Internal morphology and taphonomic history of the Neoproterozoic vase-shaped microfossils from the Visingsö Group, Sweden

MÓNICA MARTÍ MUS & MAŁGORZATA MOCZYDŁOWSKA

The morphology and mineral composition of the vase-shaped microfossils (VSMs) from phosphatic nodules of the upper Visingsö Group in the Lake Vättern area have been studied using confocal and transmitted light microscopy along with the EDX analytical technique. The taphonomic history of the microfossils and the internal anatomy of the original organism were reconstructed. An early diagenetic precipitation of phosphate accounts for the formation of phosphatic surfaces replicating the external and internal morphology of the vase-shaped organism. The vase-shaped vesicle had an internal compartment containing a reproductive cell or cyst. The presence of these structures indicates that the vesicle does not in itself represent an encystment stage of a protist as previously suggested by some authors. Hypotheses on the biological affinities of the VSMs are reviewed. The VSMs global record is considered in the palaeogeographic and palaeoenvironmetal contexts, suggesting that the vase-shaped microfossils were produced by stenothermal planktonic organisms, thriving in shallow marine seas in tropical to temperate climatic zones.

M. Martí-Mus & M. Moczydłowska, Department of Earth Sciences, Historical Geology and Palaeontology, Uppsala University, Norbyvägen 22, SE-752 36, Uppsala, Sweden

Introduction

Vase-shaped microfossils (VSMs) are a morphologically distinct group of microfossils known from Neoproterozoic marine sediments world-wide. They have a characteristic vase shape, being rounded at the aboral pole and showing a short, tapering, truncated neck with a narrow terminal opening at the oral pole. The vesicle has a smooth wall and lacks processes. VSMs were first recorded by Ewetz (1933), though at the time un-named and simply called 'single-celled organism with shell', from phosphatic nodules of the Visingsö Group, southern Sweden. Since then, several occurrences of VSMs have been reported from Neoproterozoic (850–650 Ma) sediments of many parts of the world (Table 1). The organically preserved specimens from the shales of the Kwagunt Formation (Bloeser et al. 1977; Bloeser 1985) are the best-known morphologically and the only ones formally described under the generic name *Melanocyrillium* Bloeser, 1985. Differences in preservation between these exceptionally preserved specimens and specimens from other localities have hindered detailed morphological comparisons and have generally prevented the identification of the latter ones as *Melanocyrillium*. Even so, the different microfossils summarized in Table 1 share distinct morphological similarities and have preservational features in common (perhaps associated with the chemistry of the wall; see below) that suggest close biological affinities.

VSMs occur in rocks of various lithologies: shales, carbonates, cherts and phosphatic nodules, encompassing a wide array of shallow marine depositional settings. Both their world-wide distribution and their presence in a variety of lithologic facies supports the interpretation of VSMs as representing marine planktonic organisms (Bloeser et al. 1977; Knoll & Vidal 1980; Bloeser 1985; Knoll et al. 1989; Fairchild et al. 1991). These intriguing microfossils thus constitute the earliest record of planktonic organisms showing morphological polarity (Bloeser 1985) which, together with the morphological complexity of the oral pole and the herein described internal structures, places them among the most complex Neoproterozoic microfossils recovered to date.

It has been observed that the mode of preservation of VSMs changes according to the lithology, but little is known about the details of their preservation or the taphonomic processes which they have undergone in different depositional environments. In only a few occurrences the VSMs are preserved as three-dimensional organic-walled vesicles that can be extracted from the sediment by standard palynological techniques (Bloeser et al. 1977; Vidal 1979; Vidal & Ford 1985; Bloeser 1985). In most of the localities VSMs are preserved as moulds and casts of entire, undeformed vesicles, and the organic matter seems to be partially or completely degraded. Knoll (1992, p. 57) pointed out that 'Marked taphonomic differences between these fossils and acritarchs suggest original differences in wall chemistry' (see below).

The VSMs from phosphatic nodules of the Visingsö Group were first described and figured by Ewetz (1933) and subsequently studied in more detail by Knoll & Vidal (1980). Ewetz (1933) observed that the VSMs possessed 'shells' with rough internal surfaces and that phosphate

Table 1. Global record of VSMs.

Region	Stratigraphic unit	Age	References
North America	Kwagunt Fm	Late Proterozoic	Bloeser et al. 1977
			Bloeser 1985
			Vidal & Ford 1985
			Horodyski 1987, 1993
			Porter & Knoll (in press)
	Pahrump Group	Late Proterozoic	Horodyski 1987, 1993
Greenland	Limestone-Dolomite 'Series'	Late Proterozoic	Vidal 1979
	(Eleonore Bay Group)		Green et al. 1988
Sweden	Visingsö Group	Late Riphean	Ewetz 1933
			Knoll & Vidal 1980
			This study
Saudi Arabia	Jabal Rokham Carbonates	Late Precambrian	Binda & Bokhari 1980
Svalbard	Ryssö Fm	Late Riphean	Knoll 1982
			Knoll & Calder 1983
	Draken Fm	Late Riphean	Knoll et al. 1991
	Backlundtoppen Fm	Late Riphean	Knoll et al. 1989
	Elbobreen Fm	Late Proterozoic	Knoll 1990, 1992
Tasmania	Smithton Dolomite	Late Precambrian	Saito et al. 1988

had entered the fossil vesicles through their 'mouths'. He also observed an internal, round, brownish structure, which he interpreted as a resting spore, and concluded that the Visingsö VSMs could represent fossil rhizopods. Knoll & Vidal (1980) described the morphology and dimensional variation of a greater population of VSMs and compared them structurally and ecologically with modern tintinnids.

In this study, newly observed internal structures preserved in the VSMs are reconstructed in the light of the taphonomic history of the microfossils, and their biological significance is assessed.

Geological setting and palaeoenvironments

The Visingsö Group is a sedimentary succession consisting of terrigenous rocks with minor carbonates of early Neoproterozoic age that extend in a restricted area of Lake Vättern in south-central Sweden (Fig. 1A, B). The sediments are preserved in a graben within the crystalline basement presently occupied by the lake. The succession is unmetamorphosed and exposed in the coastal cliffs of the lake and on the Vising Island (Visingsö), and is known also from a number of boreholes in the vicinity of the lake (Brotzen 1941; Collini 1951; Vidal 1974, 1976, 1982, 1985; Fig. 1B). Three informal lithostratigraphic units (lower, middle and upper) which are in the rank of formations (Vidal 1985), are distinguished in the Visingsö Group, and together they exceed 1000 m in thickness (Collini 1951).

The lower unit of the Visingsö Group consists of cross-bedded, fluvial quartz sandstone with minor conglomerate and was deposited in a delta plain environment. The middle unit is characterized by alternating feldspathic arenite, conglomerate and siltstone and was accumulated in a shallow marine prodelta environment (Vidal 1974, 1976, 1982, 1985; Larsen & Nørgaard-Pedersen 1988). The upper unit of the Visingsö Group is of major interest in this study because of the occurrence of VSMs and consists

of alternating micaceous shale and siltstone, with coarse sandstone at the bottom and interbeds of dolomitic limestone with stromatolites at the top (Vidal 1972, 1976, 1985). The total thickness of the unit was estimated as being more than 580 m (Collini 1951). The observed sedimentary structures and the presence of abundant marine planktonic microfossils in the upper Visingsö Group conform with deposition in a shallow marine environment with oscillating water depth, including shelf and subtidal to intertidal carbonate mud flats (Vidal 1972, 1976, 1985; Samuelsson & Strauss 1999). The cosmopolitan acritarch species dominating the assemblage also attest to the existence of a connection between the Vättern Basin and the global ocean (Vidal 1985) maintaining the free dispersal of microplankton. The total organic carbon (TOC) content in the whole-rock upper Visingsö samples has an average value of 3.56 mg C/g for shales (Strauss & Moore 1992; Samuelsson & Strauss 1999). This value is higher than the average value for late Proterozoic shales (2.30 mg C/g; Strauss et al. 1992) suggesting that not only high burial of organic matter, but also high organic productivity must have prevailed in the Visingsö Basin. This, together with the presence of phosphate nodules in the upper Visingsö Group is compatible with the Visingsö basin being influenced by upwelling of nutrient-rich waters, as suggested by Knoll & Vidal (1980).

The climatic conditions prevailing during the deposition of the Visingsö Group, related to the palaeogeographic position of the host craton, have been constrained by several independent lines of evidence; i.e. palaeobiology, diagenetic mineralogy and palaeomagnetic data. The presence of stromatolites in the upper Visingsö Group, characteristic of tropical and warm temperature belts, is a direct indication of the climatic conditions (Vidal 1972, 1976). The abundance of detrital biotite suggests dry climatic conditions (Vidal 1985). The early diagenetic mineral berthierine, present inside the VSMs preserved in phosphate nodules and occurring also in the host shale of the upper Visingsö Group, has been interpreted to
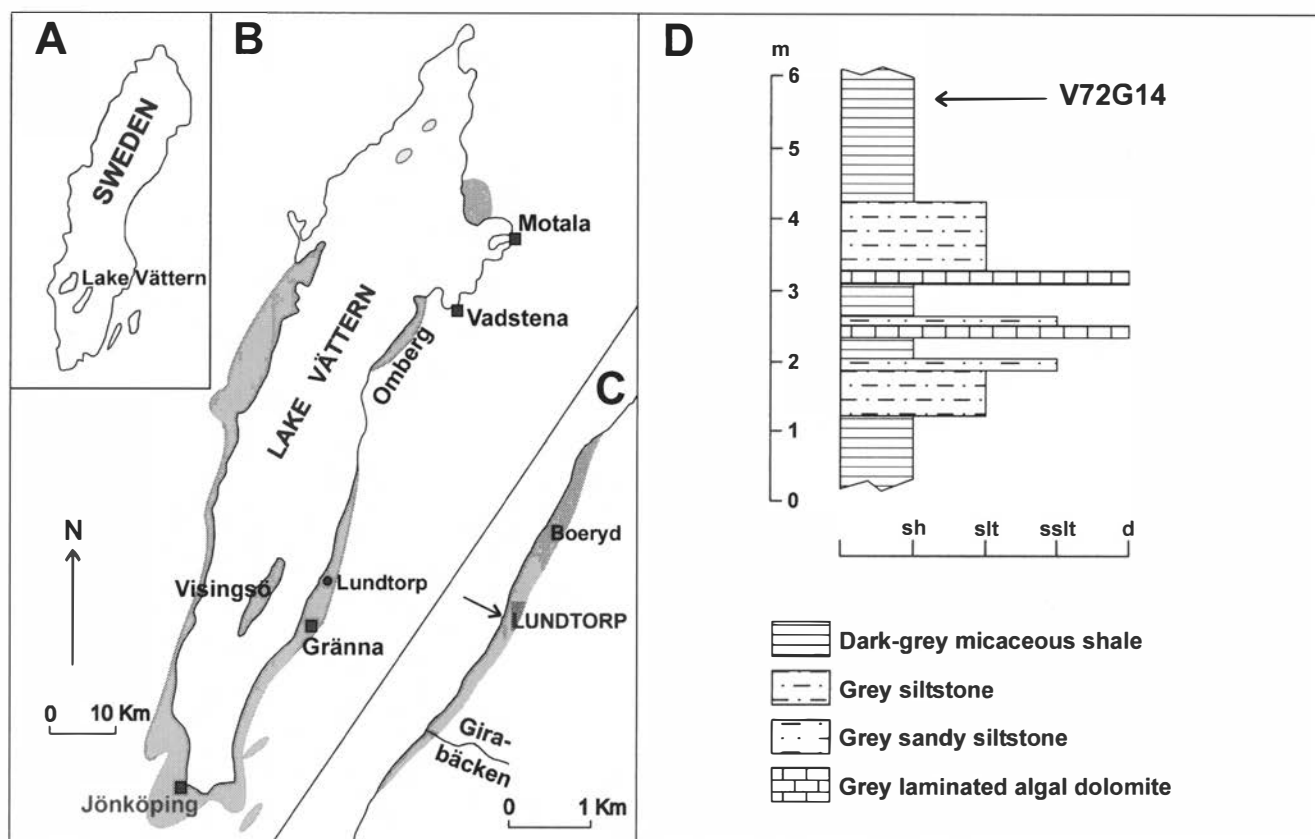
Fig. 1. A. Sketch-map of Sweden showing the location of Lake Vättern. B. Distribution of the Visingsö Group (shaded pattern) in the Lake Vättern area and location of the sampled section at Lundtorp. C. Distribution of the upper unit of the Visingsö Group (shaded pattern) at the Lundtorp area. D. Stratigraphic level of the sample studied is indicated in the geologic succession of the upper Visingsö Group at Lundtorp. sh: shale; slt: siltstone; sslt: sandy siltstone; d: dolomite.

precipitate under reducing conditions near the sediment-water interface in sediments accumulated in shallow ($<\sim$ 60 m) and probably warm ($>20°C$) seawater (Morad & Al-Aasam 1994).

The palaeolatitude of the Vättern Basin, pertaining to the Baltica craton, during the deposition of the middle unit of the Visingsö Group has been estimated from the palaeomagnetic data to be 15° to 40° (Vidal & Bylund 1981). Such latitudes, though they might have been slightly changed with geologic time, are consistent with environmental conditions suitable for the formation of phosphate nodules and Fe-silicates (berthierine) recorded in the upper Visingsö Group (Morad & Al-Aasam 1994). The suggested palaeolatitude for the Vättern Basin in the Neoproterozoic is also in agreement with recent palaeogeographic reconstructions of the Baltica palaeocontinent during the early Neoproterozoic, in which its location is in the low to middle latitudes of the southern hemisphere (Torsvik et al. 1996; Dalziel 1997).

All the above arguments corroborate the inferred position of the Vättern Basin in a subtropical to temperate climatic belt. The climatic conditions are relevant to infer the palaeoecologic aspects of the VSMs which, in turn, may help to reveal their similarities with extinct and extant organisms. Compared to the Visingsö Group, all other occurrences of the VSMs are confined to shallow marine

depositional settings in tropical to temperate climatic zones (Knoll & Calder 1983; Fairchild et al. 1991; and references in Table 1). These data suggest that the vase-shaped microfossils were produced by stenothermal organisms that thrived in tropical and warm shelfal waters, with probably no significant seasonal changes in temperature, rich in nutrients (probably associated with upwelling zones) and well-oxygenated.

Age of the Visingsö Group

Biostratigraphic constraints on the relative age of the Visingsö Group are from acritarch assemblages recorded throughout the group. A Proterozoic, late Riphean age (possibly 750–800 Ma), was assessed for the lower and middle units and a late Riphean–early Vendian age for the upper unit of the group (Vidal 1972, 1974, 1976). Subsequent re-evaluation of the microfossil ranges and biostratigraphic correlations resulted in an age estimation for the entire Visingsö Group as early Neoproterozoic, late Riphean (700–800 Ma), (Vidal 1979; Vidal & Siedlecka 1983; Vidal et al. 1993).

The isotopic Rb/Sr dating on whole-rock shales from the upper Visingsö Group, interpreted to record a diagenetic event, provides a minimum age of 663 ± 7 Ma for the
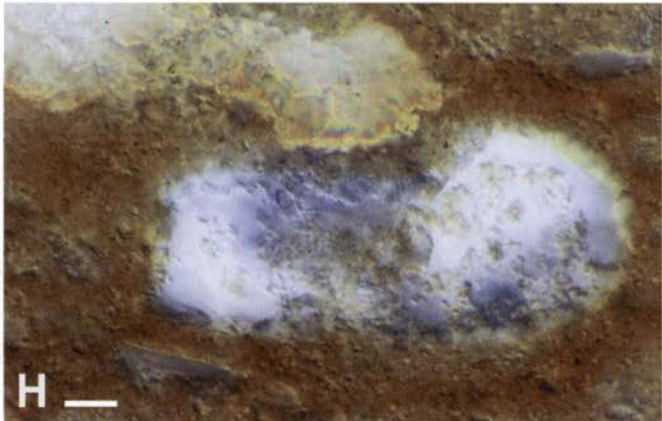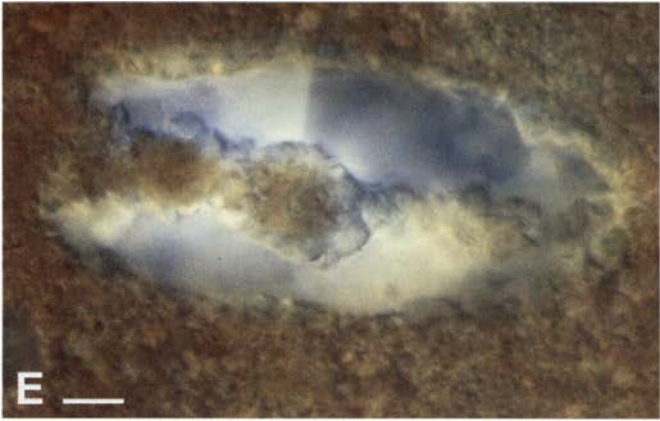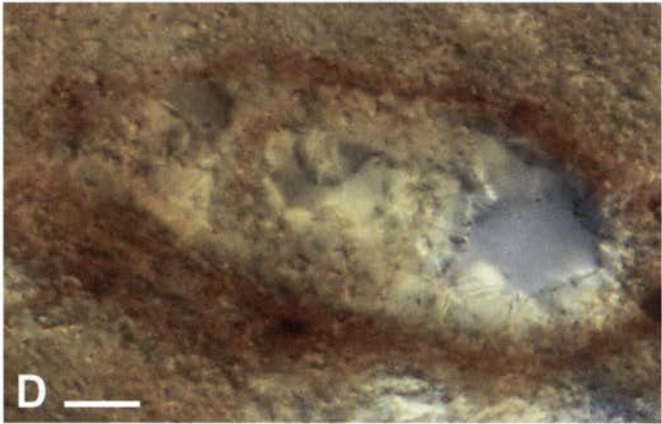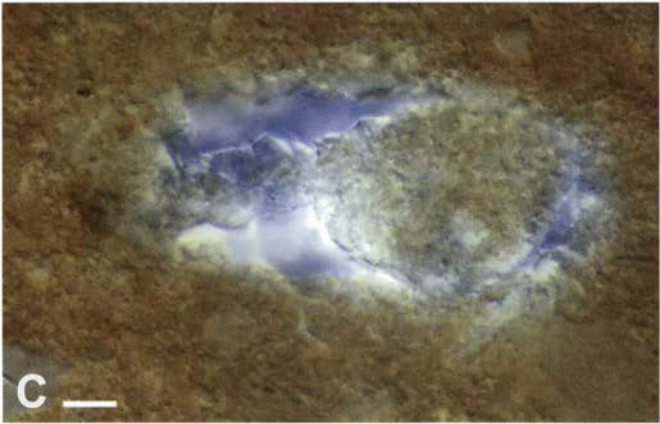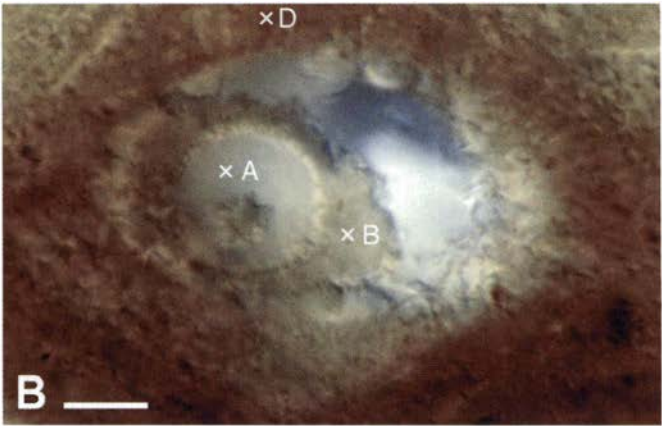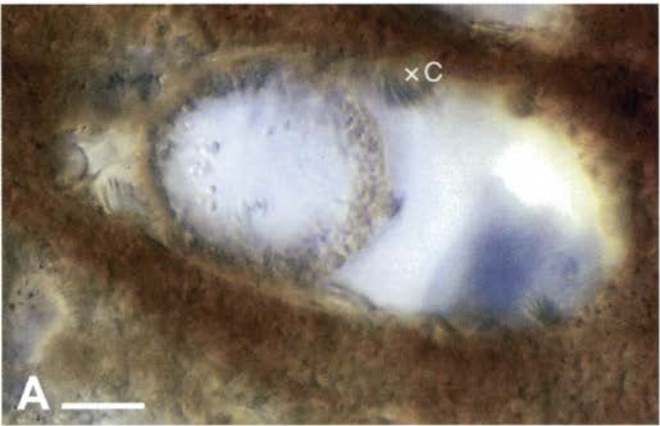
group (Bonhomme & Welin 1984), conforming in general with the biochronologic assessment.

Material and methods

Microfossils have been studied in thin-sections from phosphate nodules occurring in dark-grey and organic-rich shale of the upper Visingsö Group. The sampled succession is at Lundtorp, on the eastern shore of Lake Vättern, northeast of Gränna and between the Girabäcken Valley and Boeryd (Vidal 1976, and unpublished data; Fig. 1B, C). Strata belonging to the upper portion of the upper Visingsö Group are exposed along the ca. 4 km cliff-coast but their thickness is only a few metres. They are folded but unmetamorphosed. In this exposure, the basal and topmost beds of the upper Visingsö Group are missing. The measured succession consists of shale alternating with siltstone and thin layers of laminated algal dolomite (Vidal 1976; Fig. 1D). The phosphate nodules are lenticular in shape and randomly scattered within the shale. Detailed petrologic and geochemical analyses of phosphate nodules and host shales are provided by Morad & Al-Aasam (1994). The TOC content in shales in the Lundtorp area is high and ranges between 0.39 and 5.38 mg C/g (Strauss & Moore 1992), and it is even higher (up to 11.6 mg C/g) in the nearby locality at Boeryd (Samuelsson & Strauss 1999). The thermal alteration index (TAI) of the kerogens preserved at Boeryd (Fig. 1C) indicates a catagenesis stage of thermal alteration and burial temperatures around 150°C (Samuelsson & Strauss 1999). A similar stage of kerogen maturation is most likely in Lundtorp because of the uniform thermal alteration of the organic matter in the upper Visingsö Group, estimated previously to be around 100°C (Vidal 1976). The stratigraphic position of the sampled level with the occurrence of VSMs studied is shown in the lithologic log in Fig. 1D.

Five thin-sections with the collection reference numbers PMU-V72G14 – 1, 2, 3, 4, 5, have been examined. The VSMs are very abundant in some of the thin-sections, numbering up to several hundred specimens. The thin-sections were studied using transmitted light microscopy.

Selected specimens were further studied with confocal microscopy (Leica® TCS 4D) equipped with an Argon-Krypton laser. The autofluorescent properties of phosphate (probably francolite, Morad & Al-Aasam 1994) were used for image acquisition, and the excitation wavelength was 488 nm. Among all minerals present in the Visingsö nodules, only phosphate showed autofluorescent properties when illuminated with light in the visible spectrum. It was thus possible to obtain images showing only the morphology of phosphatised parts of the fossils. This was especially valuable since the taphonomic study of the Visingsö VSMs indicates that only the phosphatised parts of the fossils contain relevant biological information (see below). Most of the final images were obtained processing an 'image series' with the 3D software available in the Leica® system. Each 'image series' consisted of 90 optical sections scanned at successive planes of focus covering the whole volume of a specimen.

Energy dispersive X-ray analysis (EDX), together with the appearance of the different minerals under optical, confocal and scanning electron (equipped with a back-scattered electrons detector) microscopes, was used to infer the mineral composition of different parts of the microfossils. For EDX analyses the thin-sections were coated with carbon.

Each figured specimen is named with the last digit of the thin section reference number (1–5) and a code indicating its location in England-Finder co-ordinates.

The terminology established by Bloeser (1985) to describe the external morphology of the VSMs from the Kwagunt Formation is followed in this paper. Some additional terms are introduced for the newly described internal structures and all terms are shown in Fig. 8.

Description of the Visingsö VSMs

VSMs have not been recovered from acid-resistant residues of the Visingsö nodules, nor are they preserved in the host shale (Knoll & Vidal 1980). They are accumulated on the bedding planes, with their major axis oriented more or less horizontally. Their azimuthal

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Fig. 2. Vase-shaped microfossils (VSMs) from phosphatic nodules from the Visingsö Group, Sweden, photographed under transmitted light. All specimens, except 1: S-46 (B), which is an oblique section, are oriented with the oral end to the left. Note the different colour and texture of the three mineral components of the fossils. The phosphatic portions of the microfossil have a reddish coloration and a granular appearance. Quartz has mostly a white–blue coloration and a glossy appearance. Berthierine is usually whitish and is more readily distinguished by its microstructure, consisting of thin laminae radiating from the phosphatic surfaces. A. 1: Q-46-4, longitudinal section showing an internal sphere with an outer phosphatic layer and a siliceous core. The elemental composition of the spot 'C', located on the berthierine layer, was analysed by EDX and the obtained spectrum is shown in Fig. 4C. B. 1: S-46, oblique section showing an internal sphere with an outer phosphatic layer and a siliceous core. Note that the inner surface of the phosphatic layer of the sphere is smoother and has a more regular spherical shape than the outer one. The spot 'A' is located on the siliceous core of the internal sphere and its elemental composition is shown in Fig. 4A. The spot 'B' is located on the phosphatic outer layer of the internal sphere and its elemental composition is shown in Fig. 4B. The spot 'D' is located on the phosphatic matrix of the nodule and its elemental composition is shown in Fig 4D. C. 1: U-53-2, longitudinal section showing a solid phosphatic sphere connected with the oral opening by a long phosphatic tube. The internal sphere and tube as well as the surface defining the vase-shaped vesicle are coated with a berthierine layer. D. 1: T-45, longitudinal section showing an internal sphere with an outer phosphatic layer and a siliceous core. Note that berthierine is growing on both the inner and the outer surfaces of the phosphatic layer of the sphere. E. 1: T-45-2, longitudinal section showing a tubular internal phosphatic structure with several constrictions along its length. All the phosphatic surfaces of the fossil are coated with a conspicuous berthierine layer. F. 1: T-54-2 longitudinal section showing a uniform and thick berthierine layer coating the phosphatic surface defining the vesicle. G. 1: T-41-4, longitudinal section showing a short phosphatic tube connected with the oral opening and a continuous berthierine layer coating the surface defining the vesicle. H. 2: F-62-4 longitudinal section of a broken VSMs. Note the large clast above the vesicle and the corresponding shape between the clast and the fracture. Scale bars 10 μm.
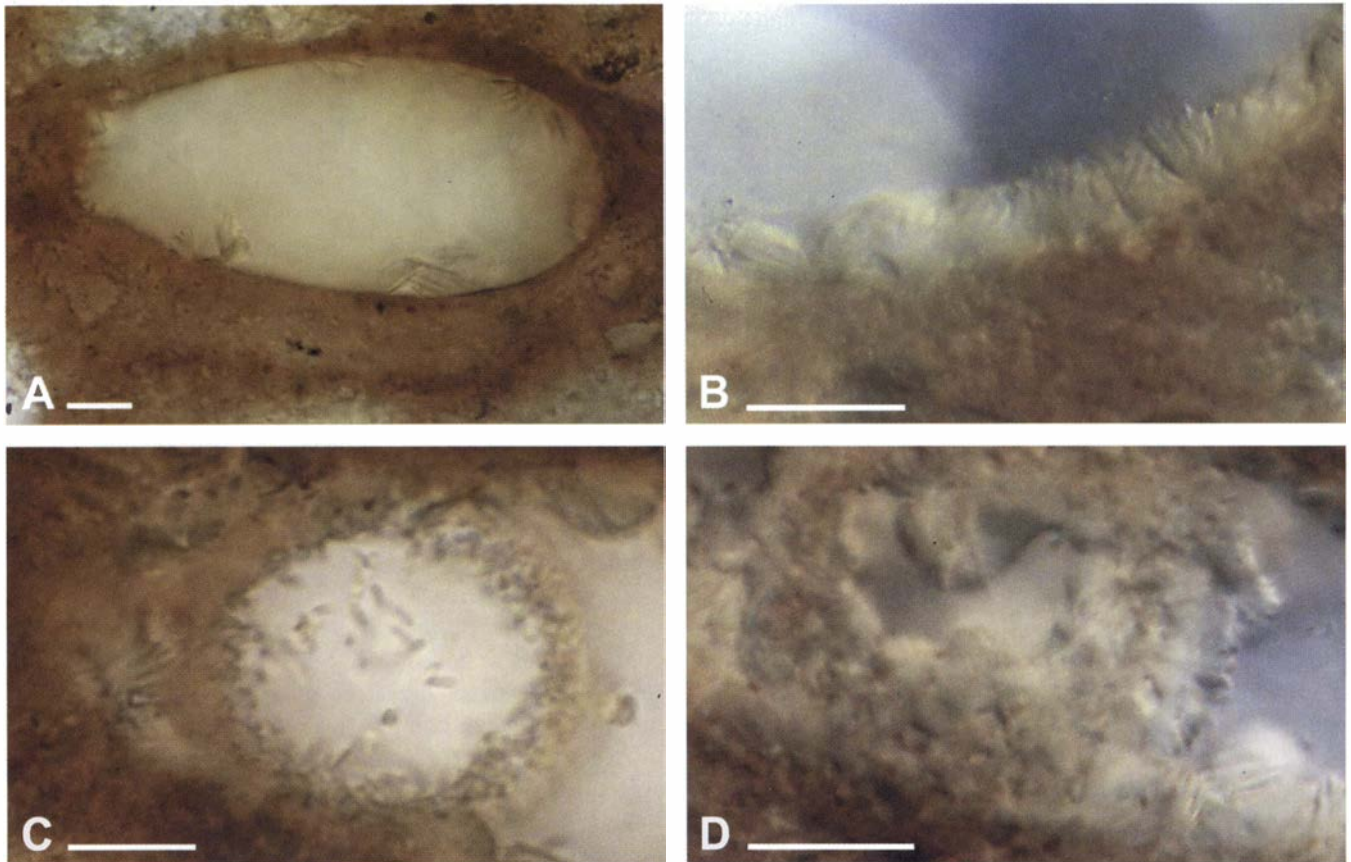
Fig. 3. VSMs from phosphatic nodules from the Visingsö Group, Sweden, photographed under transmitted light. A. 1: M-47-2, longitudinal section oriented with the oral pole to the left. The specimen shows no internal phosphatic structures. The sharp appearance of the vesicle surface is due to the very small amount of berthierine, corresponding to the few observable laminae radiating from the concave phosphatic surface; otherwise, the vesicle is filled with quartz. B. Detail of specimen 1: T-54-2 (Fig. 2F) showing the berthierine layer disposed between the phosphatic surface defining the vesicle and the quartz infilling. Note the rough internal surface of the berthierine layer and the laminae radiating from the phosphatic surface. C. Detail of specimen 1: Q-46-4 (Fig. 2A) showing a close-up of the internal sphere. The microstructure of the internal phosphate is in the form of small rod-like particles tightly aggregated in the phosphatic layer of the sphere and loosely aggregated when 'embedded' in the siliceous core of the sphere. D. Detail of specimen 1: T-45 (Fig. 2D) showing that both the inner and outer surfaces of the phosphatic layer of the sphere are coated with berthierine. The berthierine microstructure is in the form of radiating laminae.

orientation is random, so when studied in thin-sections (cut orthogonally to bedding), different individuals on the same bedding plane appear as longitudinal, transversal or oblique sections of the microfossils. The microfossils are considerably larger than the usual thickness of a petro-graphic thin section, and thus all of them have been sectioned during the preparation of the thin-sections.

The Visingsö vase-shaped microfossils are sharply distinguished from the nodule phosphatic matrix, thanks to their quartz infilling (Figs. 2, 3A). They are composed of three minerals: phosphate, berthierine and quartz (Figs. 2–4). All three minerals have a consistent distribution within the microfossils as illustrated in Fig. 5. In a few horizons there are also framboids of pyrite within the microfossils and in the surrounding host sediment. No significant amount of elemental carbon has been detected in the EDX analysis (Fig. 4).

The vesicle ranges in length from 60 to 130 μm and the diameter of the cross-section from 25 to 62 μm (Knoll & Vidal 1980). Each vase-shaped vesicle is defined by a smooth, continuous phosphatic surface that constitutes a negative of the external wall of the vase-shaped organism

(Figs. 5–8A). Phosphate is also found in the interior of the vesicle in many microfossils (Figs. 2, 5–8A). In all specimens sectioned parallel to an axial plane, the phosphate in the vesicle interior is continuous with the nodule matrix, and the connection is always through the oral pole of the fossil (Figs. 5, 6A, C–F, 7A–C, F, 8A) where an opening is found in organically preserved specimens (see Bloeser 1985).

The morphology of the internal phosphatic structure is variable, but many specimens display the same basic pattern: a sphere connected with the exterior through the oral pole by a narrow tube (Figs. 6A, C, D, 7C, 8A). The sphere, approximately 30 μm in diameter, can be found in individual specimens close to the oral pole (Fig. 6A), in the middle of the vesicle (Fig. 6D), or at the aboral pole (Fig. 6C). Regardless of its position, the sphere fits tightly inside the vesicle (since its diameter almost coincides with the diameter of the transverse section of the vesicle), but the surfaces of the sphere and the vesicle never come into contact (Figs. 6A–D, 7C, D, F). There is always a minimum separation of about 0.5 μm between both surfaces. The sphere is not always made of solid
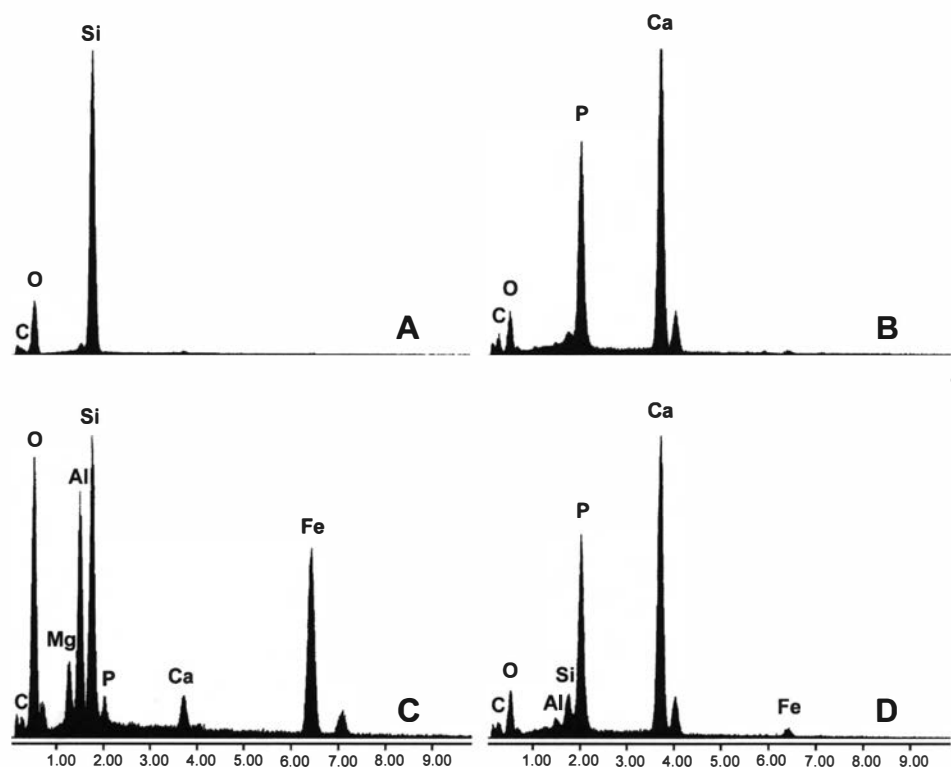
Fig. 4. Elemental composition spectra of the diagenetic minerals present in the Visingsö VSMs analysed by EDX. Each spectrum shows the elemental composition of one of the four spots indicated in Figs. 2A, B. The small C peaks correspond to the carbon coating of the thin-sections, implying that the rock does not contain 'significant' amounts of C in the selected spots.

phosphate. In many specimens, only the outer layer is phosphatic (Figs. 6A, B, D, 7C, D, 8A), whereas the interior is siliceous (Figs. 2A, B, D, 5). Still, small phosphatic particles can be found 'embedded' in the siliceous core of the sphere (Figs. 2A, 3C, 6A, 7C). In some specimens, the inner surface of the phosphatic layer is smoother and has a more regular spherical shape than the outer surface (Figs. 2B, 6B). A solid narrow tube of phosphatic composition extends inside the neck of the vesicle, connecting the sphere with the oral end (Figs. 6A, C, D, 7C, 8A). The phosphatic tube has an approximately circular transverse section, measuring about 5 µm in diameter. The length of the phosphatic tube depends on the position of the sphere inside the vesicle (Fig. 6A, C, D). Many specimens show the mentioned structures, but some others show a more or less inflated tube extending from the

Fig. 5. Schematic drawing showing the constant distribution of the three minerals forming the fossils and the variability of the internal phosphatic structures in the studied samples.

oral pole and ending somewhere inside the vesicle (Figs. 6E, F). This tube may show several constrictions along its length and can be globular or contorted in some areas. In a few specimens, the internal structure seems to get thinner towards the aboral pole, terminating close to the surface of the vesicle (Figs. 6E, F). The microstructure of the phosphate is granular in the nodule matrix, whereas in the vesicle interior it can be either granular or in the form of minute, rod-like particles (Figs. 3C, 6A, 7C) that can be tightly or loosely aggregated. Phosphatic particles in the form of micron-sized rods have been observed in both modern and ancient phosphorites and have been interpreted by some authors as phosphatized bacteria (see Krajewski et al. 1994 for a discussion).

The mineral berthierine is found coating the phosphate surfaces of the microfossil: the surface defining the vesicle and the phosphatic surfaces of the internal structure (Figs. 2, 3B, D, 5). It may form a continuous layer covering these entirely (Figs. 2C, E, F) or it may be present in a small amount as a few isolated fans (Fig. 3A). The berthierine layer has a rough internal surface and variable thickness up to 6 µm (Figs. 2, 3B, D). The berthierine microstructure is in the form of thin, tightly packed laminae that radiate in small fans from a point on the phosphatic surfaces (Figs. 3B, D). Finally, quartz occupies the rest of the vesicle as large crystals (Figs. 2, 3, 5). The quartz is separated from the phosphate by the berthierine layer in many specimens, but if the berthierine is absent, the quartz is in direct contact with the phosphate.

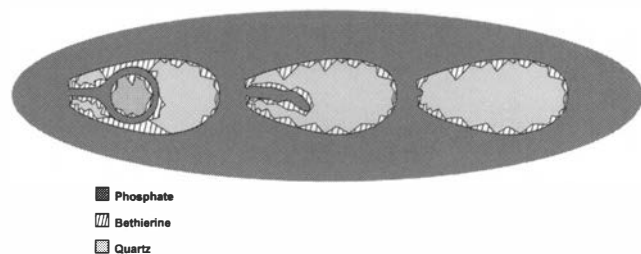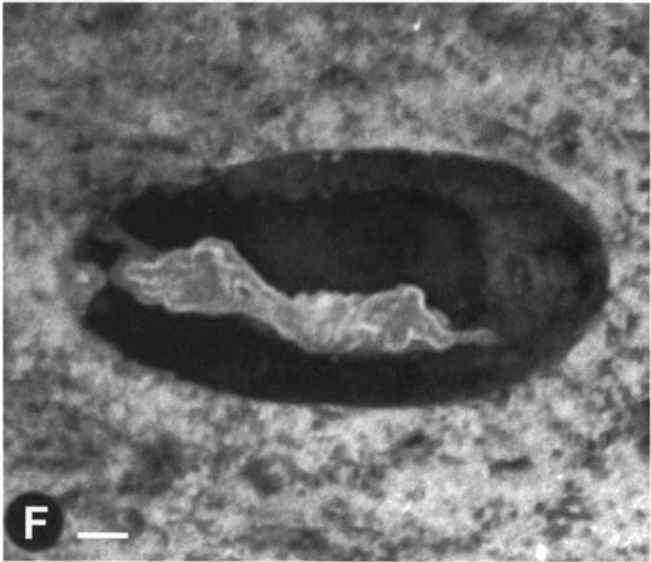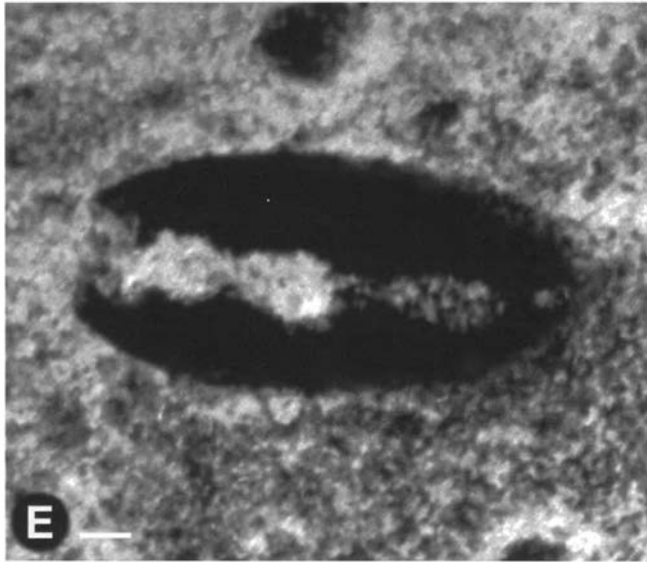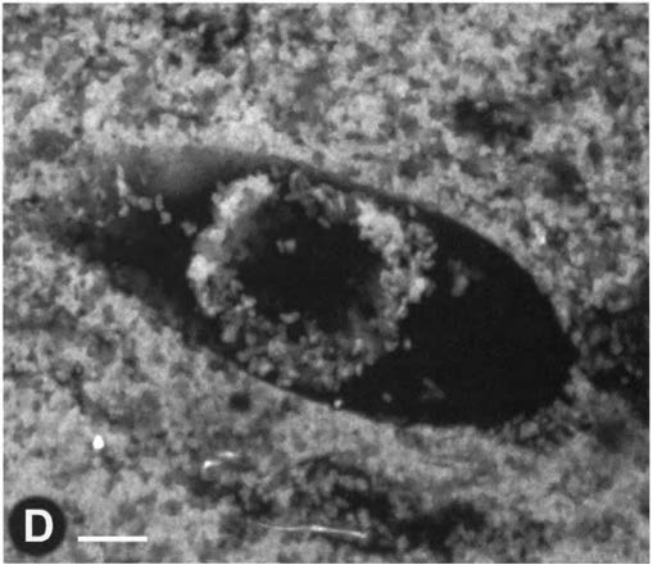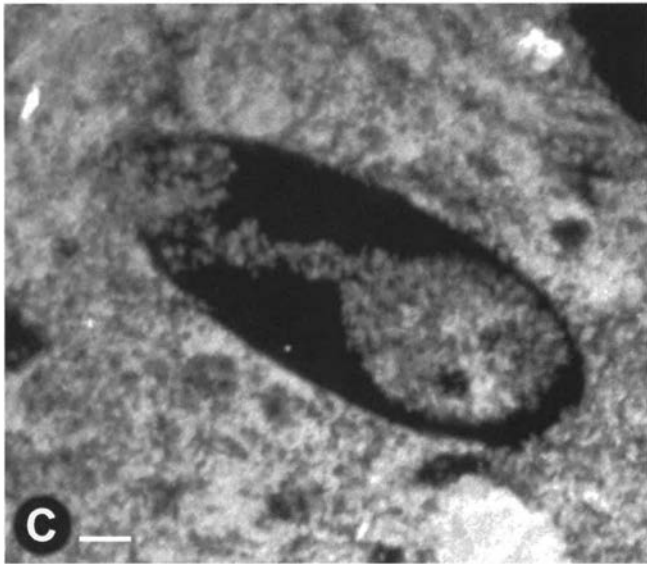The vase-shaped vesicles are rarely found broken and
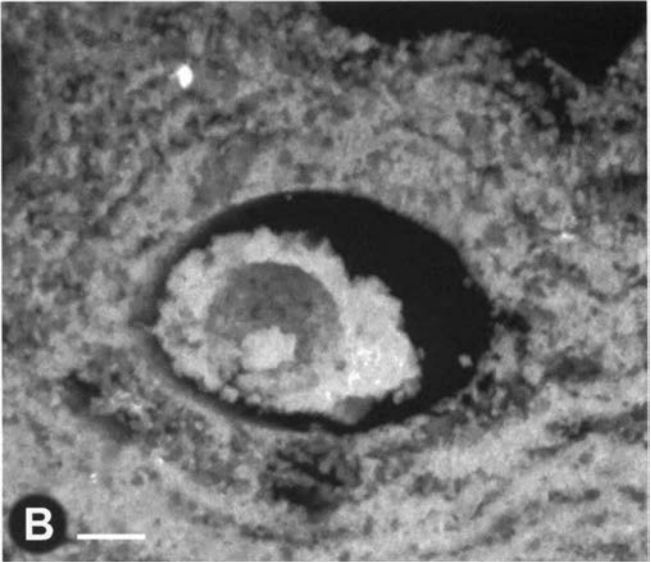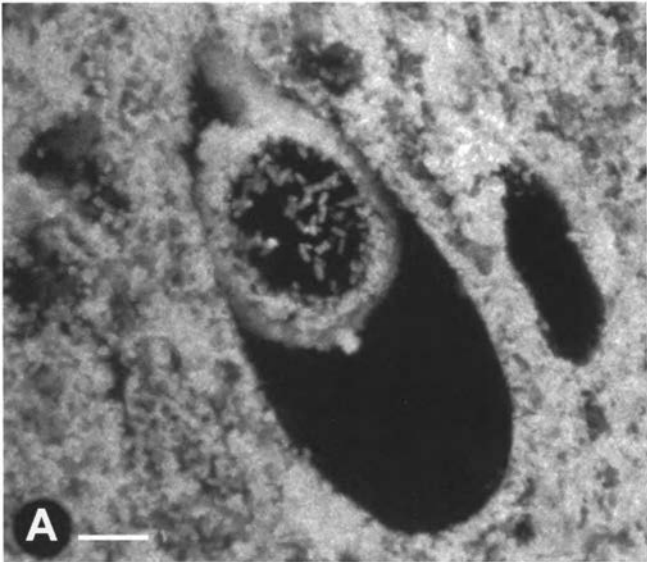
are never collapsed or deformed. In a few broken specimens, the phosphatic surface defining the vesicle shows a brittle fracture with the original curvature of the broken pieces retained (Fig. 2H, 7E, F). The fractured fragments are always directed towards the vesicle interior and, in most cases, there is a large clast in the host sediment just above or below the fractured area. The shape and size of the clast seem to correspond to the shape and size of the fracture. In specimen 2: F-62-4 (Figs. 2H, 7F) the fracture determines the shape of the internal phosphatic structure that seems accommodated to the shape of the broken vesicle. The internal structure is compressed against the side of the vesicle opposite to the breakage and shows a constriction coinciding with the most inwardly protruding broken fragment. Despite this compression, the separation distance between the internal structure and the vesicle surface is kept.
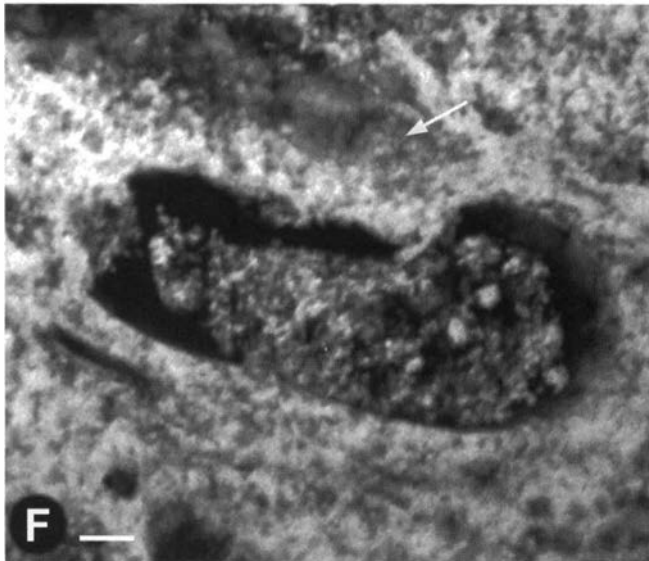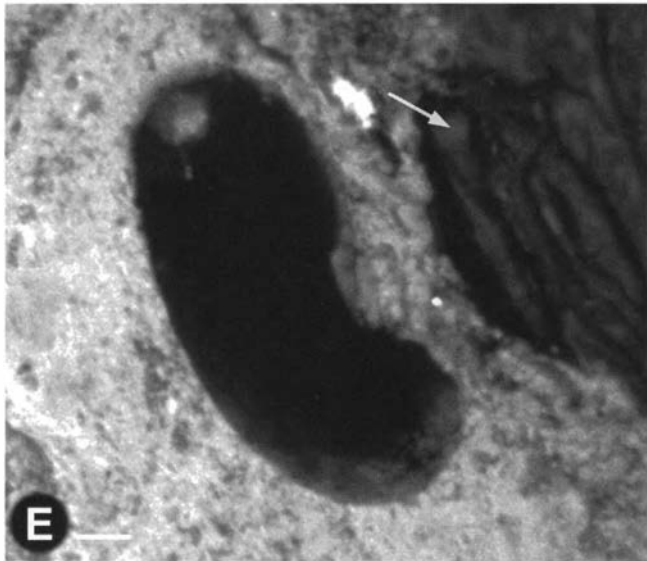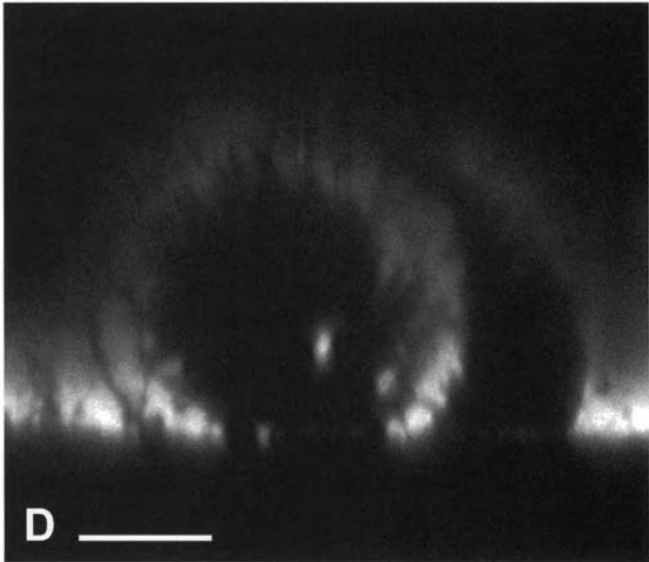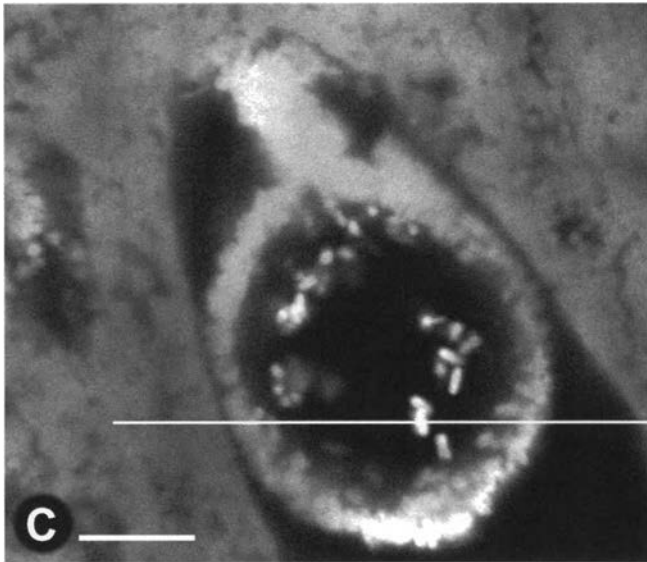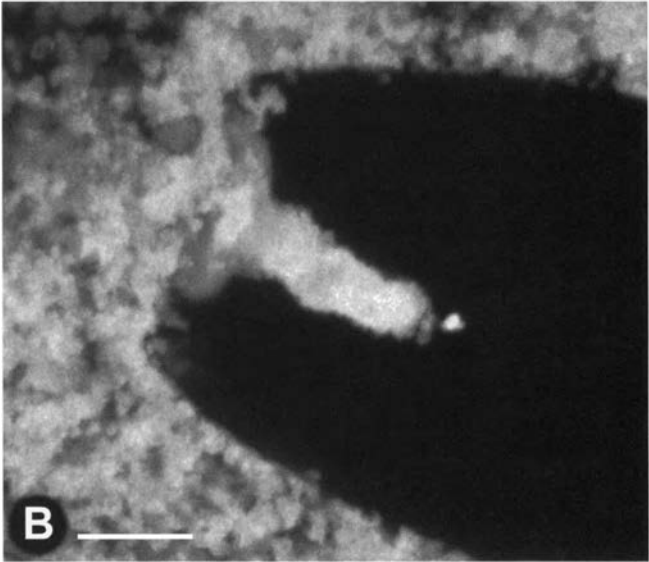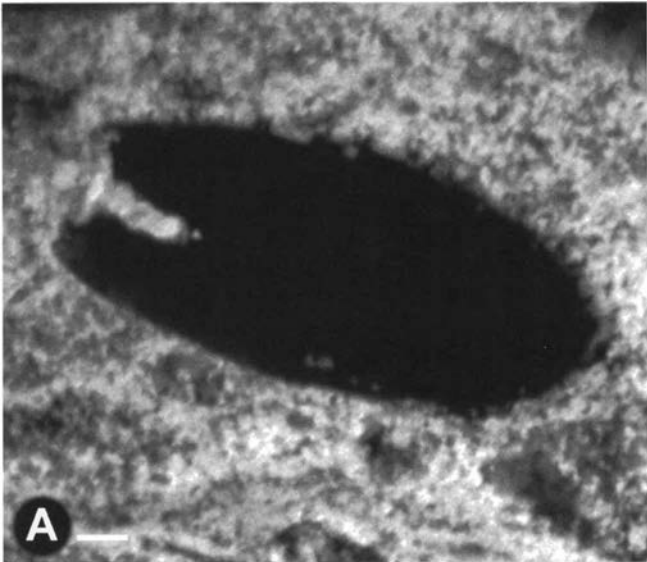
Taphonomic history of the Visingsö VSMs

The position and distribution of the VSMs in the sediment are compatible with them being suspended in the water column before deposition. The microstructure and distribution of the minerals as well as the morphology of the different mineralized parts of the microfossil allow the reconstruction of the diagenetic history of the microfossils (Fig. 9). The fact that the phosphate replicates the external morphology of the vase-shaped vesicles (Figs. 6, 7) so accurately suggests that precipitation of phosphate began in the sediment when the external wall of the organism was still intact and formed its external mould (Figs. 8B, 9C). The continuity of the phosphate between the nodule matrix and the vesicle interior through the oral pole indicates that the oral opening was unsealed, allowing pore waters to enter the vesicle. The consistent and precise morphology of the internal phosphatized area, as well as the fact that phosphate never fills the whole vesicle cavity, indicates that phosphate precipitated inside an internal compartment and formed its internal mould. Several features observable in the broken specimens (i.e. inwardly directed fractured fragments, presence of a clast in close vicinity to the broken area, the corresponding shape and size of the clast and the broken area; Figs. 2H, 7E, F) indicate that the fracture was probably formed during sediment compaction by the clast pressing against the vesicle. This implies that the fracturing occurred before the nodule was formed and the sediment was still susceptible to compression. It is possible, however, that phosphate precipitation had started

locally. In specimen 2: F-62-4 (Figs. 2H, 7F), the mould of the internal compartment reflects a plastic deformation that occurred as a response to the pressure created by the inwardly directed fracture. This deformation must have happened before phosphate precipitated in the internal compartment, since a phosphatic body is not susceptible to plastic deformation. This, along with the variability in shape and position of the internal mould in different specimens indicates that the internal compartment was defined by a flexible membrane that could be deformed and displaced inside the vesicle. The vesicle cavity must have been occupied either by fluid or was empty since the internal compartment could be displaced within it. The cavity may have escaped phosphatization by being sealed off from the pore waters by the vesicle wall and the compartment membrane (Figs. 8C, 9C). The distance between the internal and external moulds (Figs. 6A–D, 7C, D, F) is interpreted to represent the space that was occupied, when phosphatization took place, by the vesicle wall plus the membrane of the internal compartment (Fig. 9C). The existence of this space supports the suggestion that the wall was intact when phosphate precipitation took place (see above). The internal compartment membrane appears to have been attached to the inner surface of the vesicle wall at the oral pole around the opening (Figs. 8C, 9C). In some specimens, the posterior end of the internal mould is close to the vesicle surface at the aboral pole (Figs. 6E, F), which may indicate that the compartment membrane was locally attached to the vesicle wall also at that point (Fig. 8C). As mentioned above, in many specimens only the outer layer of the internal sphere is of phosphatic composition (Figs. 6A, B, D, 7C, D, 8A) and, at least in some specimens, the inner surface of this phosphatic layer is smoother and has a more regular shape than the outer one (Fig. 6B). This suggests that, at the time of phosphatization, the compartment was occupied by a spherical body. The inner surface of the phosphatic layer of the internal sphere would, thus, constitute the external mould of the spherical body (Figs. 8B, C, 9C, D). This observations also suggest that the spherical body had a smooth, rather firm surface (more so than the membrane of the compartment). Considering its location, shape and inferred surface features, this internal body is here interpreted as a reproductive cell or cyst.

The vesicle wall of the vase-shaped organism was more rigid than the membrane of the internal compartment because its external mould does not reflect any sort of plastic deformation. Rarely, the external mould shows brittle fractures. These fractures occurred early in the

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Fig. 6. Confocal microscope fluorescence images of VSMs from phosphatic nodules from the Visingsö Group, Sweden. Each image assembled from 90 horizontal scans, covering the whole volume of the specimen. Only the phosphatic structures are seen. All specimens, except 1: S-46 (B), which is an oblique section, are oriented with the oral end to the left. A. 1: Q-46-4, longitudinal section of a VSMs showing the morphology of the internal phosphatic structure. Note the separation distance between the empty internal sphere and the vesicle surface, despite the tight fit of the sphere inside the vesicle. B. 1: S-46, oblique section of a vesicle with an empty internal sphere, having a smooth and regular inner surface. The separation distance between the outer surface of the sphere and the vesicle surface is observable. C. 1: U-53-2, longitudinal section with a solid sphere connected with the oral opening by a long tube. D. 1: T-45, longitudinal section showing an empty internal sphere tightly fitted inside the vesicle. The separation between the sphere and the vesicle surface is evident. E. 1: T-45-2, longitudinal section with a tubular internal structure with constrictions along its length and ending as a narrow thread in the aboral pole of the vesicle. F. 1: T-54-2 longitudinal section showing a contorted tubular internal structure ending as a narrow thread close to the aboral pole of the vesicle.

taphonomic history of the microfossil (before the phosphatic nodule was formed and before phosphate precipitated inside the vesicle) at a time when the vesicle wall was still intact. It is thus possible that the brittle fractures were present in the original wall and therefore reflect the consistency of the original wall. Still, it is possible that phosphate precipitation had started locally, coating an unbroken vesicle wall with a thin, rigid phosphatic layer that was fractured under pressure deforming the original wall underneath. This second scenario is supported by the observation that, in the broken specimens, phosphate did not precipitate inside the vesicle through the broken area (as it could have done if the vesicle wall had an open fracture). In the broken specimens, internal phosphatization is also restricted to the internal compartment (Fig. 7F), indicating that the only connection between the exterior and the interior of the vesicle was through the oral opening.

The pattern of crystal growth and the distribution of berthierine (Fig. 2, 3B, D, 5) indicate that it started to precipitate directly on the phosphatic surfaces. Because the phosphatic surfaces are moulds that formed having as a template biological structures, berthierine could have precipitated only when both the vesicle wall and the internal compartment membrane were degraded (Figs. 9D, E). The growth pattern of the berthierine, with thin laminae radiating irregularly towards the interior of the vesicle (Figs. 3B, D) indicates that the mineral growth was not restricted in this direction, and that berthierine growth preceded quartz precipitation. Quartz was the last mineral to precipitate inside the microfossil, filling the rest of the vesicle (Figs. 2, 3, 5, 9F).

The taphonomic history of the Visingsö VSMs is summarized in Fig 9. An early diagenetic precipitation of phosphate, before significant degradation of organic matter, formed a mould of the parts of the organism that were exposed or connected to the exterior, and only the morphology of the phosphatized parts of the fossil contains relevant biological information. Both berthierine and quartz fill the void that was left after the complete degradation of the vase-shaped organism.

Morad & Al-Aasam (1994) studied the diagenetic history of the Visingsö phosphatic nodules from a geochemical point of view. They inferred the sequence of authigenic mineral precipitation that began with francolite (the cryptocrystalline phosphate) was followed by berthierine (Fe-rich phyllosilicate) and quartz, and the burial depth at which the phosphate nodules grew to be

within several decimetres to metres below the sea floor. The taphonomic history of the vase-shaped microfossils proposed in the present work (Fig. 9) is in agreement with the reconstruction of the progressive burial-diagenetic evolution of the nodules. Taking the geochemical interpretation and the present reconstruction of the vase-shaped organisms' fossilization into account, it can be concluded that the complete degradation of the most resistant materials forming the vase-shaped organism (presumably the vesicle wall) must have taken place very early during the diagenetic history, in the suboxic diagenetic zone.

Palaeobiological reconstruction

Several conclusions about the morphology (Fig. 8C) and the properties of the original material of the vase-shaped organism can be drawn from the study of the Visingsö VSMs, despite the fact that all the original material of the organism is gone. The vesicle wall was smooth and less than 0.5 μm thick (considerably thinner than the 5 to 7 μm thick wall of the specimens described by Bloeser 1985; see below). It was relatively rigid and impermeable, at least to some ions. The only opening of the vesicle wall was at the oral pole. The oral opening was about 5 μm in diameter. Inside the vase-shaped vesicle there was an internal compartment connected to the exterior through the oral opening and defined by a flexible membrane. This membrane was also impermeable to some ions. The internal compartment had an elaborate morphology, being tubular and narrow at the oral pole and extending into a more spacious spherical part that contained a reproductive cell or a cyst. The contained cell had a smooth and regular spherical surface and a relatively firm wall. The membrane of the compartment may have been locally attached to the internal surface of the vesicle wall towards the aboral pole. The vesicle cavity (the space extending between the wall and the internal compartment) was empty or filled with fluid.

Biological affinities

The biological affinities of the VSMs remain uncertain, though several ideas have been put forward since the discovery of these microfossils. The morphological resemblance to the problematic group Chitinozoa was observed

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Fig. 7. Confocal microscope fluorescence images of VSMs from phosphatic nodules from the Visingsö Group, Sweden. Only the phosphatic structures are seen. A. 1: T-41-4, longitudinal section oriented with the oral pole to the left. Image assembled from 90 horizontal scans, covering the whole volume of the specimen. The short and narrow tube is connected with the oral opening. B. Close-up of the oral pole of the previous specimen. Image assembled from 90 horizontal scans, covering the whole volume of the specimen. C. Detail of specimen 1: Q-46-4. Image corresponding to a single horizontal scan. The short tube connecting the sphere with the oral opening and the constant separation distance between the sphere and the vesicle surface are shown. Note also the continuity between the phosphate outside and inside the vesicle and how the only connection is through the oral opening. The thin white line cutting the specimen corresponds to the vertical plane scanned in the image to the right. D. Detail of specimen 1: Q-46-4. Image corresponding to a single vertical scan. The image loses resolution with depth. The internal sphere is empty and separated from the vesicle surface. E. 1: J-40-2 longitudinal section of a broken VSMs. The clast indicated with an arrow is located alongside the fractured area and its shape corresponds to the fracture. The fractured fragments retain their curvature and are directed towards the interior of the vesicle. F. 2: F-62-4 longitudinal section of a broken specimen showing an internal structure accommodated to the shape of the broken vesicle. The internal globose structure is pressed towards the opposite side of the breakage but the separation distance with the vesicle surface is retained. The clast above the fractured area is indicated by an arrow and the broken fragments are inwardly directed.
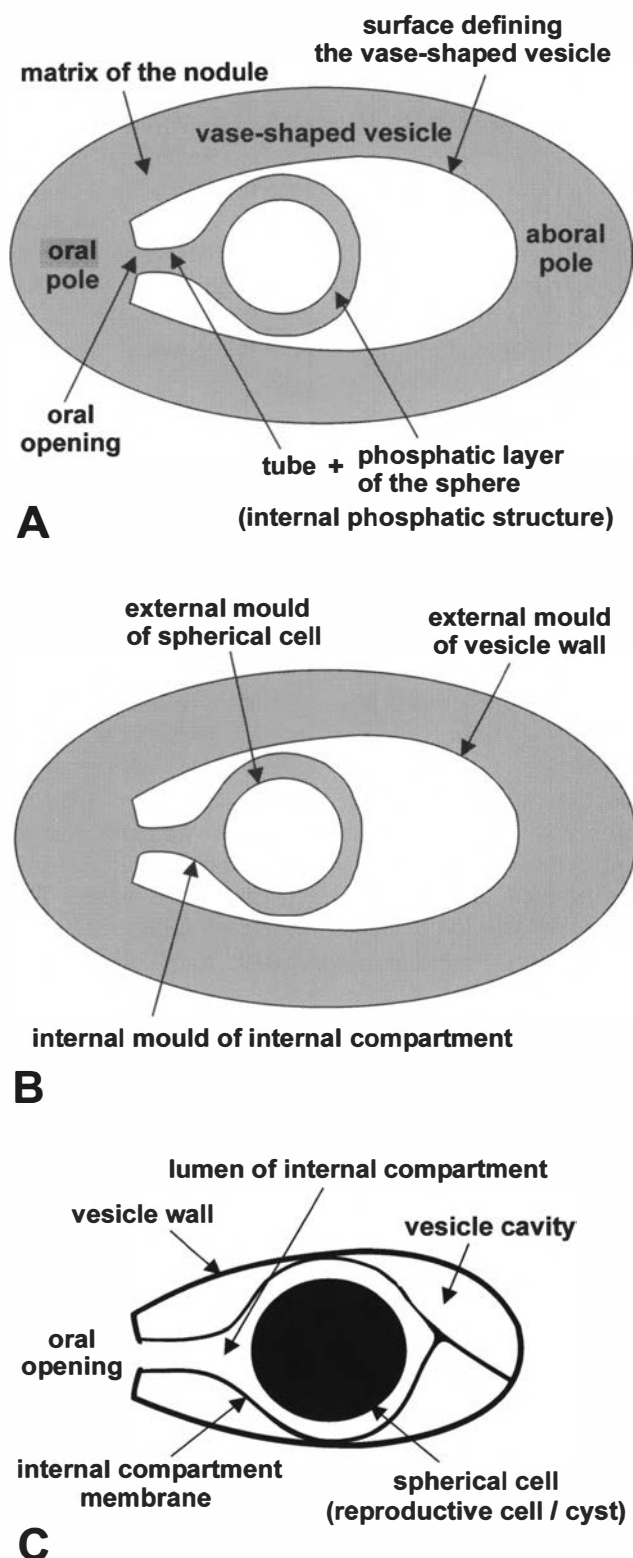
Fig. 8. A. Schematic drawing of the vase-shaped microfossil showing its phosphatic parts and the terminology used in their description. B. Interpretation of the different phosphatic surfaces as moulds of parts of the vase-shaped organism anatomy. C. Reconstruction of the vase-shaped organism showing the newly described internal structures.

Fig. 9. Schematic drawing showing the diagenetic history of the Visingsö VSMs.

and a relationship postulated (Bloeser et al. 1977), but this conclusion was challenged (Vidal 1979; Knoll & Vidal 1980) and eventually abandoned (Bloeser 1985). Until now, two contrasting hypotheses on the possible biological

affiliation of the VSMs have been considered. One hypothesis favours an autotrophic algal origin and the other a heterotrophic protistan affinity. Several modern organisms form structures morphologically similar to the VSMs vesicle, i.e. loricas of heterotrophic protists as well as some of their encystment stages (especially tintinnid cysts), 'fruiting bodies' of multicellular algae and the

encystment stages of some unicellular algae. All these possibilities have been considered by different authors since VSMs have been suggested to represent ciliate protists of Tintinnida (Fairchild et al. 1978), the oldest heterotrophic protists (Knoll & Vidal 1980), the reproductive cyst of walled amoebae (Schopf 1999), loricas of testate amoebas (Porter & Knoll, in press), as well as the encystment stage of an alga (Bloeser 1985) or the fossilized sporangium of an alga (Horodyski 1993). The internal structures described herein indicate that the vase-shaped vesicle could not by itself represent an encystment stage, either of a unicellular algae or of a heterothrophic protist. More likely, it is interpretable as a 'fruiting body' of a multicellular alga, or the lorica of a heterotrophic protist.

Although no modern multicellular algae produce structures closely comparable to VSMs, the formation of sac-like unilocular gametangia or sporangia (that contain, respectively, sexual or asexual reproductive cells) is very common among modern multicellular algae. Sometimes these sac-like structures can detach from the thallus and thus contribute to the protection and dispersal of the reproductive cells. An example of an algal gametangium frequently found in the fossil record (and which could constitute a functional analogue of VSMs) is the charophyte oogonium (common in freshwater deposits from Devonian to present). The first fossil charophyte oogonium to be described was initially identified as a foraminifer (Tappan 1980), being an example of an easily-made misinterpretation led by the morphological similarities between the tests of some heterotrophic protists and the reproductive structures of some algal groups. As mentioned above, VSMs are considered to represent planktonic organisms and they have never been reported to be attached to other fossils. Still, despite this lack of evidence and though there are no exactly comparable structures among modern algae, the possibility of them being reproductive structures of an extinct algal group cannot be ruled out (Horodyski 1993). It could be speculated that the internal structures described in this work may represent a single spherical reproductive cell held inside a spacious fruiting body by a membrane. The ability of the VSMs to float freely in the water column would have been part of the dispersal strategy of the algae.

Several groups of heterotrophic protists, particularly testate amoebae, tintinnids and some unilocular foraminifera, form loricas that are also morphologically similar to the VSMs. Although some of the mentioned organisms (especially some groups of testate amoebae) have very sophisticated mineralized tests, the three groups of protists mentioned have representatives that possess relatively simple sac-like organic tests. The living cells of both thecoamoebans and tintinnids have (unlike most foraminiferans) a very simple relation with their tests. The complete test is built after reproduction and does not grow during the lifetime of the organism. The cell is separated from the internal surface of the test, being attached to it only locally and reversibly so the test can readily be discarded at some stage of the life cycle of the organism. Both organisms are predators and capture their prey with specialized cellular structures extruded through the opening of their tests. Some species of testate amoebae have a triangular opening and others thecas with hexagonal transverse section (Deflandre 1953; Loeblich & Tappan 1964), both features comparable with those characters found in VSMs (see Porter & Knoll, in press, for a detailed comparison between testate amoebae and VSMs).

In both thecoamoebans and tintinnids, the formation of a resistant cyst inside the test is common and the lorica opening may be plugged during the encystment stage (Reid & John 1978; Deflandre 1953). Since the living cell does not usually occupy the whole volume of the test (particularly in tintinnids it may occupy considerably less than half of the test volume; Gilron & Lynn 1989), the resting cyst may also appear quite small in relation to the whole lorica volume. In some tintinnids the cyst may be enclosed within a thin, but resistant-to-decay, membrane that attaches the cyst to the lorica (Reid & John 1978). VSMs have been compared with heterotrophic protists on the basis of their external morphology, but the internal structures of the Visingsö VSMs described herein are also comparable with those found in some heterotrophic protists during the encysting stage of their life cycle.

Alternatively, a comparison can be made between the apertural apparatus of some unilocular foraminifera (Knight 1986) and the internal structures of the Visingsö VSMs. Some unilocular foraminifera possess a narrow tube that projects from the aperture towards the inside of the theca. This particular structure is similar in morphology and dimensions to the tubular proximal part of the internal compartment in the Visingsö VSMs.

Discussion

The Visingsö VSMs were previously considered to be preserved '... as chert, phosphate or, rarely, calcite casts of the original organisms ...' (Knoll & Vidal 1980, p. 209). Our study shows they are preserved as complex phosphatic moulds. Calcite has not been found in the specimens studied. Neither the berthierine coating, nor the quartz filling alone can be regarded as casts. The 'siliceous filling' (berthierine + quartz) as a whole could be regarded as a cast (a replica formed having a mould as a template) of the vesicle, but the presence of an internal phosphatic mould in many specimens complicates the matter and therefore we have preferred to avoid the term 'cast'.

Microfossils referred to as VSMs (and implied to bear similarities with *Melanocyrillium*) have been described also from several localities not listed in Table 1. A critical evaluation of these microfossils indicates that, for various reasons, they are best regarded as unrelated to the specimens referred in Table 1. Specimens reported from Brazil (Fairchild et al. 1978) should probably be regarded as dubiofossils, since they do no meet any of the criteria required of unquestionable biogenic remains (Hofmann

1972, 1987). The specimens from the Doushantuo Fm reported by Duan & Cao (1989) have been reinterpreted as non-biological structures (Zhang 1994; Zhang et al. 1998). Specimens reported from Uzbekhistan (Abduazimova 1986) and the Proterozoic of China (Yin 1980; Zang & Walter 1992; Duan & Cao 1989) are too poorly preserved to allow comparisons. The specimens reported from India (Maithy & Babu 1989) and from the Dengying Fm (Zhang & Li 1991) show distinct morphological features (e.g., wide, flaring oral ends) that have never been observed in any of the populations listed in Table 1. The occurrence of VSMs in the Uinta Mountain Group (Utah) has been reported (Nyberg 1982) but they have not been illustrated. Finally, several occurrences of VSMs have been reported from Lower Cambrian strata in China (Cao 1996, 1998; Cao et al. 1995; Duan 1985; Duan et al. 1993). These specimens have recently been reinterpreted as chancellor-iid spicules (Qian et al. 1999)

Regarding the internal morphology of the VSMs, Bloeser (1985) described and illustrated an irregular, polygonal network formed by thin carbonaceous lamellae inside the vesicle of some specimens from the Kwagunt Formation. She considered this reticulate-like organization to be the result of the diagenetic alteration of organic matter that originally could have been present inside the vesicle in the form of cell or endospore walls. The presence of internal carbonaceous membranes inside the VSM vesicle is compatible with the results presented in the present work, since we also report the existence of membranous structures inside the VSMs which could have suffered different alterations in various sedimentary environments. Horodyski (1987, 1993) reported the existence of small, organic-walled spheroids resembling acritarchs inside the vesicle of VSMs from the same formation. This led him to interpret *Melanocyrillium* as a fossilized algal sporangium. Since only one specimen is figured by Horodyski (1993; a transmitted light photograph of a thin-section) containing the reported spheroids, it is difficult to assess the significance of this feature (see Porter & Knoll in press for a re-evaluation of these internal structures).

Another disputable aspect of VSM morphology is the presence of an operculum sealing the oral opening. Only Bloeser (1985) has figured some specimens from the Kwagunt Fm with their opening plugged by a more or less amorphous body. For the Visingsö VSMs it has been argued herein that, at least at the time of their phosphatization, the oral opening was open (at least in most of the specimens) and connecting the internal compartment cavity with the external environment. The oral opening could, certainly, have been open or plugged in different specimens, depending on the stage in the life cycle of the organism.

The composition of the wall of VSMs has been a subject of controversy. The presence of a mineralized wall has been considered previously (Ewetz 1933; Vidal 1984, 1994; Vidal & Martí 1996). Ewetz (1933) reported the presence of a 'shell' of even thickness with a smooth

external and a rough internal surface in Visingsö VSMs. Knoll & Vidal (1980, p. 209), studying the populations from the same occurrence, also described the presence of a 'wall zone [...] present at the periphery of each cast'. In both studies the 'wall' was considered to be of phosphatic composition, and Knoll & Vidal (1980, p. 209) commented that '... the present mineral composition [...] may be of diagenetic origin'. There is little doubt that these authors were referring to the herein called 'berthierine layer', which coats the fossil phosphatic surfaces. It has been argued earlier in this paper that this layer was precipitated during diagenesis, once the original wall material was completely degraded. This layer is neither a replacement nor a cast of the original wall. It is a void coating and, therefore, uninformative regarding the original wall composition or structure. Another argument used to support the possible existence of a mineralized wall in VSMs is the observation that they are always preserved uncompressed and undeformed (Vidal 1994; Vidal & Martí 1996). Since some biogenic organic materials, such as lignin or chitin, are rigid, this observation alone does not confirm the presence of a mineralized wall. VSMs have been recovered as three-dimensional organic vesicles in acid-resistant residues in two localities (Bloeser et al. 1977; Vidal 1979; Vidal & Ford 1985; Bloeser 1985). In palynological preparations they are observed as uncompressed vesicles, even when the co-occurring organic-walled microfossils (e.g. acritarchs, algal remains or bacterial sheaths) are collapsed or compressed (Vidal 1979; Vidal & Ford 1985). This suggests that the vesicle wall of VSMs was originally organic, recalcitrant and rigid (Bloeser 1985). It was thus paradoxical that in many other occurrences the wall seemed to be partially or completely degraded and the VSMs were preserved as casts and moulds. This second type of preservation also suggests the presence of a rigid wall, but either composed of readily degradable organic matter or mineralized (and thus susceptible to dissolution). In the Kwagunt Fm, VSMs have been reported to occur both as organic vesicles (Bloeser et al. 1977, Bloeser 1985, Vidal & Ford 1985) and as moulds and casts (Horodyski 1987, 1993), depending on the lithology of the host rock. This further suggests that the differences in preservation of VSMs were not due to the different original composition of the wall in different populations of VSMs, but rather to the particular diagenetic processes undergone by the vesicles in different sedimentary environments. Porter & Knoll (in press), after a study of new populations of VSMs from the Kwagunt Formation and a re-evaluation of the observations of Bloeser (1985), have suggested that the organic wall of the specimens reported by Bloeser (1985) does not represent the original vesicle wall, but rather was formed by organic debris that coalesced around casts. This suggestion may explain the previously mentioned paradox regarding the preservation of VSMs, but it remains unclear how organic debris could form vesicles with coherent, continuous walls that preserve detailed morphological information and survive the process of acid maceration (Bloeser 1985).

Conclusions

The results of the present study of the VSMs from the Neoproterozoic sedimentary succession of the Visingsö Group at Lundtorp, Lake Vättern area, can be summarized as follows:

● The Visingsö vase-shaped microfossils are preserved as phosphatic moulds of the original organism filled with berthierine and quartz. The mineral berthierine is reported for the first time in these microfossils.
● The entire degradation of the vesicle was completed in the suboxic zone, early during diagenesis. The sequential precipitation of the diagenetic minerals began with phosphate, before significant organic matter degradation occurred, and it was followed by berthierine and then quartz. The last two minerals filled the voids left after the degradation of the organic matter of the organism.
● The Visingsö VSMs do not provide any information about the original composition of the vesicle wall but indicate that it was relatively rigid and impermeable. The only opening of the vesicle, the oral opening, was unsealed at the time of phophatization.
● The internal compartment described herein, extending from the oral opening and occupying part of the vesicle internal cavity, was formed by a flexible and impermeable membrane and contained a spherical reproductive cell or cyst.
● The internal structures reported herein indicate that the vase-shaped vesicle does not in itself represent an encystment stage of a protist, as previouly suggested by some authors.
● The palaeogeographic position of the Vättern Basin within low to medium palaeolatitudes and the climatic conditions prevailing during the deposition of the Visingsö Group, inferred from the sedimentary geology, palaeomagnetic, palaeobiological and diagenetic mineralogy data, suggest that the Visingsö vase-shaped organisms were living in the water column in a shallow marine, tidally influenced shelf environment in a warm climatic belt.
● The global record of the Neoproterozoic VSMs set in the context of the continental palaeogeographic reconstructions shows that their distribution at the time was confined to the tropical to temperate palaeolatitudes.
● The high content of the total organic carbon and the abundance of autotrophic planktonic protists (acritarchs) in the host sediments containing the VSMs most likely indicate high productivity (and subsequently high burial rate) in the photic zone of waters extending over the shallow shelf of the intracratonic Visingsö Basin.
● All the above data and inferences combined with the palaeoenvironments of the other VSMs occurrences (Knoll & Calder 1983; Knoll 1983; Fairchild et al. 1991) are taken to indicate that the microfossils are remains of stenothermal organisms, thriving in tropical and warm shelfal waters, with probably no significant seasonal changes in temperature, rich in nutrients (probably associated with upwelling zones) and well oxygenated.

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