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Cavernosa kapitiana (Bacillariophyceae): biogeography and morphology of the different life cycle stages

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The monospecific diatom genus *Cavernosa* is known from only two locations: Kapiti Island off the west coast of New Zealand and Ile de la Possession, Crozet Archipelago, in the southern Indian Ocean. *Cavernosa kapitiana* Stidolph is a chain-forming diatom with cylindrical frustules having an elongated valve mantle. We provide a description of the different life-cycle stages (normal frustules, globular initial cells, bell-shaped initial cells, first daughter cells of initial cells) of *C. kapitiana* based on examination of new material from Ile de la Possession and material from the type locality on Kapiti Island. The most remarkable morphological features include the complex valve face structure composed of pores, granules and ridges, the subdivision of the valve interior into marginal caverns, the complex structure of the mantle and girdle, and the presence and morphology of rimoportulae. The study concludes with an emended species description of *C. kapitiana*.

Keywords: biogeography; *Cavernosa kapitiana*; diatoms; ecology; life cycle; morphology; New Zealand; subantarctica; taxonomy

Introduction

To date, the monospecific diatom genus *Cavernosa* Stidolph 1990 has been reported from only two localities. *Cavernosa kapitiana* Stidolph was originally described from a squeezing of submerged weed and rock scrapings collected in a small stream on Kapiti Island, New Zealand (Stidolph 1990). More than a decade later, *C. kapitiana* was identified in some soil samples from coastal cliffs on Ile de la Possession, the main island of the Crozet Archipelago, situated in the southern Indian Ocean (Van de Vijver et al. 2002). Originally regarded as belonging to the genus *Melosira* s.l., a range of features suggested a separation from the latter justifying the description of a new genus (Stidolph 1990). The most prominent characters of *Cavernosa*, distinctly recognizable under the light microscope, include the caverns on the valve interior and a distinct labiate process in the valve centre. Spaulding and Kociolek (1998; p. 135) defined the term 'cavern' as being an undulation of the valve interior, evident in both valve and girdle views.

The genus *Cavernosa* is similar to some genera of the Melosiraceae, Aulacoseiraceae and Orthoseiraceae (Round et al. 1990). Table 1 lists the main discriminating features between the genera *Cavernosa*, *Orthoseira*, *Melosira* and *Aulacoseira*. The presence of the caverns is only shared with a few taxa in the genus *Orthoseira* (Spaulding & Kociolek 1998). *Orthoseira* can, however, be separated by the presence of the so-called carinoportulae in the valve centre, whereas *Cavernosa* possesses a typical rimoportula.

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Table 1 Morphological characteristics of *Cavernosa* and similar genera.

	Cavernosa	*Orthoseira*	*Melosira*	*Aulacoseira*
Presence of caverns	Yes	Yes but in few taxa only	No	No
Valve face structure	Complex	Regular or complex	Regular or complex	Regular
Mantle structure	Deep, four zones	Deep, uniform	Deep, uniform	Deep, uniform
Copulae	Open, ligulate, perforated	Open, ligulate, perforated	Open, ligulate, perforated	Open, ligulate, perforated
Spines	Ring near valve face margin	Ring near valve face margin	Small spines on valve face margin	Ring of linking spines near valve face margin[1]
Ringleiste	Yes	No	No	Yes
Rimoportulae	1; initial cells 2	No	Several–many	Several
Carinoportulae	No	Yes	No	No

[1] *Aulacoseira* possesses beside linking spines also separation spines.

A recent study of fresh and cleaned material from Ile de la Possession revealed a number of morphological structures in *Cavernosa* that, to date, were not described from the type material collected on Kapiti Island, among them the first observation of cell chains and the morphology of initial cells. In this article, we offer a detailed light and scanning electron microscope study of the type material of *C. kapitiana* from Kapiti Island and from samples taken at Ile de la Possession. The different stages of the life cycle of *C. kapitiana* that could be described from the studied samples show certain similarities with the life cycle of other Melosiraceae (Crawford 1975, 1981a, b), but the complete life cycle is not yet fully understood. However, the extended knowledge of the ultrastructure, morphology, life cycle and biogeography of *C. kapitiana* is considered in an emended diagnosis.

Materials and methods

For this study, fresh material was sampled from Ile de la Possession (Crozet Archipelago, southern Indian Ocean) during the austral summer of 2002. In addition, cleaned original material – a subsample of the true type material – used by Stidolph from Te Rere Stream, Kapiti Island, New Zealand, was studied for comparison (Fig. 1, Table 2)

Microscopic slides of fresh, untreated material were prepared with deionized water and studied with an Olympus BX51 light microscope at a magnification of × 400 or × 1000. For the study of the frustule and valve structure, the samples were prepared following the method of Van der Werff (1955). Small portions of the samples were cleaned with 37% H_2O_2 on a hot plate at 80°C for about 1 h. The reaction was then completed by adding potassium permanganate ($KMnO_4$). Following digestion and centrifugation, the cleaned material was diluted with deionized water to avoid excessive concentrations of diatom valves on the microscopic slide. Cleaned diatom valves were mounted in Naphrax™ (Brunel Microscopes Ltd., Chippenham, UK). Examination of the diatom slides was carried out with an Olympus BX51 light microscope equipped with an UPlanFl × 100/1.30 oil immersion objective and Differential Interference Contrast (DIC-Nomarski), and the Olympus Colorview I digital imaging system. Scanning electron microscopy (SEM) examination of valves of *Cavernosa* was carried out with a JEOL-5800LV at 20 kV at the National Botanic Garden of Belgium in Meise, Belgium. The studied type material and microscopic slides are stored at the National Botanic Garden of Belgium (BR), Department of Bryophytes & Thallophytes.

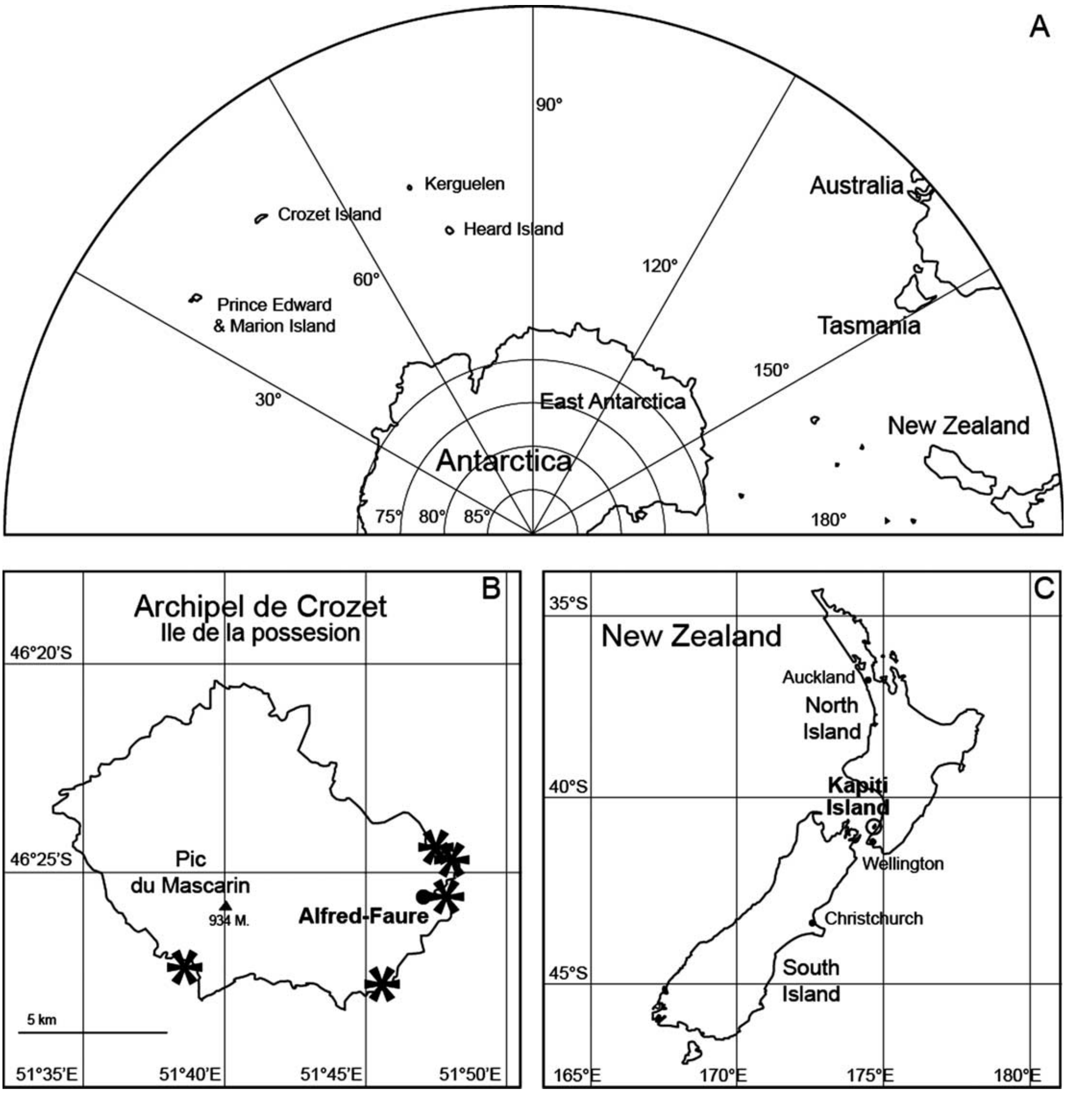

Figure 1 Map of the investigated locations. **A,** Part of the southern hemisphere with the locations of the Crozet Archipelago and New Zealand. **B,** Ile de la Possession (Crozet Archipelago) with the locations where *Cavernosa* was found. **C,** New Zealand showing the position of Kapiti Island.

Observations

The study of a population of *C. kapitiana* from Ile de la Possession and re-examination of the type material results in the description of four stages of the life cycle: bell-shaped initial cells, globular initial cells, cells originating from the first division of an initial cell with a globular epivalve and a flat concave or convex hypovalve, and vegetative cells with two flat concave or convex valves. Auxospores or siliceous scales of the auxospore wall, known, for example, from various species in *Melosira* (Round et al. 1990) were not observed, which does not necessarily indicate that siliceous-walled auxospores are not formed by *Cavernosa*.

Table 2 Material of *Cavernosa kapitiana* examined for this contribution.

Locality	Material	Habitat	Collection date	Collector	Light microscopy slide no.	Scanning electron microscopy sample no.
Kapiti Island (New Zealand), Te Rere Stream	Mixed sample of squeezings of submerged weed, rock scrapings, silt	Freshwater stream and pool in rocky outcrop	31/01/87	S.R. Stidolph	FW-217A (type material)	FW-217A
Ile de la Possession (southern Indian Ocean)	Soil scraping in shaded cliff scratches	Rocks close to spray zone of the sea	26/01/02	B. Van de Vijver	BA158	BA158

Ile de la Possession populations

Normal vegetative valves

Colony and cell form. Cavernosa kapitiana is a chain-forming diatom (Fig. 2A,B). In untreated material from Ile de la Possession, chains composed of up to 14 cells were observed. This is in contrast to the original description of Stidolph (1990) who found no evidence for chain

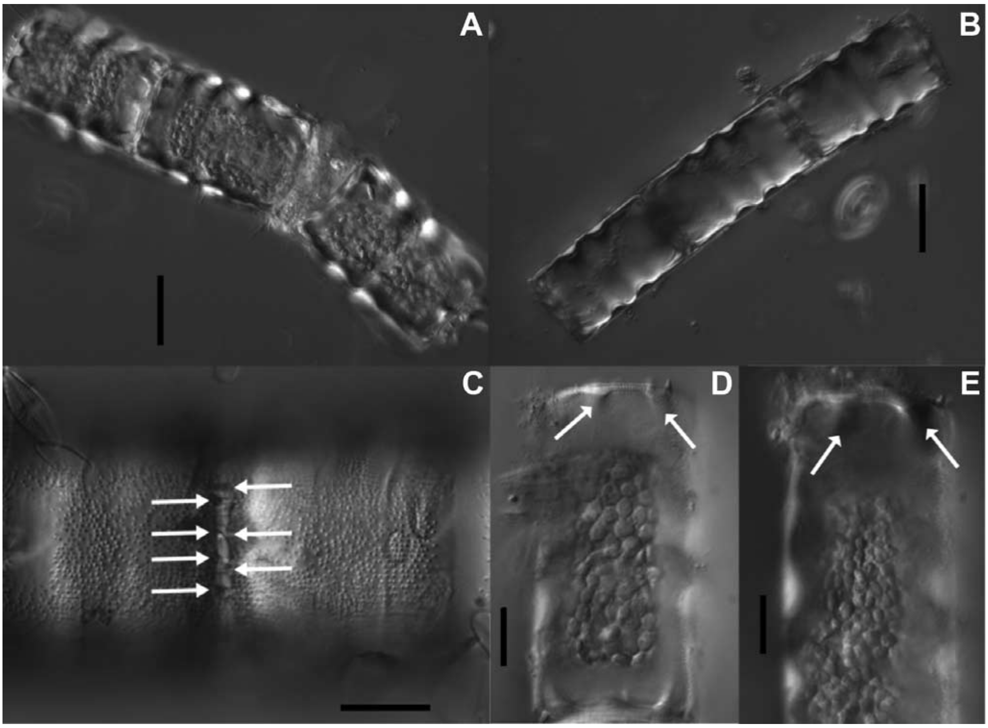

Figure 2 Chain forming (A–C) and plastids (A,D,E) in *Cavernosa kapitiana* from Ile de la Possession. **A–C,** Chains linked by spines showing multiple plastids per cell. The arrows in C indicate the position of linking spines. **D,E,** Position of the caverns indicated by arrows. Note also the large number of discoid plastids. Scale bars, 20 µm (A,B), 10 µm (C–E).

formation in the Kapiti Island material and stated '... it is considered likely that *C. kapitiana* lives in a solitary state' (Stidolph 1990; p. 99). However, Stidolph studied material cleaned using permanganate, possibly indicating that chain-forming cells in *Cavernosa* are linked by organic threads which were dissolved by the permanganate oxidation method. Frustules in the chains may also be linked by the marginal ring of unevenly spaced spines (Fig. 2C; arrows) which is, however, not clearly visible on our images. Spine morphology and arrangement clearly differ from genera such as *Aulacoseira*, which are known to possess typical linking spines (Round et al. 1990). Cells of *C. kapitiana* have a cylindrical form and contain a high, but variable number of small discoid plastids (Fig. 2A,D,E). The typical internal caverns of *Cavernosa* are also clearly visible in untreated samples (Fig. 2D,E; arrows). Frustules have a cylindrical outline with a diameter ranging from 21 to 52 µm ($n = 25$) and a frustule pervalvar length of 45–64 µm ($n = 15$).

Valve exterior. Valve faces of *C. kapitiana* are slightly to moderately concave or convex (Fig. 3C,D and Fig. 4A,B). The valve face is ornamented by three different structural elements: pores, granules and ridges. Simple, small, rounded pores (Fig. 4C–E) are surrounded by a thickened siliceous funnel-shaped rim of variable circumference, ranging from almost round to oval to polygonal (Fig. 4C,E). Pores on the valve face are usually irregularly scattered with a distinctly higher density near the valve margin compared with the valve centre (Fig. 3C,D). Granules are very small rounded projections that are scattered mainly in the central part of the valve face and around the spines (Fig. 4C). The third structural feature of the valve face includes a system of distinctly developed ridges that form a meandering pattern (Fig. 4C,E). These ridges are mainly developed in the inner two thirds of the valve face and are less prominently present along the valve margin. The convex valves are obviously less densely ornamented than the concave valves (compare Fig. 4A with 4B). The valve mantle is relatively high and perforated by an irregular pattern of well-differentiated pores. In some cases, mantle pores are also arranged in long pervalvar rows (Fig. 3A,B). The valve mantle is always deeper than the valve diameter and is composed of several (usually four) distinct zones (Fig. 5A). The uppermost zone comprises approximately three-fifths of the entire mantle depth and is irregularly perforated (Fig. 5A, I). The diameter of the mostly rimmed pores decreases with increasing mantle depth. Areas between the pores are partly covered by small raised plates. The density and size of these raised plates also increase with mantle depth. The second, underlying zone is marked by the presence of fairly larger and thicker raised plates and mostly non-rimmed pores some of which are perforating the plates (Fig. 5A, II). The subsequent zone of the mantle comprises a narrow band that is characterized by very densely packed raised plates lacking any perforation (Fig. 5A, III). This band probably corresponds to a distinct solid thickening, the so-called ringleiste, which is always present on the valve interior (Fig. 6B). The lowermost zone has a totally different structure, consisting of regular rows of pores that fuse towards the mantle edge to form elongated, slit-like openings (Fig. 5A, IV). The very edge of the mantle has an almost fimbriate structure (Fig. 5B). In some cases, the mantle is apparently stepped (Fig. 5A; arrow) although this feature has not been observed on all studied valves. Such stepped mantles – the so-called Müller step – were observed within the Melosiraceae, Paraliaceae and the genus *Eunotia*, and their formation has been described in detail, for example in *Ellerbeckia arenaria* (Crawford 1981b) and *Aulacoseira italica* (Crawford et al. 2003). The steps originate during vegetative cell division when the mantle of the new hypovalves is formed close to the cingula of the parent valves (Crawford 1981b; p. 258, Fig. 4). The girdle of the frustule is composed of several porous copulae (Fig. 5A). The copulae are open and entirely covered by

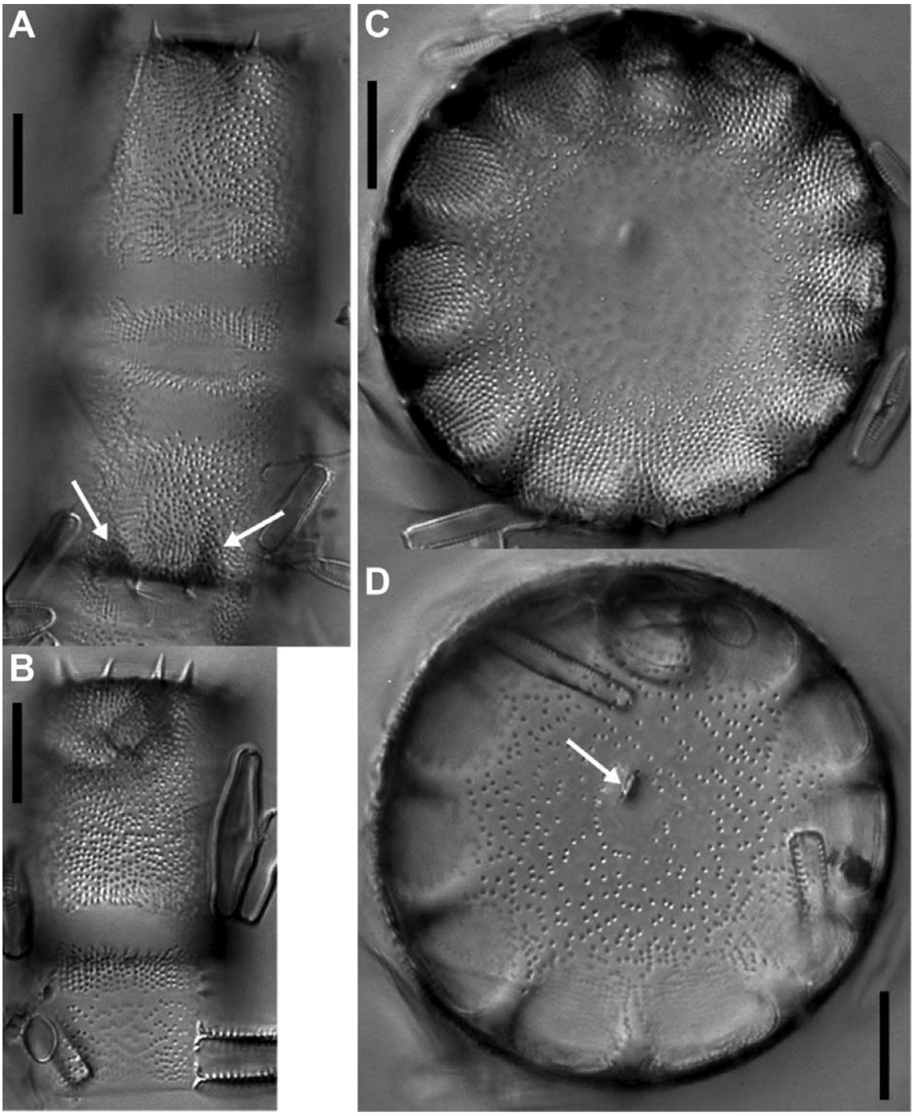

Figure 3 Light micrographs of *Cavernosa kapitiana* from Ile de la Possession. **A,B,** Entire frustules showing the zonation on the mantle and the presence of spines and caverns (indicated by arrows). **C,D,** Two micrographs of the same valve at different focus level showing the surface structure (C), the caverns (D) and the rimoportula in the valve centre (D, arrow). Scale bars, 10 µm.

small granules (Fig. 5C). The maximum number of copulae observed is four. The mantle/valvocopula transition is distinct (Fig. 5A). Each copula, apart from the valvocopula, has a relatively long ligula that fits into the slit of the adjacent advalvar copula (Fig. 5A,B). Fig. 5B shows the differentiation of a copula into a fimbriate, thin pars interior and a more solidly silicified pars exterior. The pars interior is finely perforated on its inner part, whereas the pars exterior shows a dense pattern of irregularly scattered pores bordered by a hyaline band at its abvalvar edge (Fig. 5A). A marginal ring of unevenly spaced spines is usually present

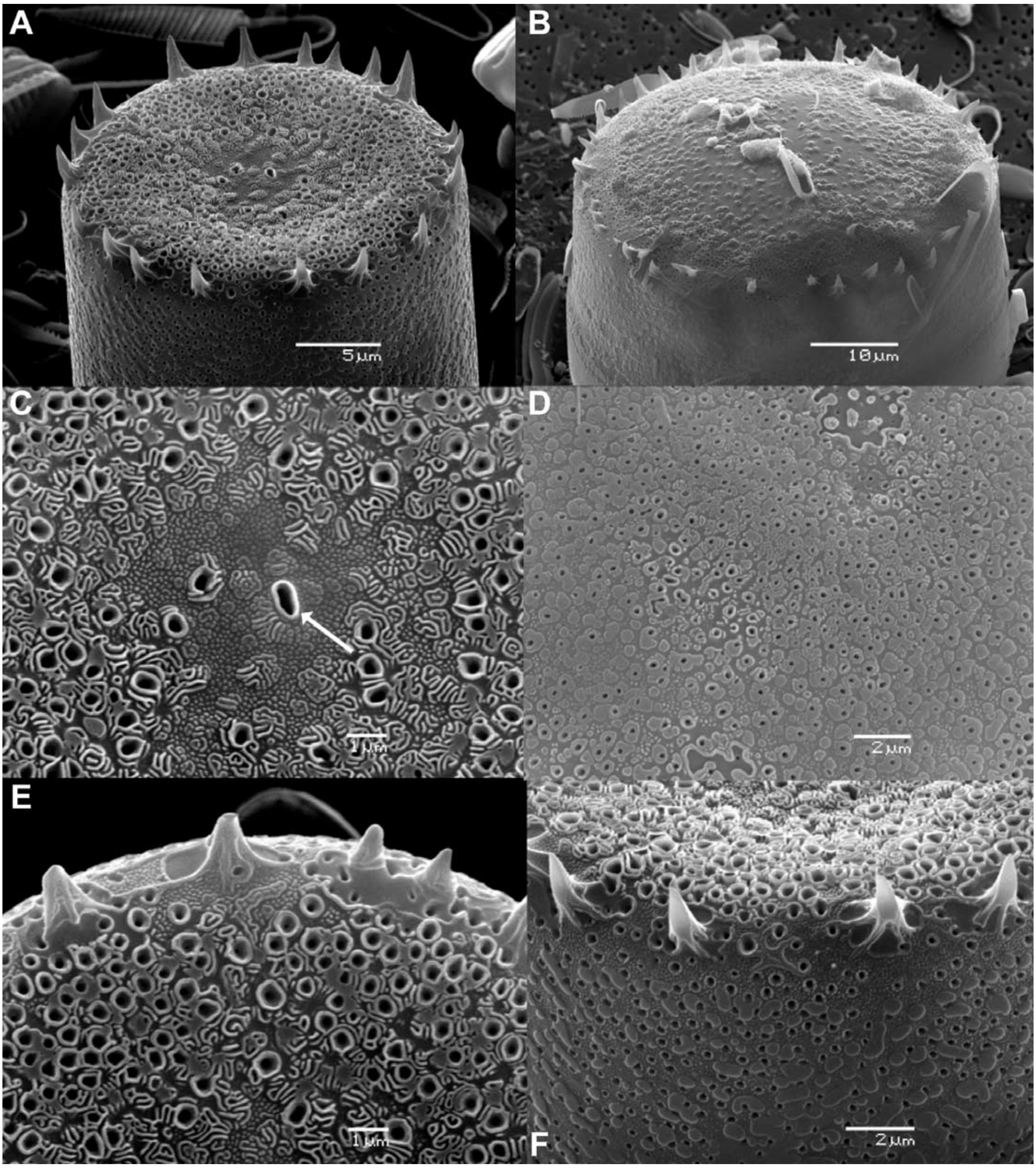

Figure 4 Scanning electron micrographs of *Cavernosa kapitiana* from Ile de la Possession. **A,** Concave valve face. **B,** Convex valve face. **C,** Detail of the surface structure of a concave valve showing three different ornamentation elements: pores, granules and ridges. The arrow indicates the position of the rimoportula. **D,** Surface structure of the valve mantle. **E,** Detailed valve face view of the stellate spines. **F,** Valve–mantle transition with the position of the spines. Scale bars, 10 µm except for (C,E), 1 µm.

(Fig. 3B). Spines are mostly thick, acute, volcano-shaped and generally slightly curved towards the valve centre, and have a stellate bottom part (Fig. 4A,E,F) on which often a complex ornamentation of granules and ridges is visible. Simple, completely solid spines without a stellate base do sometimes also occur (Fig. 4E). Valves possess usually one (or two) rimoportulae

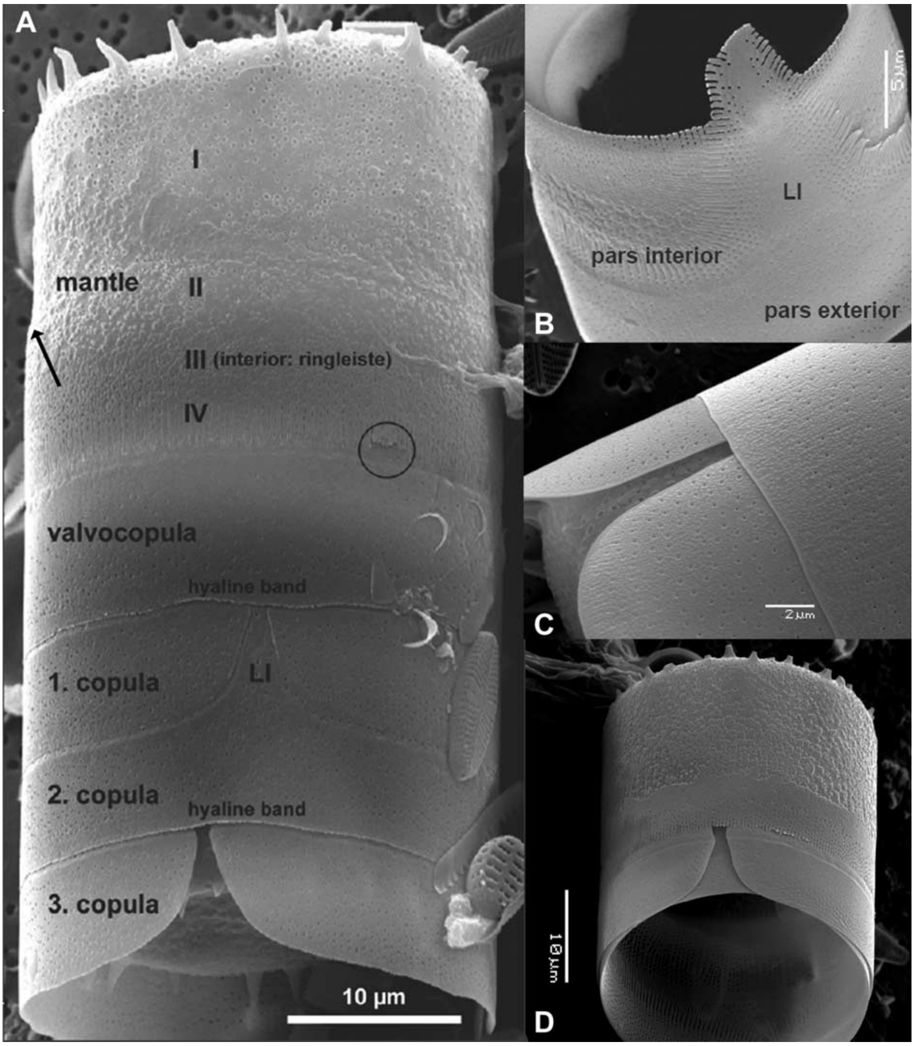

Figure 5 Scanning electron micrographs of the girdle structure of *Cavernosa kapitiana* from Ile de la Possession. **A,** Entire mantle and girdle structure with the typical zonation. The different parts of the mantle and the girdle are indicated. The area in the black circle shows the structure of the valvocopula under the mantle. **B,** Detail of the valvocopula with the fimbriate pars interior and the pars exterior. **C,** Slit of a copula in which the ligula of the following abvalvar copula fits. **D,** Interior view of the girdle. Scale bars, 10 µm.

(labiate processes) the external opening of which is usually clearly defined by its shape and relatively isolated position in the valve centre. The rimoportula is usually easily recognizable in both the light (Fig. 3D, 8B; arrows) and scanning electron (Fig. 4C; arrow) microscope. The oval to elliptical opening is also surrounded by a thickened raised rim (Fig. 4C, arrow). There are also examples of vegetative cells with two rimoportulae in the valve centre (Fig. 6B, 8B; see section ‘Initial cells’ below). Near the valve face–mantle junction, dark structures are visible that represent the internal ridges defining the so-called internal caverns (Fig. 3A; arrows). The number of caverns is variable and ranges from 6 to 11 per valve ($n = 20$). In these caverns,

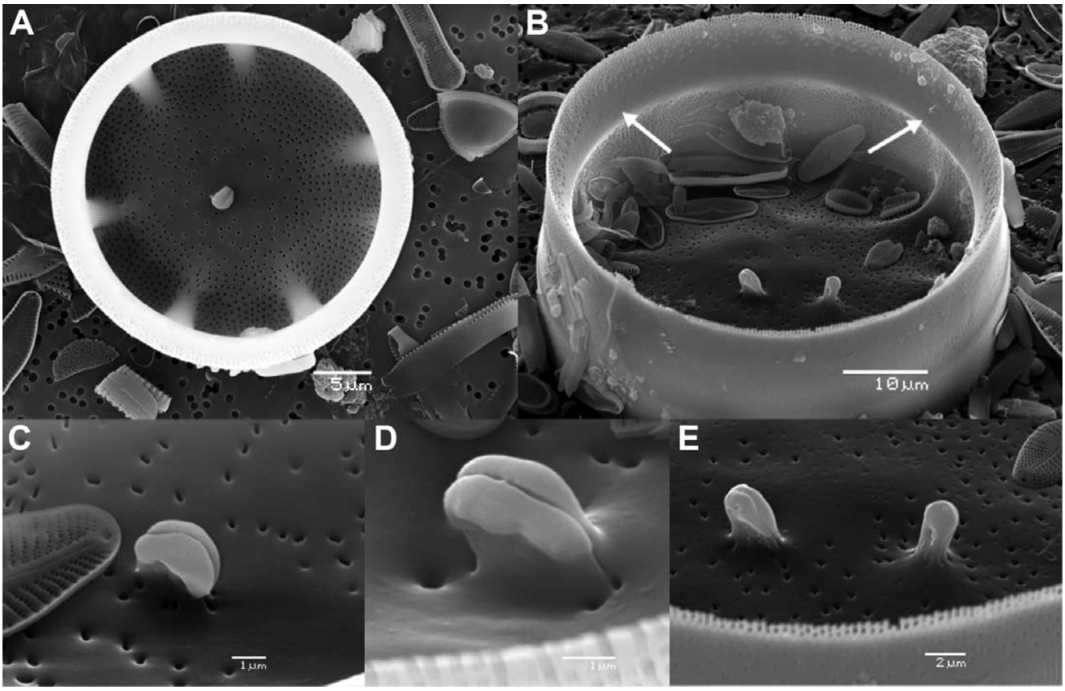

Figure 6 Scanning electron micrographs of the internal valve and rimoportulae of *Cavernosa kapitiana* from Ile de la Possession. **A,** Valve interior showing the caverns and one central rimoportula. **B,** Presence of two rimoportulae on a valve emerging from the first division of an initial cell. The arrows indicate the ringleiste. **C,D,** Structure of the rimportula seen from different angles. **E,** Detail of the two rimoportulae in (B). Scale bars, 10 µm except for (C, D), 1 µm.

the pores are usually arranged in short, parallel to slightly radiate rows (Fig. 3C, 6A) and the solid ridges separating them are always distinctly visible in valve view (Fig. 3D).

Valve interior. The internal valve view of *C. kapitiana* is marked by the presence of caverns. Each cavern represents a hollow that is bordered by two solidly silicified, imperforated braces (Fig. 6A). The interior of the caverns is densely packed with the rounded, minute inner openings of the pores. The valve centre is much more loosely perforated. Pores are seemingly not occluded by vela or hymenes (Fig. 6A,C). The rimoportula is internally shaped as a typical short-stalked labiate process with a single slit (Fig. 6C,D). Vegetative valves with two central rimoportulae were occasionally also observed (Fig. 6B,E) and are believed to be the first daughter cell of an initial cell (see sections 'Light microscopy' above and 'Initial cells' below). The internal view also unveils the presence of a ringleiste just beyond the mantle edge (Fig. 6B; arrows). As considered above, this ringleiste corresponds with the externally visible narrow band on the mantle that is entirely covered by raised plates (see above and Fig. 5A, III).

Initial cells

In addition to vegetative cells with concave or convex valves, globular frustules were also observed. These represent initial cells (Fig. 7A–D) which show the same ornamentation elements as normal vegetative cells but obviously have a much denser concentration of pores (Fig. 7C). The valve face of initial cells is also

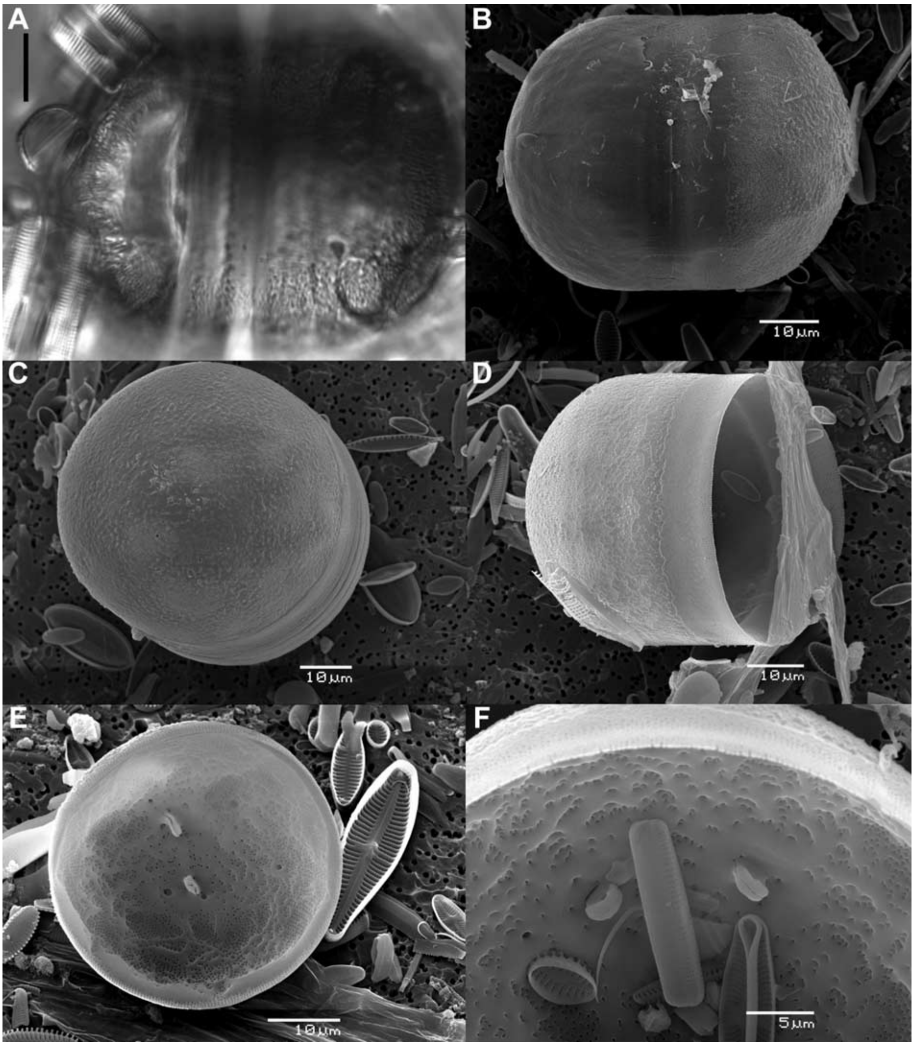

Figure 7 Light and scanning electron micrographs of a globular initial cell of *Cavernosa kapitiana* from Ile de la Possession. **A,** LM view of complete initial cell. **B,** SEM view of a complete initial cell. **C,D,** SEM view of external surface structure of an initial valve. A small ringleiste is visible on (D). **E,** SEM internal view of an initial valve with the presence of two rimoportulae and only weakly developed caverns. **F,** SEM detail of the internal surface structure showing an irregular pattern of areolae openings and two rimportulae. Scale bars, 10 µm except for (F), 5 µm.

partly covered by raised plates (Fig. 7B–D), a feature that is lacking on the valve faces of vegetative cells. Spines are lacking on initial cells of *C. kapitiana*. The valve mantle is distinctly shorter than in vegetative cells but basically shows a similar succession of zones (Fig. 7B,D). The valve interior of initial cells shows a complex pattern of caverns that are bordered by pronounced braces and cover the entire valve interior (Fig. 7E). The caverns are densely packed with simple pores. The surface of the braces and the space between the caverns are unevenly perforated by pores that are similar in shape and size to the pores in the caverns. Initial cells usually have two rimoportulae with short-stalked labiate processes, located approximately halfway between the valve centre and the margin (Fig. 7E,F). A well-developed ringleiste is present beyond the mantle edge (Fig. 7E,F). The genus *Orthoseira* possesses a similar type of initial cells with a round profile, short mantle and lacking spines (Crawford 1981a).

Cells resulting from the first division of the initial cell

The first cell division of an initial cell will result in the formation of two new hypovalves back to back. One of these cells with a normal valve and an initial cell valve is shown in Fig. 8A. The globular valve displays the morphology of a typical initial cell and lacks, for example, any spines, whereas the normal valve of this cell possesses a marginal ring of well-developed spines (Fig. 8A). The flat valves of the combined initial/normal cells possess two rimoportulae in the valve centre (Fig. 6B,E and 8B) as is typical for true globular initial cells. The formation of a single rimoportula in normal valves becomes likely realized only in successive generations. However, there is not (yet) enough evidence from our study that all first daughter cells of initial cells possess two rimoportulae and likewise the principle behind this observation remains unclear. It might be related to valve size, implying that larger valves tend to have two rimoportulae and smaller valves only one.

Bell-shaped initial cells

Cells with a bell-shaped outline were observed in both LM and SEM samples (Fig. 9A–D). These valves (are they the epivalve?) presumably belong to initial cells that were formed by auxospores possessing a projection or ‘Nabel’ *sensu* Müller (1890) and Krammer & Lange-Bertalot (2004). Such projections may form if retraction of the protoplast from the mother cell remains incomplete during initial cell formation. This phenomenon was described for example in *Melosira* (Crawford 1975, Plate 3, Figs. 14, 15). Ehrlich et al. (1982) presented with *Arataulus laevis* a nice example of funnel-shaped initial epivalves. The funnel-shaped part of such valves in *C. kapitiana* shows a subdivision in zones that is similar to the one of normal valves (Fig. 9B) including the narrow hyaline band that corresponds to the position of

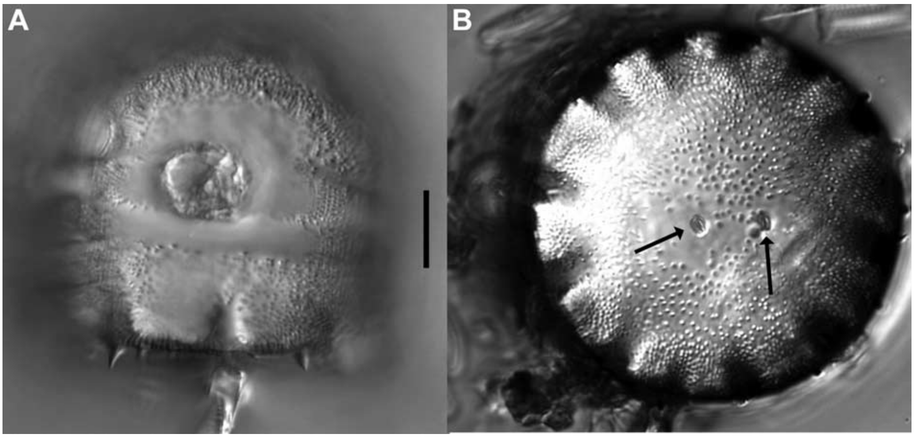

Figure 8 Light micrographs of the cell following the first division of an initial cell of *Cavernosa kapitiana* from Ile de la Possession. **A,** Girdle view of a cell with a globular valve and a flat valve. **B,** Face view of a flat valve with two rimoportulae in the valve centre (arrows). Scale bar, 10 µm.

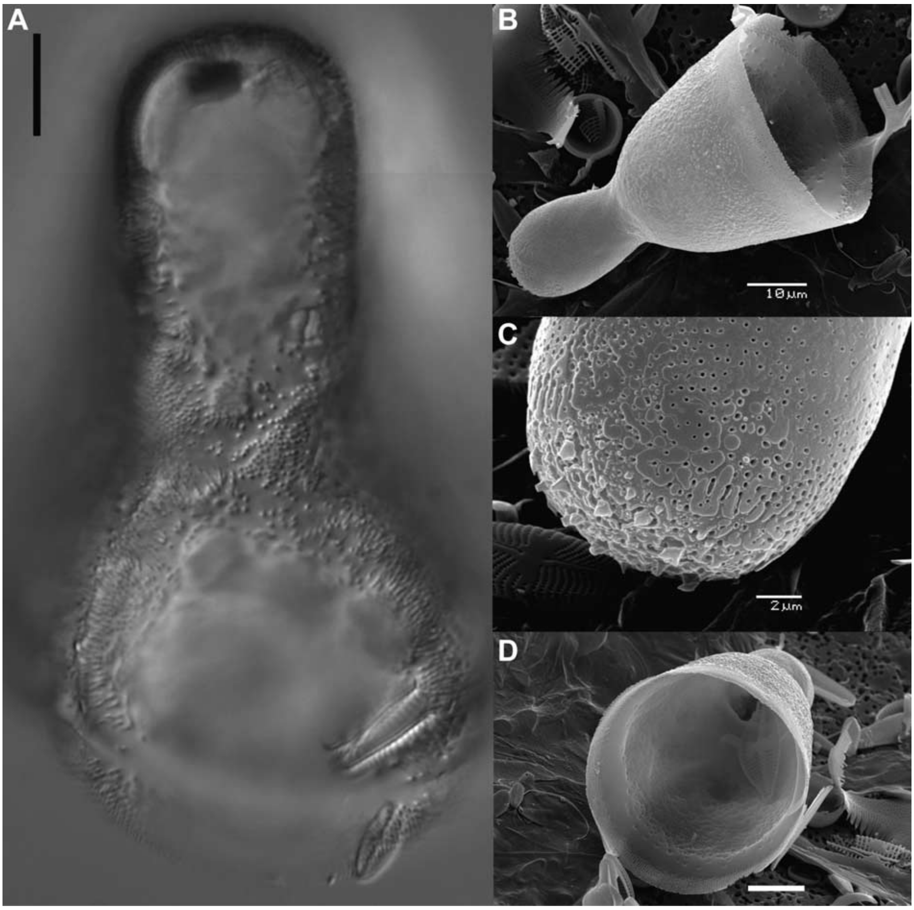

Figure 9 Light and Scanning electron micrographs of a bell-shaped initial cell of *Cavernosa kapitiana* from Ile de la Possession. **A,** LM view of a bell-shaped initial cell. **B,** SEM view of a bell-shaped initial valve. **C,** SEM view of external detail of the handle part of the bell-shaped initial valve. Spines are clearly absent and the surface ornamentation is irregular. **D,** SEM internal view of a bell-shaped initial valve. Scale bars, 10 µm except for (C), 2 µm.

the ringleiste on the valve interior (Fig. 9D). Similar to the globular initial cells, the valve interior is subdivided into numerous caverns (Fig. 9D). The handle-shaped part of bell-shaped initial valves is densely but irregularly perforated and the distal end of the handle is covered by an irregular pattern of siliceous plates and granules (Fig. 9C). Small and simple spines are visible on the valve face of the handle. Rimoportulae were not observed in the bell-shaped initial valves.

Kapiti Island population (= type population of original material)

The study of frustules and valves of the type population of *C. kapitiana* from Kapiti Island, New Zealand, revealed several morphological differences compared to cells of the population from Ile de la Possession. Table 3 summarizes the main morphometric and morphological characteristics of *C. kapitiana* based on the observations of Stidolph (1990) and on our own observations of the type (Fig. 10) and Ile de la

Possession material. Stidolph (1990) did not report the presence of chains of *C. kapitiana*, whereas in the Ile de la Possession populations chains of up to 14 cells were observed. Cell chains were similarly not found in our re-study of the type material. Stidolph considered the presence of only one rimoportula and the limited number of marginal spines as being indicative for a solitary life form of *C. kapitiana*. A re-examination of the spines in the type material confirms this point of view. Spines are usually small and basic and their number is rather limited (Fig. 10B–D) compared with the Ile de la Possession population, which has numerous large stellate spines. The valve surface of cells in the New Zealand population is less distinctly ornamented (Fig. 10D). The typical siliceous ridges, so prominently present in the Ile de la Possession population, are almost entirely absent in the New Zealand population. The raised rims surrounding the pores are much lower and less pronounced in valves of the type material. The structure of the mantle and the cingulum of frustules in type material is almost identical with the frustules from Ile de la Possession.

Stidolph (1990; p. 100, 103) reported a nipple-like process, which he named papilla, at the advalvar end of the ligula. However, Stidolph did not clearly indicate whether this is a feature occurring in all frustules. A papilla-like structure was not observed in cells of the Ile de la Possession population and is also lacking in cells

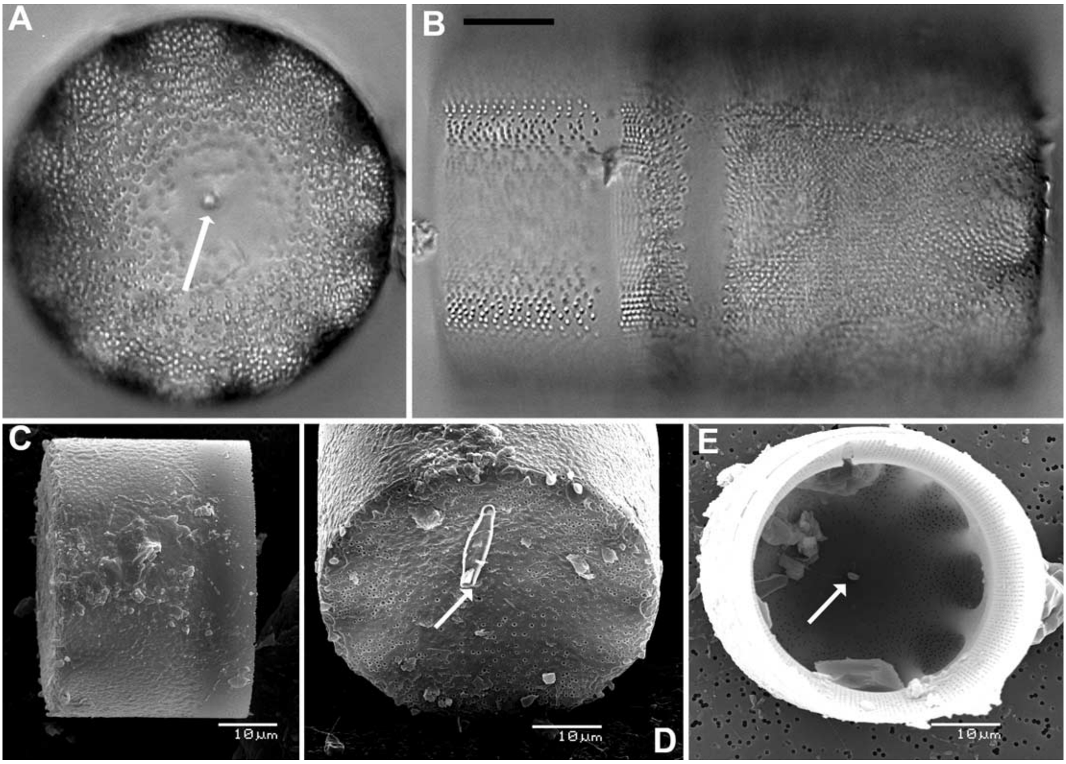

Figure 10 Light (A,B) and scanning electron (C–E) micrographs of *Cavernosa kapitiana* from the type population on Kapiti Island, New Zealand. **A,** LM valve view with the presence of a rimoportula (arrow) and the typical caverns. **B,** LM girdle view showing the mantle and part of the girdle. **C,** SEM picture of the mantle. Note the comparably small spines. **D,** SEM valve face view of a concave valve with the opening of the rimoportula (arrow) and the typically ornamented surface structure. **E,** SEM internal view with the position of the rimoportula (arrow) and the caverns. Scale bars, 10 µm.

of the re-examined material from New Zealand. Thus, the significance of such papillae remains questionable at the moment, as the obviously single observation by Stidolph could also be an occasional malformation. Initial cells were not reported in Stidolph's original description but were found in the re-study of the type material.

Ecology

Information on the ecological requirements of *C. kapitiana* is sparse, as environmental parameters were not recorded, partly due to the nature of the material sampled on Ile de la Possession. The two known populations of the species were described from rather different environments. On Kapiti Island, *C. kapitiana* is described as having a benthic life form in freshwater streams and pools (Stidolph 1990). The fact that the species has been collected in streams indicates that it might tolerate at least a certain degree of turbulence. On Ile de la Possession, *C. kapitiana* was collected in a rocky, benthic environment close to the spray zone of the Indian Ocean, indicating that the species is likely salt tolerant. Furthermore, living in the spray zone may lead to temporal periods of aerophilic life and desiccation and this might explain the generally robust silicification of the cell wall of *C. kapitiana* in the samples from Ile de la Possession. The largest population was found living in dry soil on a rocky ridge in the cliffs covered with a sparse vegetation of mosses.

The abundance of *C. kapitiana* on Ile de la Possession in all examined populations was < 5%. There, *C. kapitiana* is mostly associated with *Sellaphora tumida* Van de Vijver et Beyens, *S. subantarctica* Van de Vijver et Beyens, *Stauroneis pseudomuriella* Van de Vijver et Lange-Bertalot, *Diatomella balfouriana* Greville, *Frankophila maillardii* (Le Cohu) Lange-Bertalot and *Melosira guillauminii* Manguin ex Kociolek et Reviers. On Kapiti Island, *C. kapitiana* was associated with a number of benthic diatoms including *Cocconeis placentula* var. *euglypta* (Ehrenberg) Grunow, *Cocconeis placentula* var. *lineata* Ehrenberg, *Gomphonema berggrenii* Cleve, *Hantzschia amphioxys* var. *major* Grunow, *Paralia sulcata* (Ehrenberg) Cleve, *Rhoicosphenia curvata* (Kützing) Grunow and *Stauroneis phoenicenteron* fo. *gracilis* (Ehrenberg) Hustedt (see Stidolph 1985, for a complete species list).

A noticeable issue is the difference in cell size (valve diameter and frustule pervalvar height) among the studied populations within *C. kapitiana* (Table 3). The populations from Kapiti Island are seemingly bigger than those from Ile de la Possession. The reasons for these size differences are hard to explain but they seemingly have autecological significance. Edlund & Bixby (2001) list a number of possible factors that might influence population cell size, including protection against herbivory, adaptation to salinity or nutrient concentration, and genetic differences.

Biogeography

To date, the genus *Cavernosa* is known from only two localities and shows a very special biogeographic distribution. The genus was originally described from Kapiti Island near the coast of New Zealand (Stidolph 1990) (Fig. 1) and several other populations were found on the island Ile de la Possession (Fig. 1) in the southern Indian Ocean, almost 12,500 km away from the type location (Van de Vijver et al. 2002). *Cavernosa* was found at seven different sites on Ile de la Possession (Fig. 1), but it is not known if the taxon inhabits the other islands of Crozet Archipelago simply because diatom studies on these islands have not been carried out. *Cavernosa* is also not reported from islands that are located between Ile de la Possession and Kapiti Island such as the Kerguelen Archipelago, Heard Island or Tasmania (Van de Vijver et al. 2001, 2004, 2008). However, this might be a result of undersampling of the likely preferential habitat of *Cavernosa*. On Kapiti Island, off New Zealand, *Cavernosa* is described from only a single site. It can be speculated that specimens of this taxon would also be observed from

Table 3 Morphometric and morphological comparison of *Cavernosa kapitiana* from the type locality (Kapiti Island, New Zealand) and Ile de la Possession (southern Indian Ocean). $n = x$ refers to number of measured specimens.

	Type population according to Stidolph (1990)	Type population based on the re-study for this paper	Population from Ile de la Possession
Morphometry			
Valve diameter (µm)	35.9–64.1 ($n = 10$)	40–115 ($n = 4$)	21–52 ($n = 25$)
Frustule pervalvar height (µm)	55–60 ($n = 2$)	50–80 ($n = 2$)	45–64 ($n = 15$)
No. of caverns	10–17	10–23	6–11 ($n = 20$)
No. of copulae	2	3	2–4
Globular initial cell diameter (µm)	Not available	Not measured	55–65 ($n = 3$)
Morphology			
Chain formation	Not reported	Not found	Yes, up to 14 cells long
Valve face structure	Complex pattern of weakly rimmed pores and granules	Complex pattern of weakly rimmed pores and granules	Complex pattern of rimmed pores, granules, and ridges
Mantle structure	Subdivided into four zones	Subdivided into four zones	Subdivided into four zones
Spine structure	Small stellate or simple	Small stellate or simple	Long stellate
Rimoportulae	One	One on vegetative, one or two on initial cells	One on vegetative, two on initial cells
Initial cells	Not reported	Yes, globular	Yes; globular and bell-shaped cells
Ringleiste near lower mantle edge	Not reported	Present	Present
Papilla at advalvar end of the ligula	Present	Not found	Not found

localities in the nearer or farther vicinity of this site. It might be reliable to assume that *C. kapitiana* does not occur in Europe and North America given the intensity of diatom sampling on both continents.

At the moment, the observed biogeography of *Cavernosa* cannot be convincingly explained because it is unclear which of the two populations should be considered the oldest. Possible reasons for this disjunct biogeography include undersampling, confusion with other, similar taxa such as *Orthoseira* (Spaulding & Kociolek 1998) or long-distance transport (such as by wind or birds) of *Cavernosa* from or to Ile de la Possession. The latter seems less likely considering the long distance and the fact that freshwater diatom species hardly survive in purely marine environments.

Conclusions

Based on the results of this study, it is clear that the *Cavernosa* populations of both islands represent the same species, *C. kapitiana*. The observed morphological differences are too weak for a taxonomic separation of both populations. However, the results also indicate that the original description of *C. kapitiana* needs to be emended to include the newly discovered features.

Emended diagnosis

Cavernosa kapitiana Stidolph emend. Cremer et Van de Vijver

Cells in living state connected in long chains and with numerous small discoid plastids. Frustules of vegetative cells cylindrical with concave or convex valves and a deep mantle consisting of several distinct structural zones. Frustule pervalvar height 45–80 µm, valve diameter 21–115 µm. Valve faces irregularly ornamented by granules, ridges and raised plates. Pores irregularly scattered on the valve face with a denser arrangement near the valve margins compared to the valve centre. Spines irregularly spaced around the valve face margin, either solid and simple or long and stellate. Valve interior occupied by marginal caverns and with ringleiste on the lower part of the mantle. One or two short-stalked rimoportulae located in the valve centre. Cingulum composed of ligulate copulae. Initial cells of globular shape with comparably short mantle, surface ornamentation comparable with vegetative cells, and no spines. Valve interior of initial cells entirely occupied by irregularly formed caverns, with two rimoportulae halfway between valve centre and margin, and a ringleiste on the valve mantle. Irregularly formed bell-shaped initial cells with a deep, structured mantle occasionally may occur.

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References

Crawford RM 1975. The frustule of the initial cells of some species of the diatom genus *Melosira* C. Agardh. Nova Hedwigia Beihefte 53: 37–55.

Crawford RM 1981a. The diatom genus *Aulacoseira* Thwaites: its structure and taxonomy. Phycologia 20: 174–192.

Crawford RM 1981b. Some considerations of size reduction in diatom cell walls. In: Ross R ed. Proceedings of the Sixth Symposium on Recent and Fossil Diatoms. Budapest, September 1–5, 1980. Koenigstein, Otto Koeltz Science Publishers. Pp. 253–266.

Crawford RM, Likhoshway YV, Jahn R 2003. Morphology and identity of *Aulacoseira italica* and typification of Aulacoseira (Bacillariophyta). Diatom Research 18: 1–19.

Edlund MB, Bixby RJ 2001. Intra- and inter-specific differences in gametangial and initial cell size in diatoms. In: Economou-Amilli A ed. Proceedings of the 16th International Diatom Symposium, 25 August–1 September 2000, Athens & Aegean Islands. Athens, Amvrosiou Press. Pp. 169–190.

Ehrlich A, Crawford RM, Round FE 1982. A study of the diatom *Grataulus laevis* – the structure of the auxospore and the initial cell. British Phycological Journal 17: 205–213.

Krammer K, Lange-Bertalot H 2004. Bacillariophyceae. 3. Teil: Centrales, Fragilariaceae, Eunotiaceae. In: Ettl H, Gerloff J, Heynig H, Mollenhauer D eds. Süßwasserflora von Mitteleuropa. Band 2/3, Bacillariophyceae 3. Teil. Heidelberg, Spektrum Akademischer Verlag. Pp. 1–599.

Müller O 1890. Bacillariaceen aus Java, I. Berichte der Deutschen Botanischen Gesellschaft 8: 318–331.

Round FE, Crawford RM, Mann DG 1990. The diatoms. Biology and morphology of the genera. Cambridge, Cambridge University Press. p. 747.

Spaulding SA, Kociolek JP 1998. The diatom genus *Orthoseira*: ultrastructre and morphological variation in two species from Madagascar with comments on nomenclature in the genus. Diatom Research 13: 133–147.

Stidolph SR 1985. Some benthic diatoms from kapiti Island, near Cook Strait, New Zealand. Nova Hedwigia 41: 393–409.

Stidolph SR 1990. *Cavernosa kapitiana*, a new diatom genus and species from Kapiti Island, New Zealand. Nova Hedwigia 50: 97–110.

Van de Vijver B, Ledeganck P, Beyens L 2001. Habitat preferences in freshwater diatom communities from subantarctic Iles Kerguelen. Antarctic Science 13: 28–36.

Van de Vijver B, Frenot Y, Beyens L 2002. Freshwater diatoms from Ile de la Possession (Crozet Archipelago, Subantarctica). Bibliotheca Diatomologica 46: 1–412.

Van de Vijver B, Beyens L, Vincke S, Gremmen NJM 2004. Moss-inhabiting communities from Heard Island, sub-Antarctic. Polar Biology 27: 532–543.

Van de Vijver B, Gremmen NJM, Smith V 2008. Diatom communities from the sub-Antarctic Prince Edward Islands: diversity and distribution patterns. Polar Biology 31: 795–808.

Van der Werff A 1955. A new method for cleaning and concentrating diatoms and other organisms. Internationale Vereinigung für Theoretische und Angewandte Limnologie, Verhandlungen 12: 276–277.