously described external wall surface, a psilate internal surface of *Chuar* vesicle was observed. Transmission electron microscopy revealed a single-layered, electron-dense and homogeneous wall ultrastructure of the microfossil. Similar wall ultrastructure has been observed in other acid resistant microfossils from Lower Cambrian rocks. Various stages of the microfossils' wall degradation were observed and are discussed in the paper. An overview of morphological interpretations and the history of research of *C. circularis* is presented. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: *Chuar* (*acritarcha*); Morphology; Ultrastructure; Neoproterozoic; Visingsö Group; Sweden

1. Introduction

The morphological and ultrastructural study of *Chuar* *circularis* (Walcott, 1899) Vidal and Ford (1985) presented herein was carried out on abundant and well-preserved specimens from the Vis-

ingsö Group in Sweden. The species comprises macroscopic organic-walled spheroid vesicles, ranging between 70 and 3000 µm in diameter, preserved as compressed carbonaceous discs on bedding planes. Though unnamed at the time, the microfossils from the Visingsö Group (Vidal, 1976, 1985), formerly referred to as 'beds', are one of the first *Chuar* specimens that have been recorded and mentioned in geological literature

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(Nathorst, 1879a,b; Linnarsson, 1880; Holm, 1885; Wiman, 1894). However, the microfossil was not described as a new species until the year 1899 when Walcott reported it as *C. circularis*, being a 'discinoid shell' from the Late Precambrian Chuar Group in the Grand Canyon, Arizona, USA (Walcott, 1899). In the perspective of the present knowledge of the Precambrian macrobiotic records Walcott's specimens of *Chuararia* have been considered 'the first true cellularly preserved Precambrian organisms ever recorded' (Shopf, 1999, p. 28). Similar independent discoveries of unicellular microfossils from the Grand Canyon were made by White, cited by Powell (1876) (see also Ford and Breed, 1973; Sun, 1987), and almost simultaneously from the Visingsö shale of the same age by Swedish naturalist Nathorst (Nathorst, 1879a,b). Since then, the microfossil has been frequently mentioned in the literature dealing with the Precambrian successions of the southwest Sweden (Linnarsson, 1880; Nathorst, 1884, 1886, 1888, 1894; Holm, 1885; Wiman, 1894). Wiman (1894) was the first who illustrated the microfossil and recognized the acid-resistant nature of its vesicle referred to as 'chitinous'.

The microfossils described a century ago as *C. circularis* Walcott (1899) have been a subject of a continuous palaeontological debate concerning their systematic affiliation. Walcott considered them to be phosphatic shells of brachiopods (Walcott, 1899). Earlier, Holm (1885) wrote that the rounded objects from the Visingsö Beds look similar to either brachiopods from the genus *Discina* or plant remains of unknown affinity. In his opinion, circular folds indicated that the microorganisms were globular objects flattened due to a compression. Wiman (1894) suggested that they might have been trilobite eggs considering their acid-resistant nature. Wenz (1938) attributed rounded carbonaceous fossils to gastropods whereas Brotzen (1941) considered *Chuararia* to be a chitinous foraminiferan. Muir and Sarjeant (1971) suggested that some *Chuararia* fossils may have a close relationship with *Tasmanites* and therefore probably belong to prasinophycean algae. Hofmann (1977, 1985) proposed that among other possible affinities this could be a medusoid

organism or photosynthesizing eukaryote of algal affinity. Sun (1987) classified *Chuararia* as a colonial cyanobacterium.

At present, *C. circularis* has been placed among acritarchs, an informal grouping of organic-walled microfossils mainly considered to be marine photoautotrophic plankters, but its closer biological affinity remains uncertain. During the last 20 years, two concepts concerning the possible affiliation of *Chuararia* have been discussed. In the first concept it is assumed that the microfossil might be remains of eukaryotic organism, probably of algal affinity (Tappan, 1980; Vidal and Knoll, 1983; Vidal, 1984). The other view is that this fossil could represent an external envelope of prokaryotic colonial cyanobacterium (Sun, 1987; Steiner, 1994, 1996). Jux (1977) reported the presence of radial canals in the American specimens suggesting a prasinophycean algal affinity of *Chuararia*. Similar structures have been also observed by Amard (1992) in specimens from West Africa. However, the presence of pores had not been confirmed by Steiner (1994), who described a fine-layered wall ultrastructure of *Chuararia*, and compared it with the modern *Nostoc* cyanobacterium based on detailed light and electron microscopy studies of its envelopes. The latter study was mainly performed on the *Chuararia* specimens from the Liulaobei Formation in China with a few additional scanning electron images of specimens from the Visingsö Group. However, as noted by Knoll (personal communication), the living nostocalean cyanobacteria do not show the tightly regular size frequency distribution as *Chuararia* and are absent in waters with full marine salinity.

The present paper presents analysis of the *Chuararia* microfossils from Sweden using reflected and transmitted light, scanning electron (SEM) and transmission electron (TEM) microscopy techniques in order to re-examine the monospecific genus from one of the classical localities.

2. Materials and methods

The sedimentary rocks of the Visingsö Group extend along the graben structure which is now

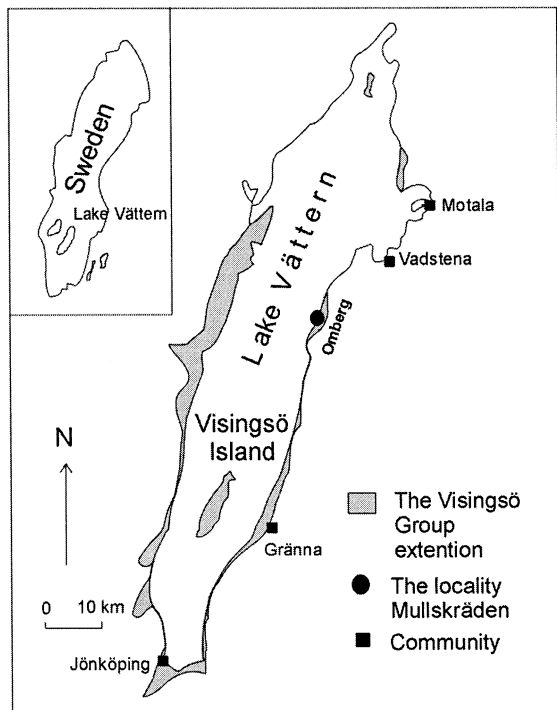


Fig. 1. The sketch-map of the Lake Vättern area showing the locality studied. Modified from Vidal (1974).

occupied by the Lake Vättern and they unconformably overlay the Proterozoic basement and are covered by the Quaternary deposits (Collini, 1951; Vidal, 1974, 1976, 1985). The contact with the Lower Palaeozoic sequence in the northwestern part of the Lake Vättern is not observed. The microfossils were collected from the locality Mullskräden (Vidal, 1976) situated in the Omberg region (Fig. 1) on the eastern coast of the Lake Vättern (Fig. 2). In this locality, the lithological succession is composed of grey to greenish silty shale in some places interbedded with thin arkosic, feldspathic sandy and silty layers. The samples have been collected from the silty grey-green shales. The detailed lithologic log of the Visingsö Group (previously called Beds) has been provided by Vidal (1976).

The Visingsö Group contains numerous organic-walled microfossils described as acritarchs. Based on palynological analysis the pre-Varangian, late Riphean-early Vendian age for the Visingsö sediments was assessed (Vidal, 1976, 1985).

The *Chuar* specimens for transmitted light, SEM and TEM analyses were extracted from the rock matrix using HF and HCl acids and filtration in water using the 250 μm mesh filter. Then the relatively big best-preserved *Chuar* specimens were picked up with a pipette. The isolated



Fig. 2. The Early Neoproterozoic rock succession at the locality Mullskräden where the samples were collected.

specimens as well as those preserved in situ on the rock bedding planes were studied in reflected light under Wild Heerbrugg M 400 binocular microscope. Permanent preparations for the transmitted light microscopy were made using Held & Schyberg AB liquid glass. Specimens selected for SEM were mounted on a preparation stub and coated with a 22 nm layer of gold. Two specimens were sectioned for the TEM analysis. These specimens were dehydrated using ethanol and acetone and then embedded in a TAAB 812 Epoxy resin. The serial sections of 40–50 nm thick were cut perpendicularly to compressed surface of a specimen using a LKB Ultramicrotome system and placed on copper grids.

The studied preparations have a reference abbreviation PMU-M-, followed by a number of a microscopic slide or a number of a stub for the scanning electron microscopy and are stored in the micropalaeontological collections of Palaeontologiska Museet, Uppsala. The copper grids with fossil sections for TEM are kept at the Department of Physiological Botany, Uppsala University.

Observations in transmitted light were made under Leica DM IRBE microscope. SEM studies were carried out using Philips XL 30 microscope with PC computerized system attached and thin sections for TEM were examined using a transmission electron microscope Philips CM 10.

The colour of microfossils is red–brown, corresponding to the thermal alteration index (TAI) 3 (Hayes et al., 1983) which means that the temperature affecting the sediment was approximately 100–120°C.

The elemental analysis of *C. circularis* (Walcott) Vidal and Ford was made using the EDAX energy dispersive system (EDS) attached to the SEM mentioned above.

3. Palaeontological descriptions

Group Acritarcha Evitt, 1963

Genus *Chuararia* Walcott, 1899

Chuararia circularis (Walcott, 1899) Vidal and Ford, 1985

Plates I, II and III

1894 Unnamed, Wiman, p. 109–113, pl. 5 (1–5).

1899 *Chuararia circularis* Walcott nov. g. and sp., p. 234–235, pl. 27 (12–13).

1941 *Chuararia wimani* n. nom.; Brotzen, p. 258–259.

1966 *Chuararia wimani* Brotzen; Eisenack (1966), p. 52–55 (1–2).

1970 *Kildinella magna* Timofeev; Timofeev (1970), pl. 1 (A, B).

1973 *Chuararia circularis* Walcott; Ford and Breed, p. 539, pl. 61 (1–7), pl. 62 (1–6), pl. 63 (1–4).

1974 *Chuararia circularis* Walcott, 1899; Vidal, p. 6–8, pl. 1 (3–6).

1976 *Chuararia circularis* Walcott, 1899; Vidal, p. 18–19, pl. 8 (A–H).

1977 *Chuararia circularis* Walcott; Hofmann, p. 3–5, Fig. 2.

1977 *Chuararia circularis* Walcott; Ford and Breed (1977), p. 171–173, pl. 1 (1–6).

1979 *Chuararia circularis* Walcott, 1899; Vidal, p. 19–21, pl. 4 (a–b).

1981 *Chuararia circularis* Walcott, 1899; Vidal, p. 23–25, pl. 11 (J–K).

1985 *Chuararia circularis* Walcott emend. Vidal and Ford, p. 355–359, pl. 3 (A).

1987 *Chuararia circularis* Walcott; Sun, p. 115, pl. 1 (1–8), pl. 4 (1–2).

1990 *Chuararia circularis* (Walcott) Vidal (1990); Vidal, p. 488, Fig. 1.

1993 *Chuararia circularis* (Walcott) Vidal and Ford (1985); Vidal, Moczydlowska and Rudavskaya, p. 390–393, pl. 3 (A–D), pl. 4 (D).

1994 *Leiosphaeridia wimani* (Brotzen, 1941), Butterfield, n. comb.; Butterfield, Knoll and Swett, p. 42–43, fig. 13 (D–F).

1994 *Chuararia circularis* Walcott 1899; Butterfield, Knoll and Swett, p. 32–34, pl. 8 (G–H), pl. 13 (G–I).

1994 *Chuararia circularis* Walcott; Yin and Sun (1994), p. 99–100, pl. 4 (b).

1994 *Chuararia circularis* Walcott; Steiner, p. 95–101, pl. 1 (4–17), pl. 3 (1–7), pl. 4 (1–4), pl. 8 (2), pl. 9 (1–2), pl. 11(8–10), pl. 12 (4–11).

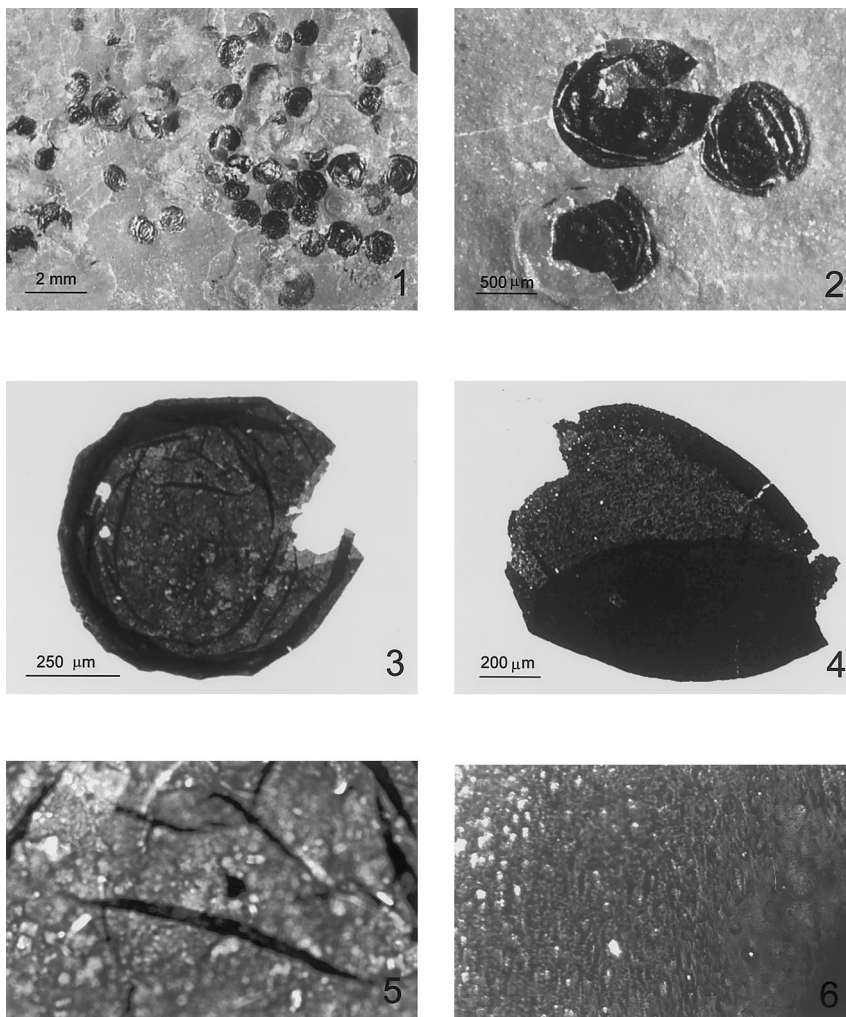


Plate I. The reflected and transmitted light micrographs of *Chuarina circularis* (Walcott, 1899) Vidal and Ford (1985) from the Visingsö Group. (1–2) Reflected light micrographs. Sample PMU-V-Ch. (1) The abundant accumulation of specimens on the bedding plane. (2) Median rupture of *Chuarina*. Note large concentric folds in all three *Chuarina* specimens. (3–6) Transmitted light micrographs. (3) Specimen PMU-M-2-E/44. (4) Specimen PMU-M-2-M/38/3. 5. Enlarged wall fragment of the specimen in 3 (see above). (6) Enlarged wall fragment of the specimen in 4 (see above).

1995 *Chuarina circularis* (Walcott, 1899) Vidal and Ford (1985); Hofmann and Rainbird (1995), p. 724–725, pl. 1 (1–6).

1997 *Chuarina circularis* Walcott, 1899, emend. Vidal and Ford (1985); Samuelsson, p. 173–174, pl. 7 (A, D).

Remarks. The genus *Chuarina* Walcott, 1899 includes a single species *C. circularis* (Walcott,

1899) Vidal and Ford (1985).

3.1. Emended diagnosis by Vidal and Ford (1985)

‘Acid-resistant, extremely robust, single-walled vesicle circular to subcircular in outline (originally spherical) after compaction. The external surface is psilate or chagrinat.’

3.2. Description

The vesicle wall of *C. circularis* (Walcott, 1899) Vidal and Ford, 1985 is carbonaceous (Fig. 3). The external and internal surfaces of the vesicle wall are psilate or chagrinate (Plate I, 3–6) as observed in the transmitted light microscope. The wall is strongly folded due to compression (Plate I, 2–5; Plate II, 1–4 and Plate III, 3–4). Small irregular

foldings are randomly distributed on the wall surface (Plate II, 3) and large concentric folds extend around the vesicle periphery (Plate I, 2; II, 2). Both kinds of folds are clearly recognized in transmitted light and SEM images. The holes within the fossil wall, which are observed in some specimens on parts of the vesicle (Plate II, 6 and Plate III, 1, 2) are caused by degradation. Median rupture of the vesicle is observed in some specimens (Plate I, 2).

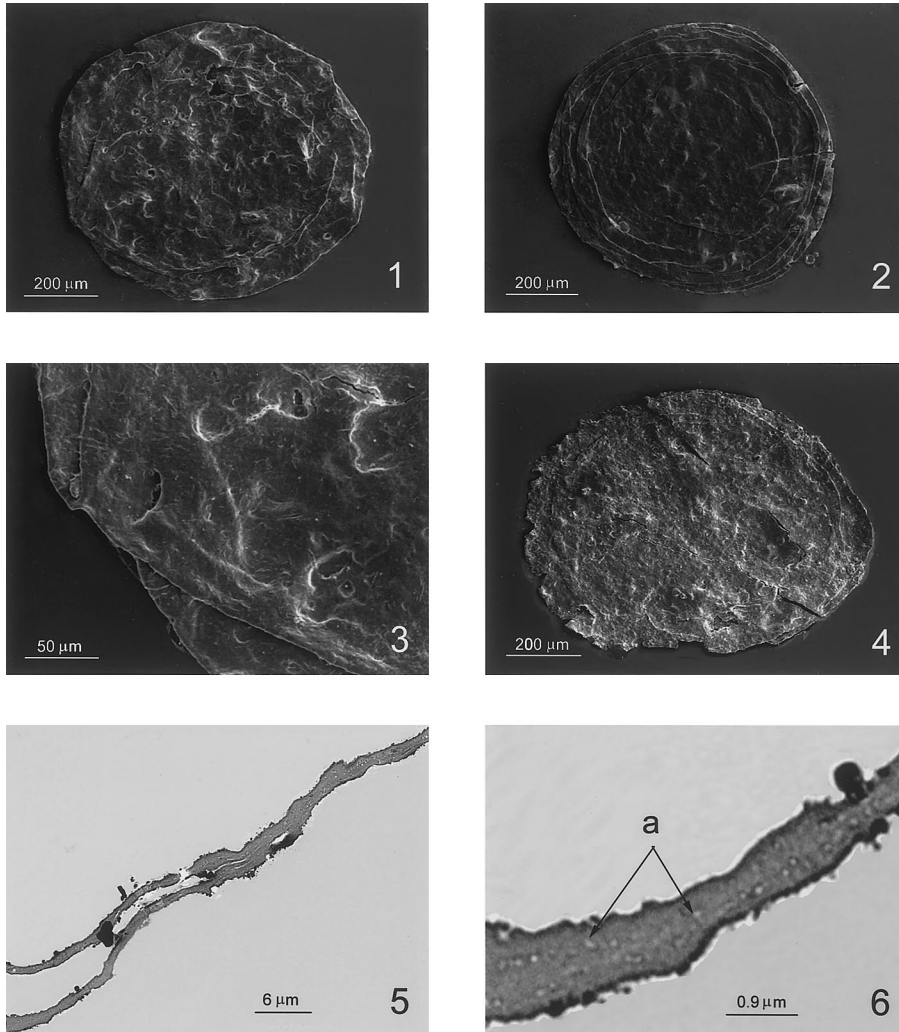


Plate II. Scanning electron and transmission electron micrographs of *Chuarina circularis* from the Visingsö Group. (1–2, 4). Scanning electron micrographs. Note concentric folds and small irregular folds of *Chuarina* vesicle wall. Scanning electron microscopy (SEM) preparation stub V-2. (3) Enlarged wall fragment of the specimen in micrograph 1. (5, 6) Transmission electron micrographs of the degraded, thin-walled specimen. The holes caused by degradation penetrate the microfossil wall (6, a). Sample M-2-96.

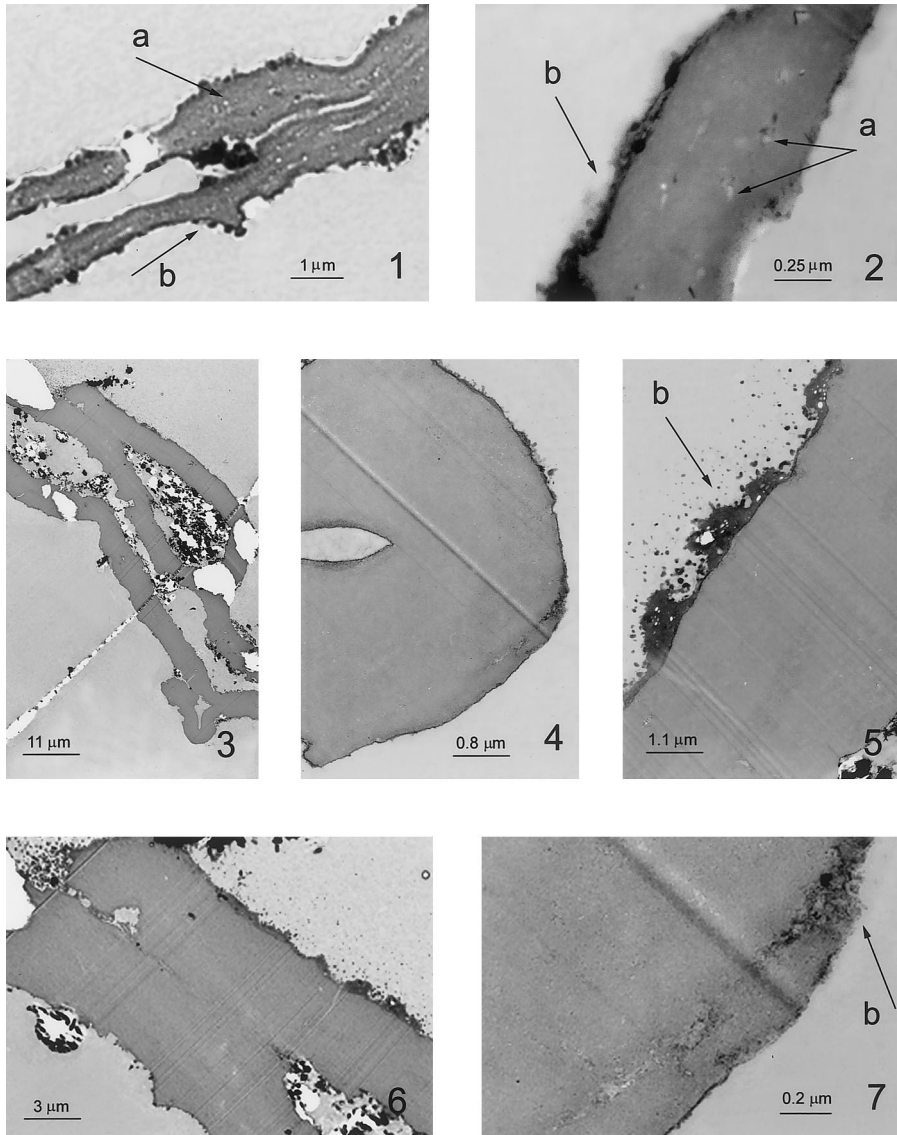


Plate III. Transmission electron micrographs of *Chuarina circularis* from the Visingsö Group. (1–2) Wall fragments of the degraded, thin-walled specimen (1 is detail of Plate II, 6). Note the degradation holes inside the microfossil wall (a) and surface degradation (b). M-2-96. (3–6) Wall fragments of the well-preserved specimen. The specimen displays some degradation of the wall surface (5, b; 7, b). Sample M-2-96.

The vesicle wall is single-layered. Under transmission electron microscope it appears to be electron-dense and homogeneous (Plate III, 2–7). The cavities which are observed inside the wall of some specimens (Plate II, 6; Plate III, 1, 2) are caused by degradation (probably biodegradation) processes. The wall thickness varies from 0.5 to

2.5 μm in the degraded specimen (Plate II, 5, 6; Plate III, 1, 2) and from 2.3 to 5.4 μm in the sectioned well-preserved specimen (Plate III, 3–7). The vesicle wall surfaces, especially the external one, are clearly corroded as seen in the TEM and SEM images (Plate II, 5, 6, Plate III, 1, 2, 5–7). No radial canals penetrating through the wall that

could be compared to those of *Tasmanites* are observed. The diameter of the studied specimens ranges 250–2000 μm .

3.3. Occurrence

The Chuar Group, Grand Canyon (Walcott, 1899; Ford and Breed, 1973; Vidal and Ford, 1985) and the Red Pine Formation, Uinta Mountains, USA (Hofmann, 1977); the Little Dal Group, Mackenzie Mountains, Canada (Hofmann and Aitken, 1979; Hofmann, 1985) and the Shaler Supergroup, Arctic Canada (Hofmann and Rainbird, 1995); the Eleonore Bay Group, East Greenland (Vidal, 1979) and the Thule Group, northern Greenland (Vidal and Dawes, 1980); the Ryssö and Hunneberg Formations, Svalbard (Knoll and Calder, 1983; Knoll, 1984); the Svanbergfjellet Formation, Spitsbergen (Butterfield et al., 1994); the Visingsö Group, Sweden (Wiman, 1894; Vidal, 1976); the Vadsø, Tanafjord and Vestertana Groups, East Finnmark, (Vidal, 1981) and the Barents Sea Group, Varanger Peninsula,

Norway (Vidal and Siedlecka, 1983); the Debengdin, Khajpakh, Maastakh and Khatyspyt Formations of Yakutia, eastern Siberia (Vidal et al., 1993); the Kildinskaya Group of the Kildin Island and the Sredni and Rybachi Peninsulas, and the Chapoma Formation, Kola Peninsula, Russia (Samuelsson, 1977); the Liulaobei, Jiliqiao and Nanfen Formations, China (Duan, 1982; Sun, 1987; Steiner, 1994).

The relative age of all mentioned occurrences is consistent with Early Neoproterozoic, late Riphean, predating the Varangerian glacial event.

4. Discussion

The *Chuar* specimens studied from the Visingsö Group conform morphologically to the diagnosis of *C. circularis* Walcott, 1899 emended by Vidal and Ford (1985). The psilate external surface, and thick, solid and single-layered vesicle have been observed using different kinds of microscopy. In addition to previously reported morphology of the external wall surface, the psilate or chagrinate internal surface is also observed. Some *Chuar* vesicles from the Visingsö Group possess a median rupture (Plate I, 2). However, it is not clear whether this feature reflects an excystment structure or a rupture due to compaction.

The concentric wrinkles of the wall are abundant in the Visingsö specimens. This is probably the most prominent feature of *C. circularis* that has been noted in the first diagnosis by Walcott (1899). Although very common in *Chuar*, this feature is certainly not unique for the genus. It is characteristic of thick-walled specimens of other taxa and probably indicates a thick vesicle wall. Similar kinds of folds have been observed in some Precambrian *Leiosphaeridia* (Knoll, 1994, p. 6746, Fig. 4, B), but this does not necessarily mean that these two genera are related.

The concentric folds and a large size of the vesicle have been treated as the main diagnostic features of *C. circularis* by some researchers (Duan, 1982; Butterfield et al., 1994). The reason is that although the folds are a secondary taphonomic feature, they are very common in *Chuar* specimens (Butterfield et al., 1994) and, as men-

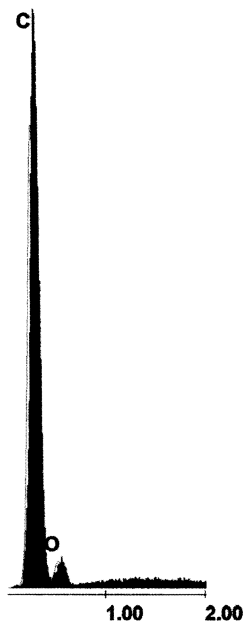


Fig. 3. The elemental composition of *Chuar* *circularis* (Walcott, 1899) Vidal and Ford (1985) using the energy dispersive system (EDS) attached to the scanning electron microscopy (SEM). SEM preparation stub V-1.

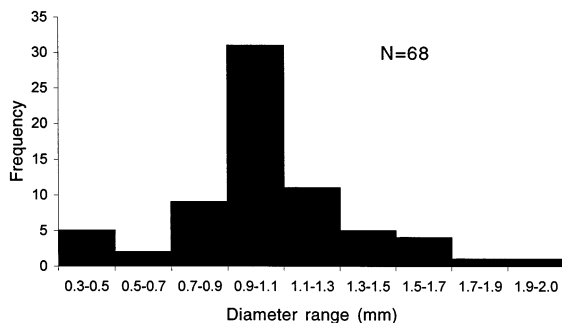


Fig. 4. Size distribution of *Chuarina* specimens, Visingsö Group, Sweden.

tioned above, probably correspond to the wall thickness and its flexibility. Arbitrarily chosen dimension limit alone has neither taxonomic nor systematic value. As noted by Vidal et al. (1993) ‘...From this lack of clearly diagnostic characters emanates the suspicion that *C. circularis* may in fact be a taxonomic waste-basket containing true biogenic, as well as various non-biogenic objects such as films of organic sapropel and carbonaceous intraclasts’. However, the artificial size limitation of *Chuarina* might be convenient, taken along with other features, allowing distinction between specimens of the megascopic acritarch, which is abundant at a certain level of Proterozoic, and numerous leiosphaerids, which are widely distributed in successions throughout the geological time.

The distribution diagram of diameters of a large in situ population of *Chuarina* (Fig. 4; Plate I, 1) from the Visingsö Group basically corresponds to a standard size distribution for a taxon (see range from 0.5 to 2.0 mm). However, the presence of a mode at the range of 0.3–0.5 mm allows to suggest that the fossil probably represent a vegetative state which grows in the course of the life cycle of the organism. A similar polymodal size distribution of *Chuarina* specimens from Uinta Mountain Group, USA is reported by Hofmann (1977, Fig. 3).

The Visingsö Group specimens have the vesicle wall resistant to HCl and HF. This property of the acid-resistance of *Chuarina* wall was mentioned in the emended diagnosis (Vidal and Ford, 1985) and was recognized in the type spe-

cies of the genus. The test on the wall resistance is significant in the definition of *C. circularis* and in contrary to suggestion of Duan (1982), it is more appropriate to exclude non-acid resistant specimens from the genus of *Chuarina*.

A variation of transparency and the wall colour from light brown to dark brown was observed in the specimens studied. Apart from the thermal alteration index mentioned above, the intensity of colour depends on the wall thickness. Comparison of thin sections from one light brown and one dark brown specimen under TEM showed that the wall of the first specimen is thinner, and is penetrated by abundant secondary degradational cavities. Furthermore, it has significantly distorted margins (Plate II, 5, 6; Plate III, 1, 2) resulting from a substantial degradation of the specimen. The dark brown specimen (Plate III, 3–7) is devoid of the degradational internal cavities and has better preserved margins. Simple polygonal cavities, favus or compound faviform cavities and compound cribrate cavities have been previously reported in *Chuarina* specimens from the Visingsö Group (Vidal, 1974) and explained as a result of a pyrite crystal growth caused by bacterial activity (reducing bacterial metabolism and precipitation of sulfides). Such a kind of degradation possibly caused the difference observed in the wall thickness between *C. circularis* from the Grand Canyon, USA and specimens from the Visingsö Group referred to as *Chuarina wimani* Brotzen and revised as *Leiosphaeridia wimani* (Brotzen, 1941) Butterfield, n. comb. (Butterfield et al., 1994).

No lamellar structure comparable to that reported by Amard (1992) in specimens from West Africa has been observed in *Chuarina* from the Visingsö Group. This structure could be taphonomic and caused by a degradation. Illustrations of in situ specimens (Amard, 1992 on Plate I, 3, 4) show highly corroded surface of the fossil, with cracks following distortions in the rock matrix. The ‘radial canals’ first noted by Jux (1977) and illustrated by Amard (1992) are probably comparable to the cavities in the wall of the Visingsö *Chuarina*, interpreted here as biodegradational.

The SEM and TEM studies of specimens from the Liulaobei Formation in China (Steiner, 1994) did not reveal any canal structures. The reported 'fine-layered' ultrastructure in these specimens (Steiner, 1994, Plate 8, Fig. 2) was interpreted as a feature of an external envelope of a colonial cyanobacterium *Nostoc*. At a magnification of $\times 34\,500$ similar ultrastructure was observed in the Visingsö *Chuarina* specimens. However, this feature seems to be common for other acritarchs, which have homogeneous and electron-dense wall. A similar ultrastructure of the wall has been observed in specimens of *Tasmanites tenellus* Volkova from the Lower Cambrian in Estonia (Talyzina and Moczydlowska, submitted, plate V, 5), the genus which is assumed to be a prasinophyte (Wall, 1962; Guy-Ohlson and Boalch, 1992). This makes the association of *Chuarina* with the *Nostoc*-like prokaryotes rather doubtful.

5. Conclusions

(1) *C. circularis* (Walcott, 1899) Vidal and Ford (1985) from the Visingsö Group possesses a single-layered and homogeneous vesicle wall. The external and internal wall surfaces are psilate in well preserved specimens and may appear shagrinated due to degradational processes. Neither radial canals comparable to pores of *Tasmanites* nor lamellar structure have been observed. The latter observations are considered taphonomic.

(2) Morphological and ultrastructural features of *C. circularis* (Walcott, 1899) Vidal and Ford (1985) are insufficient for a firm biological classification. Combination of morphological study with other methods may improve our understanding of the biological nature of this presently enigmatic microfossil.

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