R e s e a r c h   a r t i c l e

Revision of the non-marine centric diatom flora (Bacillariophyta) of the sub-Antarctic Campbell Island (southern Pacific Ocean) with the descriptions of five new species

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Abstract. During a survey of the moss-inhabiting diatom flora of the sub-Antarctic Campbell Island, located in the southern Pacific Ocean, several unknown centric diatoms were observed that could not be identified using the currently available literature. Detailed light and scanning electron microscopical observations and comparisons with the characters of several species of *Melosira*, *Angusticopula*, *Ferocia* and *Arcanodiscus* worldwide indicated that five of them should be described as new to science: *Angusticopula cosmica* Goeyers & Van de Vijver sp. nov., *Arcanodiscus crawfordianus* Goeyers & Van de Vijver sp. nov., *A. indistinctus* Goeyers & Van de Vijver sp. nov., *A. saundersianus* Goeyers & Van de Vijver sp. nov. and *Ferocia houkiana* Goeyers & Van de Vijver sp. nov. A sixth species, *Angusticopula chilensis*, was illustrated for the first time using SEM and as a result is considered to differ sufficiently from *A. dickiei* to warrant epitypification as *A. chilensis*. The new species were first described in genera that formerly were included within the genus *Melosira*. All six species are morphologically characterized and compared with similar species within their respective genera. Their presence and distribution on Campbell Island are discussed based on the observations made in the available samples.

Keywords. Sub-Antarctica, Campbell Island, centric diatoms, new species, morphology.

Introduction

The non-marine diatom flora of the sub-Antarctic Islands in the southern Pacific Ocean has received far less attention than the flora in the (sub-)Antarctic parts of the Indian and Atlantic Oceans (see for instance Van de Vijver *et al.* 2002; Zidarova *et al.* 2016 and references therein). The Pacific sector of the sub-Antarctic region comprises only a few small islands: Macquarie Island (128 km^2), Snares Island (3.3 km^2), Auckland Island (626 km^2), Campbell Island (113 km^2), Antipodes Island (21 km^2) and Bounty Island (1.35 km^2) (Chown *et al.* 1998). Only a few studies have been published on the diatom flora of these islands (Van de Vijver & Beyens 1999). Most published information comes from

Macquarie Island, a small Australian island situated between Tasmania and the Antarctic Continent. The oldest records of Macquarie Island date back to 1954 when Bunt made a first account of 64 terrestrial diatoms of the island. Most of the reported diatoms on his list were either cosmopolitan or marine taxa. Evans (1970, reporting 84 taxa), Keenan (1995), and especially the work of Dr T.P. McBride (McBride & Selkirk 1999; McBride *et al.* 1999; McBride 2009) and Dr K. Saunders (Saunders *et al.* 2009) dealt with some aspects of the Macquarie Island diatom flora, although none of them made a thorough taxonomic analysis of the non-marine diatom flora of this island. Three new diatom species have recently been described from Macquarrie Island and, to date, only from there: *Gomphonema isabellae* Van de Vijver & T.P.McBride (2006), *Navicula bergstromiana* Van de Vijver & Verleyen (in Sabbe *et al.* 2019) and *Psammothidium hodgsonianum* Van de Vijver (2019). The analysis of the latter species was made when revising all taxa showing some similarity with *Psammothidium manguinii* (Hust.) Van de Vijver. During this revision, a first new species for Campbell Island, *Psammothidium mannensianum* Van de Vijver, was described (Van de Vijver 2019). A second new species was recently described in the genus *Frankophila*, living on wet mosses collected on Campbell Island (Van de Vijver *et al.* 2020).

The diatom flora of Campbell Island was studied by Hickmann & Vitt (1973) who found 59 taxa living epiphytically on mosses. A second study in 2015 by Saunders *et al.* analyzed the relationship between aquatic diatom communities and water chemistry in 54 lakes and ponds on the island. They observed a high floristic similarity between Campbell Island and the sub-Antarctic Islands in the southern Indian Ocean (Van de Vijver *et al.* 2002) and with the flora in the Tasmanian and New Zealand mountain lakes (Vyverman *et al.* 1995; Hodgson *et al.* 1997; Kilroy 2007; John 2018).

During a visit to the moss herbarium at the British Antarctic Survey (Cambridge, UK), the original moss samples that were collected by Dale Vitt and used in their diatom survey (Hickmann & Vitt 1973) were retrieved and subsampled in the BAS herbarium. After preparation for diatom analysis, it was clear that the diatom flora in these moss samples was very well preserved. Analysis of the slides revealed the presence of several centric taxa that could not be identified using the currently available literature.

The genus *Melosira* was originally published in 1827 by Agardh but it was Kützing (1844) who included a large number of taxa in the genus. Later authors revised parts of the genus and split off several, often newly described, genera such as *Aulacoseira* Thwaites (1848), *Orthoseira* Thwaites (1848), *Paralia* Heib. (Heiberg 1863) and *Ellerbeckia* R.M.Crawford (1988). Nevertheless, a large number of taxa remained in the genus *Melosira*. In 2017, the genus *Melosira* was revised, which resulted in the description of several new genera: *Ferocia* Van de Vijver & Houk (in Van de Vijver *et al.* 2017), *Angusticopula* Houk *et al.* (2017) and *Arcanodiscus* Maidana & E.Morales (in Maidana *et al.* 2017). The description of the new genera resulted in a revision of all diatom taxa belonging or formerly belonging to the genus *Melosira* in the sub-Antarctic region. Four new taxa were described: *Ferocia ninae* Van de Vijver (in Van de Vijver *et al.* 2017), *F. subantarctica* Van de Vijver & Houk (2019), *Arcanodiscus desmetianus* Van de Vijver (in Van de Vijver & Houk 2019) and *Melosira jeanbertrandiana* Van de Vijver & Crawford (2019) whereas the correct taxonomic identity of two other taxa was established: *Angusticopula dickiei* (Thwaites) Houk *et al.* and *A. chilensis* (Grunow) Houk *et al.* (Houk *et al.* 2017). These revisions, however, only concerned those taxa that were observed on the islands in the southern Indian Ocean. The recent survey of the Campbell Island moss samples partly fills this gap in our knowledge of the sub-Antarctic melosiroid diatom flora.

Five unknown taxa were found and after a thorough analysis of light and scanning electron microscopy observations and comparison with previously described taxa worldwide, they are described as new to science: *Angusticopula cosmica* sp. nov., *Ferocia houkiana* sp. nov., *Arcanodiscus crawfordianus* sp. nov., *A. indistinctus* sp. nov. and *A. saundersianus* sp. nov. Several populations of a sixth species, *Angusticopula chilensis*, were analyzed in more detail and compared with published images of the

Grunow type slide (in Houk *et al.* 2017: pl. 63, figs 1–6). As unmounted material of this taxon is no longer available (A. Igersheim, Vienna, pers. comm.), one of the Campbell Island populations will be designated as epitype for this species. In the present paper, the morphology of the new species is discussed and the species are compared with similar species worldwide and more specifically with taxa described from the sub-Antarctic region.

Material and methods

Campbell Island (52°32′24″ S, 169°8′42″ E) is the main island of a small volcanic archipelago situated in the southern Pacific Ocean, at approx. 600 km south of New Zealand and 3800 km north of the Antarctic Continent. The island has a total surface area of 113 km^2, reaching an altitude of 569 m. Saunders *et al.* (2015) provide details on the climate, geomorphology and vegetation of the island.

During a National Science Foundation expedition between December 1969 and February 1970, a large number of moss samples were collected by Prof. Dale Vitt (Southern Illinois University Carbondale, USA) (Hickmann & Vitt 1973; Vitt 1974). Part of the samples were retrieved from the British Antarctic Survey herbarium (Cambridge, UK). Several of these samples contained fairly large populations of several melosiroid diatoms. Three samples in particular, containing large populations of the unknown centric diatoms, were chosen for further analysis:

- BAS284: Moubray Hill, 818 ft, *Holomitrium perichaetiale*, on rocks (coll. date 12/01/1970);
- BAS286: South side Mt. Fizeau, *Hypopterygium novae-seelandiae*, dark wet recess (coll. date 22/01/1970);
- BAS303: North side Perseverance Harbour, East of Moubray Hill, *Racopilum strumiferum*, wet rock (coll. date 12/01/1970).

Subsamples of the selected material were prepared for light microscopy (LM) observation following the method described in Van der Werff (1955). Small parts of the samples were cleaned by adding 37% H_2O_2 and heating to 80°C for about one hour. The reaction was completed with the addition of saturated $kmnO_4$. After digestion and centrifugation (3 × 10 minutes at 3700 g), the material was diluted with distilled water to avoid excessive concentrations of diatom valves. Cleaned diatom valves were mounted in Naphrax®. Samples and slides are stored at the BR-collection (Belgium). The slides were analyzed using an Olympus BX53 microscope, equipped with Differential Interference Contrast (Nomarski) and the UC30 camera connected to the Cell Sense Standard program. For scanning electron microscopy (SEM), part of the suspension was filtered through polycarbonate membrane filters with a pore diameter of 1 μm, pieces of which were fixed on aluminum stubs after air-drying. The stubs were sputter-coated with 10 nm of Pt and studied in a JEOL JSM-7100F at 2 kV (Meise Botanic Garden, Belgium). For each new taxon, the number of specimens measured at random on the type slide is indicated (n = X). Terminology follows Round *et al.* (1990), Maidana *et al.* (2017), Van de Vijver *et al.* (2017) and Houk *et al.* (2017). The morphology of the new species was compared with species described or discussed in Maidana *et al.* (2017), Van de Vijver *et al.* (2002, 2017) and Houk *et al.* (2017 and references therein) and Van de Vijver & Houk (2019).

For the typification of the new species, we chose to use the entire slide as the holotype following Art. 8.2 of the International Code for Botanical Nomenclature (Turland *et al.* 2018). Diatoms show a broad variability along their cell cycle making the choice for the entire population on the slide more obvious.

Results

<div align="center">

Class Coscinodiscophyceae Round & R.M.Crawford in Round *et al.* (1990) emend.
Medlin & Kaczmarska
Subclass Coscinodiscophycidae Round & R.M.Crawford in Round *et al.* (1990)
Order Melosirales R.M.Crawford in Round *et al.* (1990)
Family Melosiraceae Kütz. (Kützing 1844) emend. R.M.Crawford in Round *et al.* (1990)
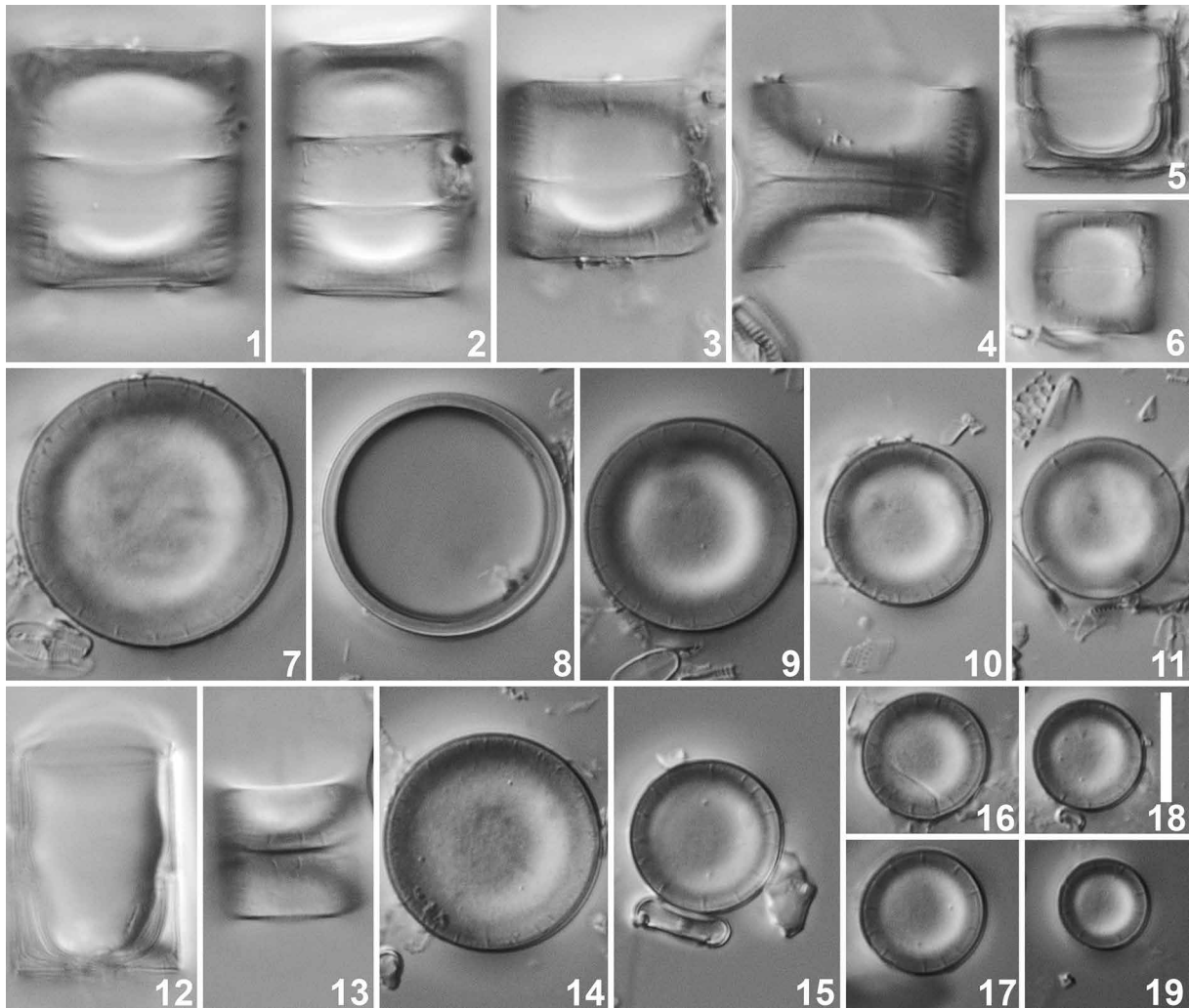Genus *Angusticopula* Houk *et al.*

Angusticopula chilensis (Grunow) Houk *et al.*
http://phycobank.org/102314
Figs 1–27

</div>

Basionym

Melosira dickiei forma *chilensis* Grunow in Van Heurck (1882: pl. 90, figs 13–14).
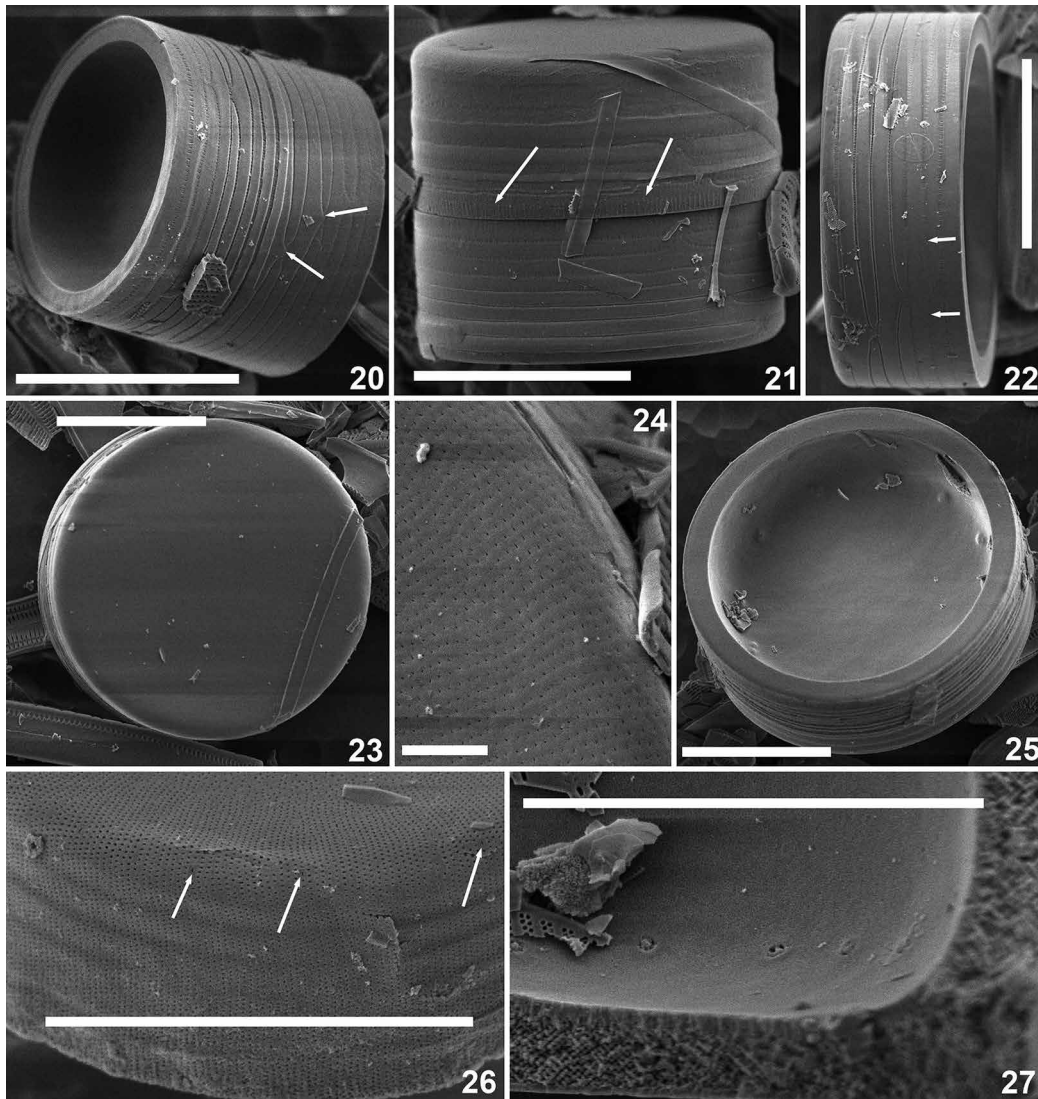

Figs 1–19. *Angusticopula chilensis* (Grunow) Houk *et al.* LM. Campbell Island epitype population, sample BAS286. **1–6, 12–13**. Several frustules in girdle view. **5, 12**. Internal valves. **7–11, 14–19**. Several valves in valve face view clearly showing the marginal rimoportulae. Scale bar = 10 µm.

Material examined

Since only the original slide 1015 in the Grunow collection (V) is available as type material and unmounted material is no longer present (A. Igersheim, Grunow Collection, Vienna, pers. comm.), we designate sample BAS286 as epitype to illustrate in more detail the morphological structures of this species.

Epitype (here designated)
CAMPBELL ISLAND • sample BAS286; 12 Jan. 1970; D. Vitt leg.; BR-4576.

Figs 20–27. *Angusticopula chilensis* (Grunow) Houk *et al.* SEM. Campbell Island epitype population, sample BAS286. **20–22**. SEM view of several valves in girdle view showing the ligulate, open, narrow girdle bands. The arrows indicate the ligulae in Fig. 20, the rimmed mantle edge in Fig. 21 and the fimbriate pars interior of the copulae in Fig. 22. **23**. External view of a valve face. **24**. External detail of the very fine striae and the small, rounded areolae. **25**. Internal view of an entire valve showing the rimoportulae and the thick mantle. **26**. External view of the mantle/valve face junction with several openings of the rimoportulae (arrows). **27**. Internal detail of the valve mantle with some rimoportulae. Scale bars: 20–23, 25–26 = 10 μm; 24, 27 = 1 μm.

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Description

Light microscopy (Figs 1–19)

Frustules cylindrical to short barrel-shaped. Cells most likely forming short chains, as often two sibling valves are found attached to each other. Valve diameter (n = 20): 8–25 μm, mantle height (n = 10): 4.5–11 μm. Valves showing thick wall (Fig. 8), having a relatively low mantle and rounded, flat valve face. Internal valves occasionally present (Figs 5, 12). Rimoportulae organized in marginal ring close to the valve face margin, visible as a series of tube-like channels. Striae and areolae not discernible in LM.

Scanning electron microscopy (Figs 20–27)

Girdle composed of a large number (up to 8) of narrow, open copulae (Figs 20–22) showing a fimbriate pars interior (Fig. 22, arrows). Small ligulae fill the gaps created by the open copulae (Fig. 20, arrows). Mantle rather high, densely punctated, clearly rimmed (Figs 21, arrows, 26). Valve faces clearly flat (Fig. 23), lacking granules and spines (Figs 23–24), finely perforated by very small areolae, arranged in irregular, uniseriate striae, ca 80 in 10 μm (Fig. 24). External rimoportula openings visible as slightly elongated slits (Fig. 26, arrows). Valves very thick (Fig. 27). Internally, sessile rimoportulae arranged in an irregular ring near the valve face/mantle junction, visible as slightly raised projections (Figs 25, 27).

Ecology and distribution

The largest populations of *A. chilensis* were found in mosses growing on cliffs next to a waterfall dominated by several species of *Humidophila*, *Diatomella balfouriana* Grev. and *Achnanthes muelleri* C.F.W.Carlson emend. Van de Vijver & Goeyers. The latter species are all known to thrive mostly in aerophilic, moist environments (Van de Vijver *et al.* 2002). *Angusticopula chilensis* was also found on several sub-Antarctic islands located in the southern Indian Ocean such as Iles Crozet (Van de Vijver *et al.* 2002), Iles Kerguelen (Van de Vijver *et al.* 2001) and the Prince Edward Islands (Van de Vijver *et al.* 2008). The species was almost always incorrectly identified as *Melosira* sp. or *Melosira varians* C.Agardh.

Angusticopula cosmica Goeyers & Van de Vijver sp. nov.
http://phycobank.org/102315
Figs 28–43

Etymology

The specific epithet refers to the general outlook of the valves in scanning electron microscopy giving the impression, due to the many granules, of a cosmos with numerous stars.

Material examined

Holotype

CAMPBELL ISLAND • sub-Antarctic region; sample BAS303; 12 Jan. 1970; D. Vitt leg.; BR-4577.

Isotype

CAMPBELL ISLAND • same collection data as for holotype; slide at University of Antwerp, Belgium; PLP-368.

Description

Light microscopy (Figs 28–36)

Frustules rectangular with valve diameter much larger than the mantle height. Cells always solitary; chains, even short ones, never observed. Numerous discoid plastids present. Valve diameter (n = 50): 18–45 μm, mantle height (n = 1): ca 8 μm. Valves with a low mantle and flat valve face. Internal valves never observed. Central area large, diameter 10–25 μm (50–60% of the total valve diameter, irregularly
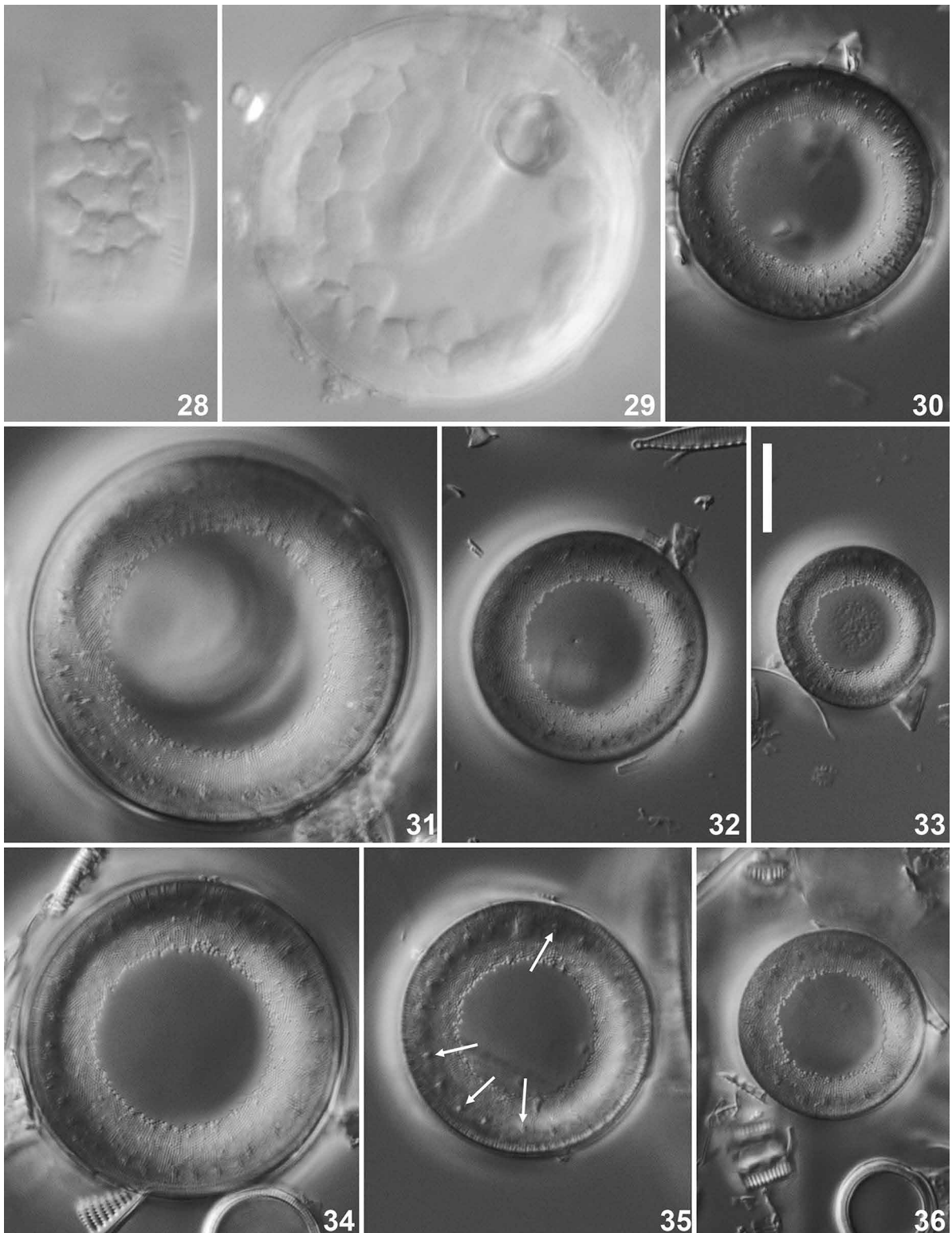
Figs 28–36. *Angusticopula cosmica* Goeyers & Van de Vijver sp. nov. LM. Campbell Island holotype population, sample BAS303 (BR-4577). **28**. Frustule in girdle view showing the discoid chloroplasts. **29**. Frustule in valve face view showing the discoid chloroplasts. **30–36**. Several valves in valve face view showing clearly the submarginal ring of rimoportulae (arrows) and the striated valve face margin. Scale bar = 10 μm.
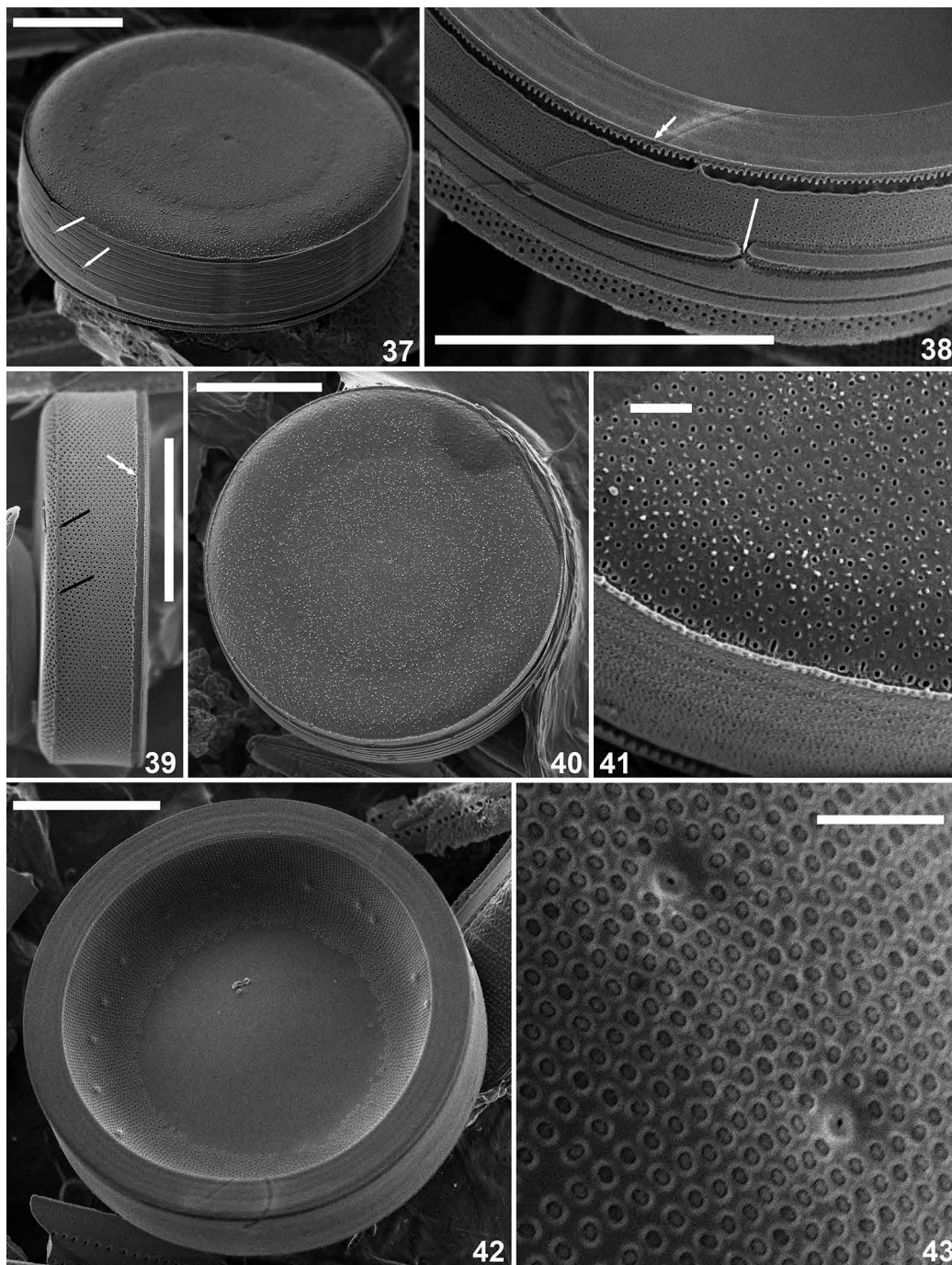
Figs 37–43. *Angusticopula cosmica* Goeyers & Van de Vijver sp. nov. SEM. Campbell Island holotype population, sample BAS303 (BR-4577). **37**. Frustule showing both the valve face and girdle formed by open, narrow copulae. The arrows indicate the ligulae. **38**. Detail of the mantle valve with the serrated mantle edge (double arrow) and the ligulate copulae (single arrow). **39**. Valve in girdle view showing the striated mantle, the narrow ridge bordering the mantle/valve face junction (black arrows) and the typical groove bordering the mantle edge (double white arrow). **40**. External view of a valve face showing the dense pattern of granules. **41**. External detail of the very fine striae, the small, rounded areolae and the narrow ridge bordering the valve margin. **42**. Internal view of an entire valve showing the rimoportulae and the thick mantle. **43**. Internal detail of the valve with some rimoportulae. Scale bars: 37–39, 42 = 10 µm; 40 = 5 µm; 41, 43 = 1 µm.

bordered by marginal striae. Marginal striae radial, clearly punctate, 31–35 in 10 μm, clearly visible in LM. Ring of rimoportulae visible close to the valve face/mantle junction (Fig. 35, arrows).

Scanning electron microscopy (Figs 37–43)
Girdle comprising a large number (up to 8) of narrow, open, non-perforated copulae (Fig. 37). Small ligulae filling the gaps created by the open copulae (Figs 37, arrows, 38). Mantle rather shallow, with dense uniseriate striation pattern, composed of very small, rounded areolae. Mantle edge with a constricted rim bordered by a serrate marginal edge (Figs 38, 39, double white arrows). Valve face/mantle junction gently sloping showing a shallow marginal ridge (Figs 39, black arrows, 40). Valves faces clearly flat (Fig. 40), entirely covered by irregularly scattered small granules (Figs 40–41). Central area weakly raised, clearly visible in oblique view (Fig. 37). Spines absent (Fig. 40). Valve face striation restricted to a broad marginal zone. Striae uniseriate, forming rather irregular series of small areolae bordered by a very shallow siliceous rim (Fig. 41). Internally, valves weakly dome-shaped (Fig. 42), perforated by a marginal pattern of small areolae, closed by individual hymenes. Areolae clearly arranged in striae, separated by very narrow interstriae. Irregular ring of rather large rimoportulae present near the mantle edge (Figs 42–43). Rimoportulae visible internally as short raised tubes (Fig. 43).

Ecology and distribution

Angusticopula cosmica sp. nov. was described from a *Racopilum* moss vegetation collected from a wet rock east of Moubray Hill. The sample was dominated by *Frankophila dalevittii*, a recently described endemic species for Campbell Island (Van de Vijver *et al.* 2020), *Diatomella balfouriana* and *Diatomella colonialis* Van de Vijver & Le Cohu.

Class Coscinodiscophyceae Round & R.M.Crawford in Round *et al.* (1990) emend.
Medlin & Kaczmarska
Subclass Coscinodiscophycidae Round & R.M.Crawford in Round *et al.* (1990)
Order Melosirales R.M.Crawford in Round *et al.* (1990)
Family Melosiraceae Kütz. (Kützing 1844) emend. R.M.Crawford in Round *et al.* (1990)
Genus *Ferocia* Van de Vijver *et al.*

Ferocia houkiana Goeyers & Van de Vijver sp. nov.
http://phycobank.org/102316
Figs 44–73

Etymology

The species is named in honour of our colleague and friend Dr Václav Houk (Institute of Botany, Czech Republic) to acknowledge him for his work on melosiroid diatoms.
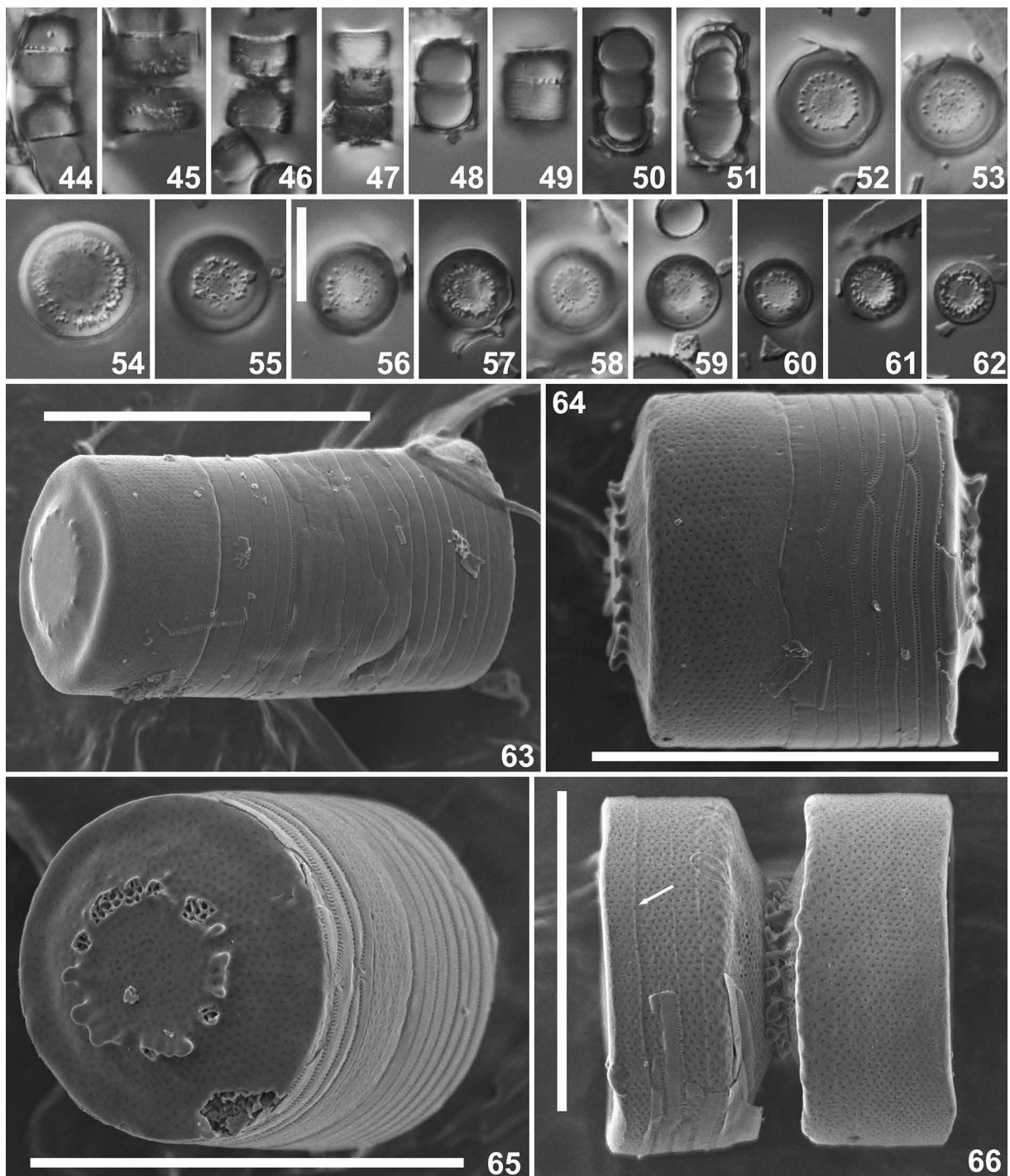
Material examined

Holotype
CAMPBELL ISLAND • sub-Antarctic region; sample BAS284; 12 Jan. 1970; D. Vitt leg.; BR-4578.

Isotype
CAMPBELL ISLAND • same collection data as for holotype; slide at University of Antwerp, Belgium; PLP-369.

Figs 44–66. *Ferocia houkiana* Goeyers & Van de Vijver sp. nov. LM and SEM. Campbell Island holotype population, sample BAS284 (BR-4578). LM. **44–49**. Several frustules in girdle view, often connected to each other. **50–51**. Internal valves. **52–62**. Several valves in valve face view clearly showing the central ring of spines. SEM. **63**. Frustule in girdle view with the narrow copulae. **64**. Frustule in girdle view with the narrow copulae on one side and one the side showing the broad mantle with one indicated rimoportula. **65**. External view of a valve face and the girdle. Note the central ring of partly hollow spines. **66**. External view of two valves connected via their linking spines. The arrow indicates the Müller step. Scale bars = 10 μm.
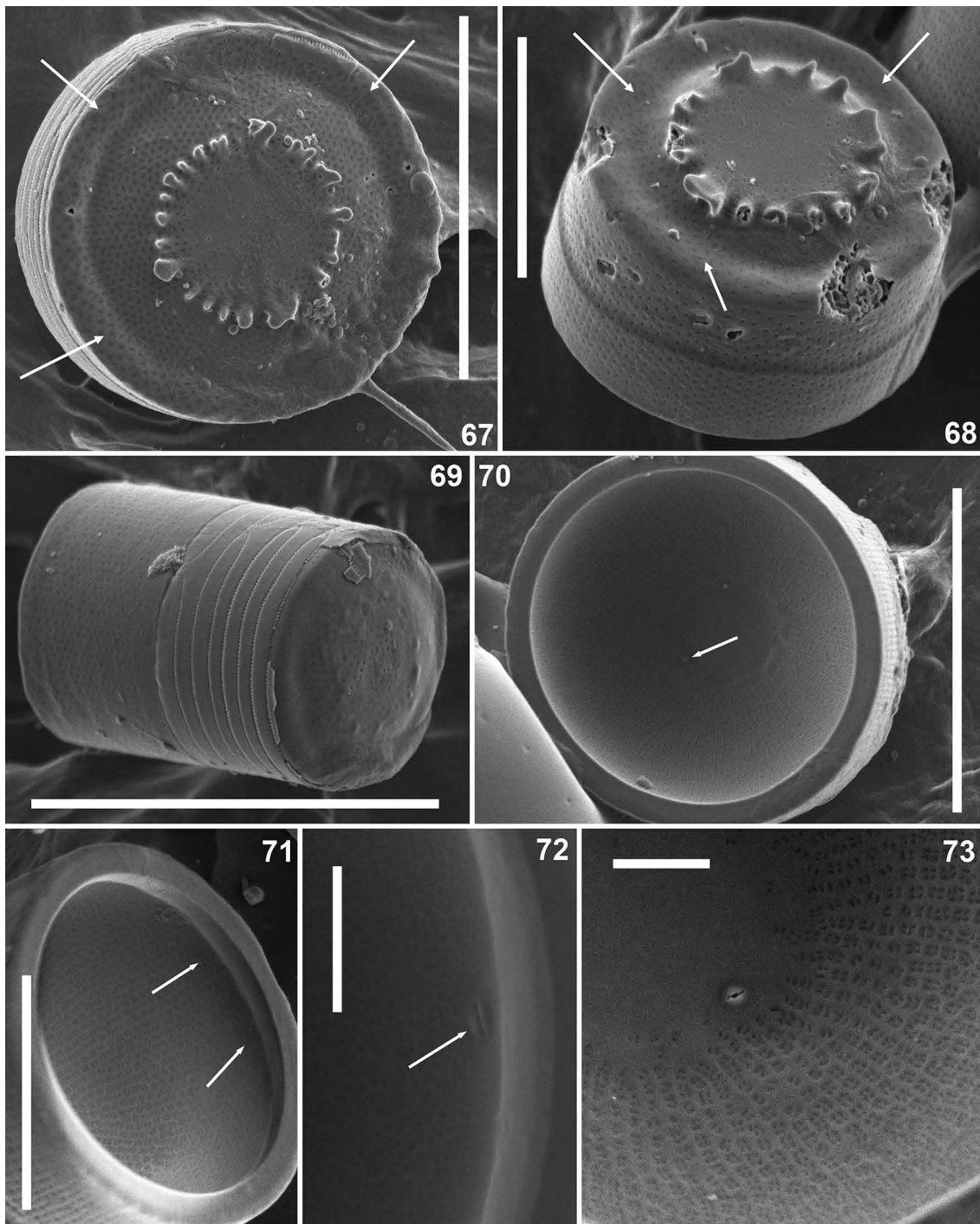
Figs 67–73. *Ferocia houkiana* Goeyers & Van de Vijver sp. nov. SEM. Campbell Island holotype population, sample BAS284 (BR-4578). **67–68**. Two external valve face views with the typical spines, the rounded to slit like areolae and the Müller step. **69**. External girdle view of a valve lacking the typical central ring of spines. Note the spines vestiges that are present in the central area. **70**. Internal view of an entire valve showing clearly the central rimoportulae (arrow) and the small central area. **71**. Internal view of an entire valve showing clearly the submarginal rimoportulae (arrows). **72**. Internal detail of the valve with one rimoportula indicated by the arrow. **73**. Internal detail of the valve central area with the central rimoportula. Scale bars: 67, 69–70 = 10 μm; 68, 71 = 5 μm; 72–73 = 1 μm.

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Description

Light microscopy (Figs 44–62)

Frustules rectangular. Cells connected via a central ring of spines, forming short chains. Numerous discoid plastids present. Girdle composed of large number of very narrow copulae, covering two adjacent valves. Valve diameter (n = 20): 4–11 μm, mantle height (n = 5): 4.0–5.5 μm. Valves with a relatively low mantle and rounded, flat valve face. Internal valves occasionally observed (Figs 50–51). Central area dominated by a regular crown of spines. Scattered spines present on the entire valve face. Striae not discernible in LM.

Scanning electron microscopy (Figs 63–73)

Girdle composed of a large number (up to 20) of narrow, open, non-perforated copulae (Fig. 63). Girdle bands attached to one of the valves of a cell extending over one of the new daughter valves after each cell division, meeting and overlapping with the bands attached to the other parent valve, covering that way two new valves of the daughter cells (Fig. 63). Copulae fimbriate on pars inferior giving the misleading impression of perforated girdle bands in non-eroded girdles (Figs 63, 65). Valves connected via central crown of large, wedge-shaped spines (Fig. 64). Müller step on mantle occasionally observed (Fig. 66, arrow). Mantle striae straight, composed of small, rounded areolae (Figs 64, 66). Near mantle edge, areolae very much smaller than near and at valve face/mantle junction, areolae irregularly scattered (Fig. 64). Mantle edge not rimmed. Rimoportula openings on the mantle not distinguishable from mantle areolae. Valve face/mantle junction thickened, relatively abrupt (Figs 63, 66). Valve face dominated by a central regular ring of large, relatively low, wedge-shaped spines (Figs 67–68). Spines hollow but apparently chambered with small silica walls inside the spines (Fig. 68). Spines occasionally lacking or reduced to series of low silica outgrowths (Fig. 69). Central area clearly raised, bordered by a narrow flat valve face edge, covered by an irregular pattern of small, rounded to slit-like areolae (Figs 67, 68, arrows). Striation pattern not detectable in the areolae. Internally, a few sessile rimoportula visible close to the mantle edge (Figs 71, 72, arrows), irregularly scattered. One rimoportula present near the valve center on the valve face (Figs 70, 73, arrow). Internal valve surface covered by numerous small areolae (Fig. 73).

Ecology and distribution

Ferocia houkiana sp. nov. is a frequently observed species on Campbell Island. It was found in several moss samples on rocks and next to waterfalls, usually dominated by species belonging to the genera *Pinnularia*, *Pinnunavis* and *Eunotia*. The type sample is dominated by the new species of *Ferocia* and is accompanied by *Pinnularia borealis* s. lat. Ehrenb. which points to a drier character of the environment, often influenced by sea spray (Van de Vijver *et al.* 2002).

Class Coscinodiscophyceae Round & R.M.Crawford in Round *et al.* (1990) emend.
Medlin & Kaczmarska
Subclass Coscinodiscophycidae Round & R.M.Crawford in Round *et al.* (1990)
Order Arcanodiscales E.Morales & Maidana in Maidana *et al.* (2017)
Family Arcanodiscaceae E.Morales & Maidana in Maidana *et al.* (2017)
Genus *Arcanodiscus* E.Morales & Maidana in Maidana *et al.* (2017)

Arcanodiscus crawfordianus Goeyers & Van de Vijver sp. nov.
http://phycobank.org/102318
Figs 74–80, 116–124

Etymology

The species is named in honor of our colleague Dr Richard M. Crawford to acknowledge his work on melosiroid diatoms.

Material examined

Holotype
CAMPBELL ISLAND • sub-Antarctic region; sample BAS303; 12 Jan. 1970; D. Vitt leg.; BR-4579.

Isotype
CAMPBELL ISLAND • same collection data as for holotype; slide at University of Antwerp, Belgium; PLP-370.

Description

Light microscopy (Figs 74–80)
To date, frustules in girdle view not observed in LM. Valves strongly silicified, rounded with a thick mantle and clearly convex, weakly domed valve face. Valve dimensions (n = 10): valve diameter 9–18.5 μm. Central area formed by a large, smooth, hyaline zone, 6–11 μm, ca 60% of the total valve diameter, surrounded by a striated, irregularly bordered marginal zone. Thick spines, scattered in the marginal zone distinctly present. Marginal striae discernible in LM, 30–33 in 10 μm. Visible tube processes lacking.

Scanning electron microscopy (Figs 116–124)
Frustules discoid with very heavily silicified valves, visible as a thick mantle (Figs 116, 123–124). Frustule height approx. 11 μm. Cingulum comprising at least 4, rather narrow, very thin, non-perforated, open, ligulate copulae (Figs 116, 120, double arrow). Pars interior clearly fimbriate (Figs 116, 117, arrows) giving the impression of perforated copulae. Valve face with large, flat hyaline, almost rounded central area, free of areolae, but with a dense covering of small silica granules (Figs 119–121). Marginal zone distinctly sloping towards the mantle with a very narrow flat zone immediately next to the valve face/mantle junction. Regular striation pattern present on sloping marginal zone. Irregular marginal ring of large, acute, solid spines present (Figs 120–122) close to the hyaline central area, placed between the areolae. Irregular pattern of small granules (Fig. 122) extending between the spines, though never reaching the mantle. Striae composed of small, strictly rounded areolae. Areolae externally covered by perforated occlusions (Figs 118, 120). Openings of portulae not distinguishable from areolae even in SEM. Striae continuing over the valve face/mantle junction, interrupted by a thick marginal ridge running entirely around the mantle (Fig. 119), usually covered by girdle bands. Mantle edge rather narrow. Between marginal ridge and mantle edge, relatively deep groove present, bearing several rows of strictly rounded areolae.
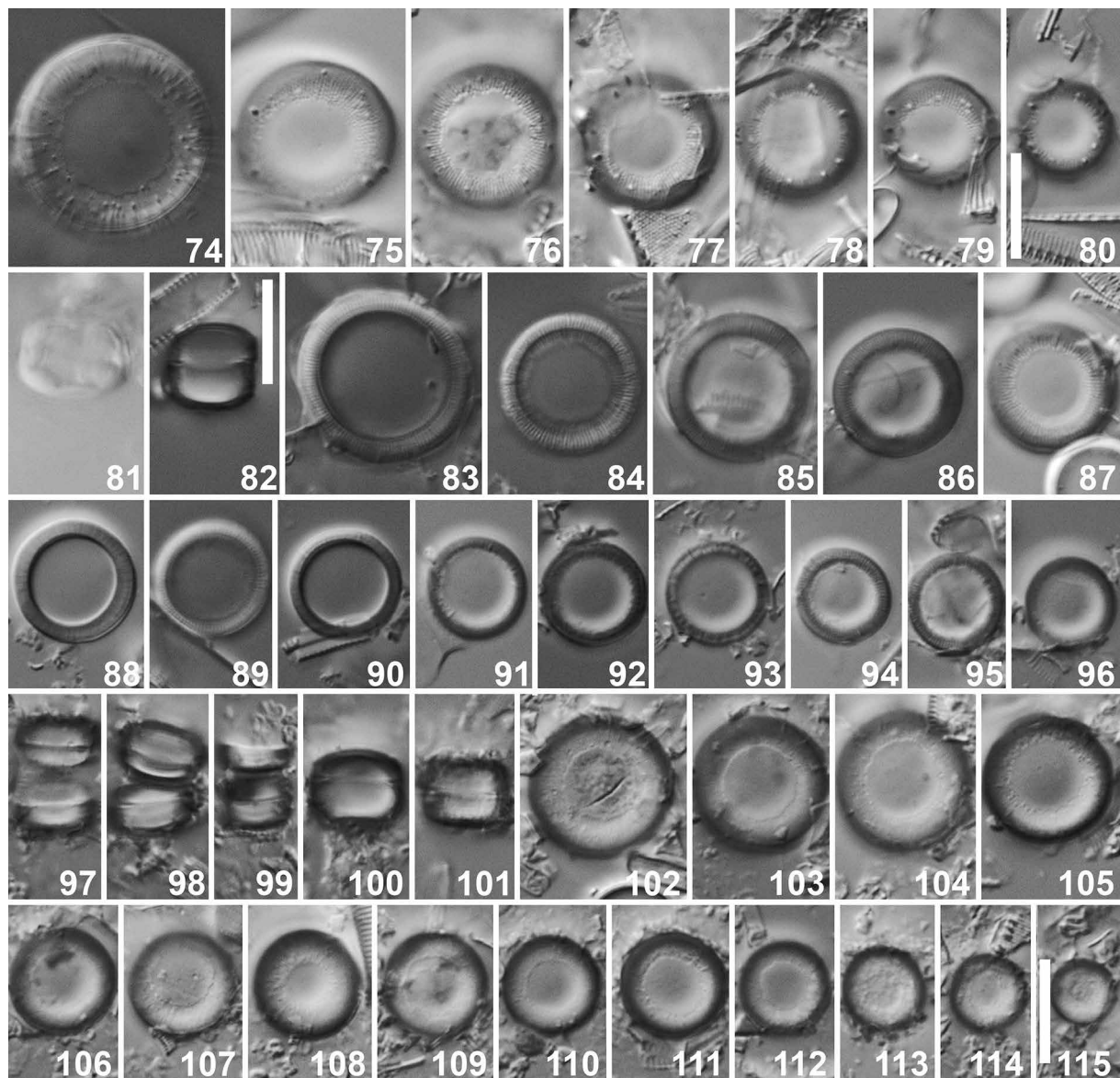
Figs 74–115. Three new *Arcanodiscus* species from Campbell Island. **74–80**. *Arcanodiscus crawfordianus* Goeyers & Van de Vijver sp. nov. LM. Campbell Island holotype population, sample BAS303 (BR-4579). Several valves in valve face view showing clearly the large central area, the irregularly scattered spines and the marginal striae. **81–96**. *Arcanodiscus indistinctus* Goeyers & Van de Vijver sp. nov. LM. Campbell Island holotype population, sample BAS303 (BR-4580). **81**. Frustule in girdle view showing the discoid chloroplasts. **82**. Frustule in girdle view. **83–96**. Several valves in valve face view. Note the thick mantle in some of the valves and the large central area. **97–115**. *Arcanodiscus saundersianus* Goeyers & Van de Vijver sp. nov. LM. Campbell Island holotype population, sample BAS272 (BR-4581). **97–101**. Several frustules in girdle view, often connected to each other. **102–115**. Several valves in valve face view. Note the thick mantle in some of the valves and the relatively small central area. The marginal striae are hardly visible in LM. Scale bars = 10 μm.
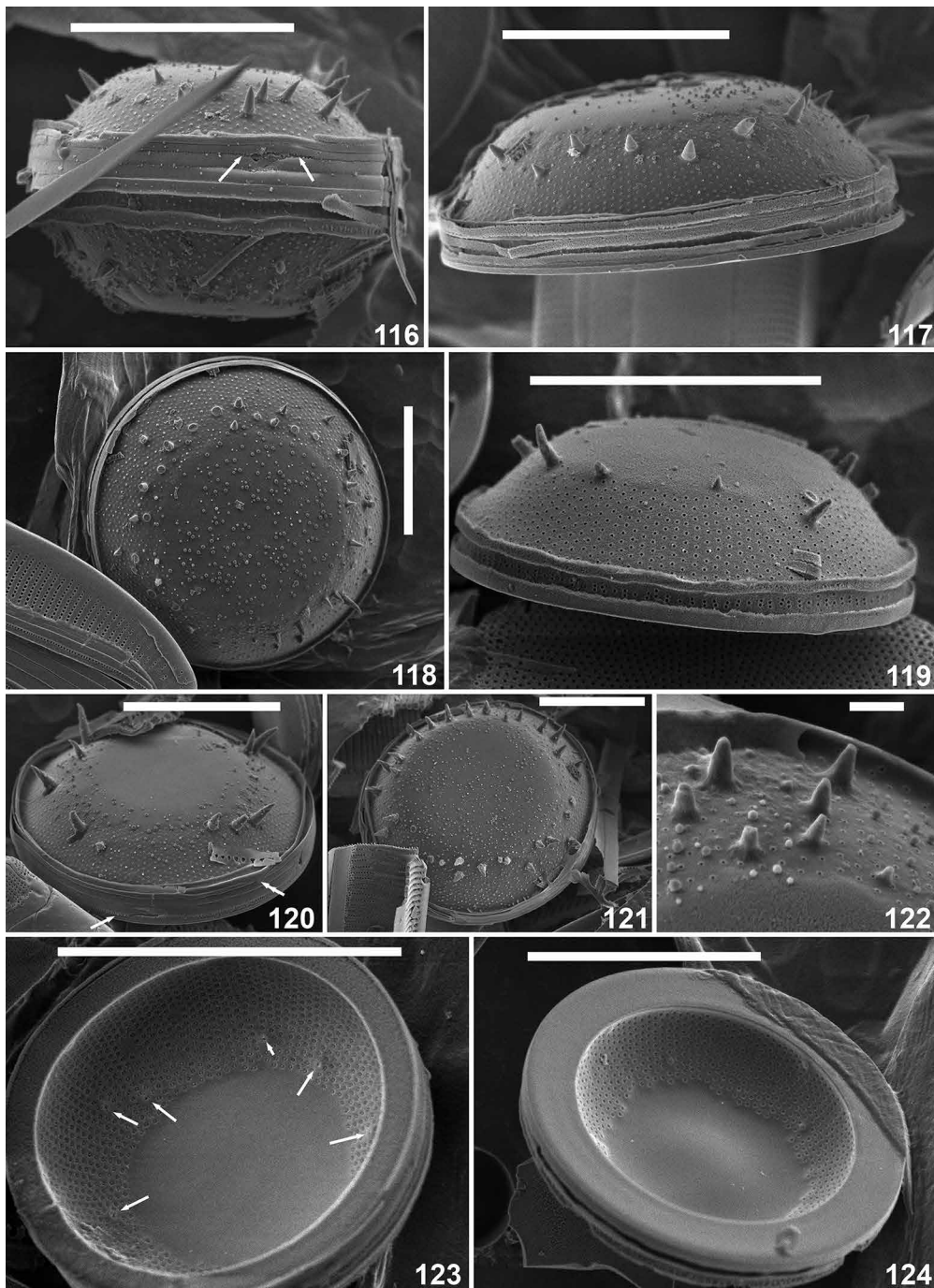
Figs 116–124. *Arcanodiscus crawfordianus* Goeyers & Van de Vijver sp. nov. SEM. Campbell Island holotype population, sample BAS303 (BR-4579). **116**. Frustule in girdle view. The arrows indicate the fimbriate pars interior of the copulae. **117**. External view of a valve in girdle view showing the domed valve face, the marginal spines and some of the narrow, unperforated copulae. **118**. External valve face view of an entire valve. Note the spines, the granules in the central area and the striae on the sloping margin. **119**. External view of a valve in girdle view showing the domed valve face, the marginal spines, the distinct marginal ridge and the mantle edge bordered by the relatively large groove. **120–121**. Several valve face views to show the irregular rings of spines. **122**. External detail of the spines and the granules. **123–124**. Internal views of an entire valve showing the rimoportulae (arrows). Scale bars: 116, 118–121, 123–124 = 10 μm; 117 = 5 μm; 122 = 1 μm.

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Internally, areolae large, clearly rounded, each showing a distinct rota, organized in a regular striation pattern (Fig. 123). Mantle edge very broad, heavily silicified (Figs 123–124). Central area formed by a large hyaline, irregularly bordered, central zone (Fig. 123). Several perforated, thickened protuberances which we presume to be the inner openings of portulae are irregularly scattered between the areolae, never organized in a regular marginal ring (Fig. 123, arrows). Inner openings of these processes rounded, smaller than the areolae, weakly raised above the surface (Fig. 124).

Ecology and distribution

Arcanodiscus crawfordianus sp. nov. was described from a *Racopilum* moss vegetation collected from a wet rock east of Moubray Hill. The sample, in which also the newly described *Arcanodiscus indistinctus* sp. nov. and *Angusticopula cosmica* sp. nov. were observed, was dominated by *Frankophila dalevittii* (Van de Vijver *et al.* 2020), *Diatomella balfouriana* and *Diatomella colonialis*. The presence in other samples needs to be confirmed with SEM observations.

Arcanodiscus indistinctus Goeyers & Van de Vijver sp. nov.
http://phycobank.org/102319
Figs 81–96, 125–131

Etymology

The specific epithet '*indistinctus*' refers to the lack of any specific peculiarity of this species as a distinguishing feature.

Material examined

Holotype
CAMPBELL ISLAND • sub-Antarctic region; sample BAS303; 12 Jan. 1970; D. Vitt leg.; BR-4580.

Isotype
CAMPBELL ISLAND • same collection data as for holotype; slide at University of Antwerp, Belgium; PLP-371.

Description

Light microscopy (Figs 81–96)
Frustules discoid, almost square to rectangular with broadly rounded edges and convex valve faces. Frustules never seen attached to each other, always solitary. Multiple discoid chloroplasts present. Girdle bands not discernible in LM. Valves rather strongly silicified, rounded with a thick mantle and convex, weakly domed valve face. Valve dimensions (n = 25): valve diameter 9–17 μm, frustule height (n = 2): 7–9 μm. Central area comprising a large, smooth, hyaline zone, almost 75% of the total valve diameter, surrounded by a clearly striated marginal zone, 27–35 striae in 10 μm. Visible processes lacking.

Scanning electron microscopy (Figs 125–131)
Frustules discoid with very heavily silicified valves, visible as a thick mantle (Figs 125, 130).

Girdle composed of several, narrow, non-perforated copulae (Fig. 126). Pars interior of the copulae clearly fimbriate giving the impression of perforate bands (Fig. 126). Valve face with large, flat hyaline, almost rounded central area, lacking areolae or any other ornamentation (Figs 127–128). Marginal zone gently sloping towards the mantle, entirely covered with short slit-like to almost rounded areolae (the latter when clearly eroded), ca 45 in 10 μm, roughly organized in irregular striae. Areolae externally covered by small, weakly raised, individual occlusions (Fig. 127). No obvious tube process openings apparent. Striae continuing over the valve face/mantle junction, interrupted by a series of up to 3 thin,

parallel ridges running entirely around the mantle (Fig. 129). Irregular silica thickenings, often connected to the first marginal ridge, present at the valve face/mantle junction (Fig. 128, arrows). Mantle areolae small, clearly rounded. Mantle edge very narrow, irregularly bordered (Fig. 129).

Internally, areolae large, each showing a clear rota, covered by very thin hymenes, organized in irregularly running striae (Fig. 130–131). Central area consisting of a large hyaline, irregularly bordered, central zone (Fig. 130). No thickened protuberances (called 'portulae') observed (Fig. 130). Mantle edge very broad, strongly silicified (Figs 130–131).
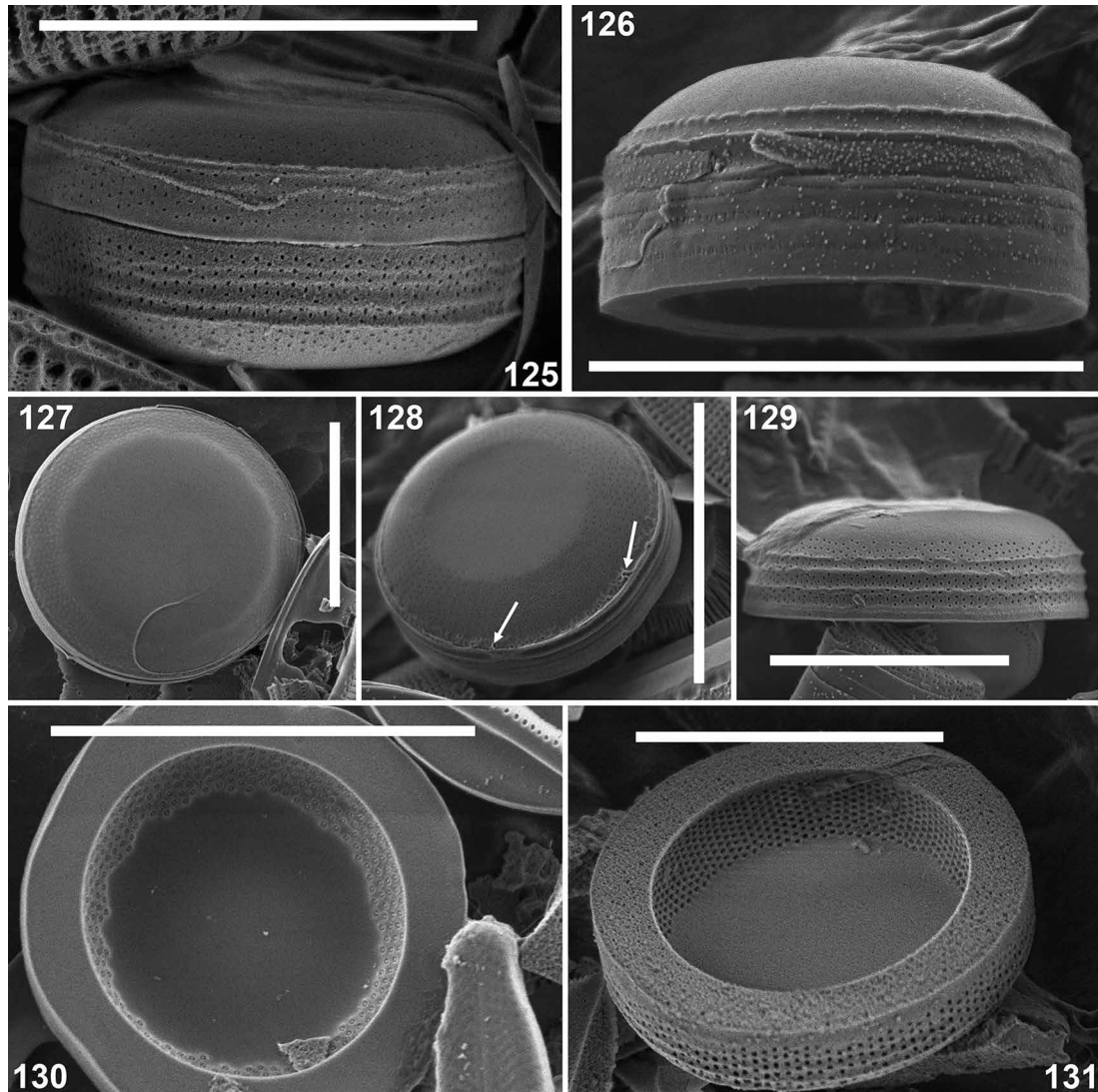
Figs 125–131. *Arcanodiscus indistinctus* Goeyers & Van de Vijver sp. nov. SEM. Campbell Island holotype population, sample BAS303 (BR-4580). **125**. Frustule in girdle view with eroded girdle showing the mantle with the parallel ridges. **126**. External view of a valve in girdle view showing the domed valve face, several marginal ridges and some of the narrow, unperforated copulae. **127–128**. External valve face view of an entire valve. Note the large central area and the striae on the sloping margin. On Fig. 128, note the siliceous outgrowth on the valve face margin. **129**. External view of a valve in girdle view showing the domed valve face, the distinct marginal ridges and the narrow mantle edge. **130–131**. Internal views of an entire valve showing the lack of rimoportulae. Scale bars = 10 μm.

Ecology and distribution

Arcanodiscus indistinctus sp. nov. was described from a *Racopilum* moss vegetation collected from a wet rock east of Moubray Hill. The sample was dominated by by *Frankophila dalevittii* (Van de Vijver *et al.* 2020), *Diatomella balfouriana* and *Diatomella colonialis*. In the same sample, *Arcanodiscus crawfordianus* sp. nov. and *Angusticopula cosmica* sp. nov. were also observed. The presence in other samples needs to be confirmed with SEM observations.

Arcanodiscus saundersianus Goeyers & Van de Vijver sp. nov.
http://phycobank.org/102320
Figs 97–115, 132–138

Etymology

The species is named in honour of our colleague Dr Krystyna Saunders (Australian Nuclear Science and Technology Organisation, Kirrawee, Australia) to acknowledge her for her ecological and paleo-ecological diatom research on the sub-Antarctic islands in the Pacific Ocean.

Material examined

Holotype
CAMPBELL ISLAND • sub-Antarctic region; sample BAS272; 26 Dec. 1969; D. Vitt leg.; BR-4581.

Isotype
CAMPBELL ISLAND • same collection data as for holotype; slide at University of Antwerp, Belgium; PLP-372.

Description

Light microscopy (Figs 97–115)
Frustules broadly discoid, almost square to rectangular with broadly rounded edges and convex valve faces. Frustules often found attached to each other. Chains composed of more than 2 cells however never observed. Multiple discoid chloroplasts present. Girdle bands not discernible in LM. Valves rather strongly silicified, rounded with a thick mantle and convex, weakly domed valve face. Valve dimensions (n = 25): valve diameter 6–17.5 μm, frustule height (n = 10): 4.5–7.0 μm. Central area is a large, smooth, hyaline zone, 3.0–7.5 μm, 50–55% of the total valve diameter, surrounded by a more rugose, irregularly shaped, marginal zone where striae are difficult to distinguish. Visible processes lacking.

Scanning electron microscopy (Figs 132–138)
Frustules discoid with very heavily silicified valves, visible as a thick mantle (Figs 132, 137). Cingulum comprises several, narrow, very thin, non-perforated, open copulae (Fig. 132). Pars interior of the copulae clearly fimbriate giving the impression of perforations on the copulae when girdle not eroded (Figs 132, 133, arrows). Copulae clearly open, ligulate (Fig. 132, double arrows).

Valve face with large, flat hyaline, clearly rounded central area, lacking areolae and any other ornamentation (Figs 134–136). Marginal zone gently sloping towards the mantle, entirely covered with rounded to slit-like areolae, ca 45 in 10 μm, organized in irregular striae, the latter ca 40 in 10 μm. Areola occlusions externally not observed (Figs 134–135). External openings of portulae not distinguishable from areola openings. No silica thickenings, close to valve face/mantle junction (Fig. 135). Striae continuing over the valve face/mantle junction, usually interrupted by a series of up to 3 parallel ridges running entirely around the mantle (Figs 134–135). Parallel ridges, usually covered by girdle bands (Fig. 133), occasionally lacking and resulting in a broad, flat mantle (Fig. 136). Areolae on the mantle strictly rounded. Mantle edge indistinct.
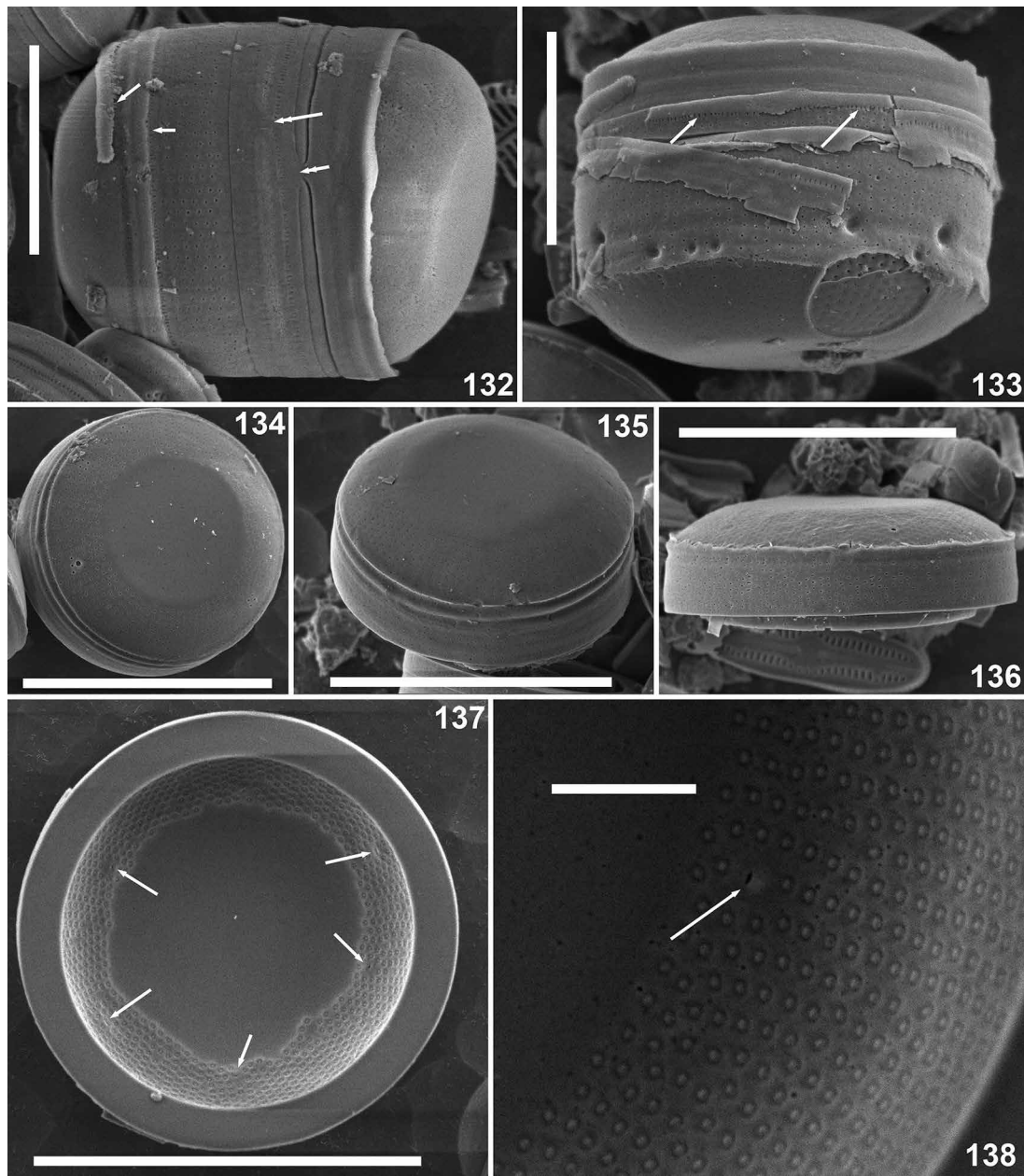
Figs 132–138. *Arcanodiscus saundersianus* Goeyers & Van de Vijver sp. nov. SEM. Campbell Island holotype population, sample BAS272 (BR-4581). **132**. Frustule in girdle view with the narrow copulae. The arrows indicate the ligulae. **133**. Frustule in girdle view with the narrow copulae. The arrows indicate the fimbriate pars interior of the copulae. Note also the domed valve face. Parts of the upper layer are eroded showing small areolae. **134–135**. External valve face views showing the relatively small central area and the well-developed marginal ridges. **136**. External view of a valve in girdle view showing the low, almost flat valve face, the absence of marginal ridges and the broad mantle edge. **137**. Internal views of an entire valve showing several rimoportulae (arrows). **138**. Internal detail of the valve with an indicated rimoportula. Note also the rota on the areolae. Scale bars: 132–137 = 10 μm; 138 = 1 μm.

Internally, areolae rather large, each showing a clear rota, covered by very thin hymenes, organized in irregularly running striae (Fig. 138). Central area a large hyaline, irregularly bordered, central zone (Fig. 137). Large number of perforated, thickened protuberances visible, irregularly scattered between the areolae, never organized in a regular marginal ring (Fig. 137, arrows). Inner openings of these protuberances rounded, smaller than the areolae, lacking rota (Fig. 138).

Ecology and distribution

Arcanodiscus saundersianus sp. nov. was found in a sample collected from a dripping bluff limestone. The sample is entirely dominated by the new species of *Arcanodiscus*. Sub-dominant species include *Achnanthes muelleri*, *Diatomella balfouriana* and several species of *Humidophila*.

Discussion

The centric diatom flora of Campbell Island is represented by at least three different genera: *Angusticopula*, *Ferocia*, both belonging to the Melosirales, and *Arcanodiscus* that was placed in the order of the Arcanodiscales (Maidana *et al.* 2017). All species are characterized by the presence of numerous narrow, often unperforated girdle bands which is typical of these genera but entirely different from *Melosira* s. str. which has broad, perforated copulae (Houk *et al.* 2017). Additionally, the position and number of rimoportulae separate the three genera further from *Melosira* s. str. Table 1 gives an overview of the four genera and highlights the distinguishing features. Based on this table, it is possible to place each of the new species in one of the new genera. Characterizing features guiding these decisions include the presence/absence and position of rimoportulae, presence/absence of internal cells, the shape of the valve (domed, flat, sloping mantle or not), the presence/absence of marginal rings and the presence/absence of large, linking spines.

Both *Ferocia* and *Angusticopula* contain a large proportion of species that prefer aerial habitats (Van de Vijver *et al.* 2017; Houk *et al.* 2017). As these habitats are likely to dry out occasionally, cells should protect their content from drying out. The presence of internal valves might be an important way to protect the cells against desiccation. The two genera possess these internal valves in many of their species. *Melosira*, considered to be a more aquatic genus (Round *et al.* 1990) is not known to present internal valves (Houk *et al.* 2017). Species of *Arcanodiscus* also seem not to present internal valves but still can be found in aerial habitats. It is, however, unclear why internal valves are lacking.

The description of the three new taxa of *Arcanodiscus* requires slight, but important changes to the original genus description (Maidana *et al.* 2017). Careful reanalysis of the original description of the type species and the accompanying illustrations shows that the girdle bands are open and not closed as stated in the genus description. Each new species of *Arcanodiscus* presents narrow, thin open girdle bands with clear ligulae (see Figs 116, 132, arrows). Moreover, the girdle bands are not perforated, but in fact possess a fimbriate pars interior that could give the impression of being perforated. This is actually clearly visible on fig. 17 in Maidana *et al.* (2017). In the description of *A. desmetianus* (Van de Vijver & Houk 2019), a similar fimbriate pars interior was also observed although in the description, the copulae were considered being perforated. Other features that seem to be different from the original genus description is the apparent lack of portulae in *A. indistinctus* sp. nov., the presence of external, though open areolar coverings, the presence of spines in *A. crawfordianus* sp. nov. and the position of the portulae, being more irregular than organized in a submarginal ring as in *A. crawfordianus* sp. nov. and *A. saundersianus* sp. nov. Therefore, the original genus description by Maidana *et al.* (2017) needs to be emended.

Table 1. Morphological characters of *Melosira* s. str. and several genera recently split off from *Melosira* s. lat.

	Melosira	*Angusticopula*	*Ferocia*	*Arcanodiscus*
	Houk *et al.* (2017)	Houk *et al.* (2017)	Van de Vijver *et al.* (2017)	Maidana *et al.* (2017)
girdle	several very broad, perforated copulae	large number of narrow, unper-forated copulae	large number of narrow, unper-forated copulae	numerous, narrow, closed perforated copulae
spines	present or absent	present or absent	very large, well-developed	absent
internal valves	absent	present	present	absent
granules	present or absent	present or absent	present	absent
rimoportulae	valve face + marginal ring	marginal ring	marginal ring	absent
mantle	broad	broad	broad	narrow, showing typical raised parallel ridges
colonies	present	present	present	absent

Arcanodiscus Maidana & E.Morales in Maidana *et al.* (2017) emended Van de Vijver

Frustules discoid, solitary or in short chains. Valves with flat and solid hyaline central area and a thicker mantle, the latter with faint radial lines corresponding to the mantle tubular areolae. Striae continuous from valve face margin to mantle. Areolae disposed in a quincunx arrangement, internally covered by rotae. Gradual or abrupt transition between valve face and mantle. Mantle usually bearing several parallel undulations upon which the girdle elements rest. Rimoportulae and fultoportulae absent, but a reduced type of portula with an internal opening situated on a prominence and a simple external opening is often present, usually scattered between the areolae but occasionally forming a submarginal ring at the abvalvar portion of the mantle. Cingulum comprising numerous, thin, open, ligulate, non-perforated elements. Pars interior of the copulae clearly fimbriate, suggesting the copulae being perforated.

The genus *Arcanodiscus* shows some resemblance to two marine genera: *Podosira* Ehrenb. and *Hyalodiscus* Ehrenb. (Round *et al.* 1990). *Podosira* possesses rimoportulae scattered over the entire valve face whereas *Hyalodiscus* shows a ring of marginal rimoportulae. Maidana *et al.* (2017) already discussed the differences between *Hyalodiscus*, *Podosira* and *Arcanodiscus*, and based most of the discrimination on the presence/absence of these rimoportulae and the girdle structure. *Hyalodiscus* shows bullulate areolae, a feature however never observed in any of the species of *Arcanodiscus* known at present, and the girdle bands in the latter are clearly closed, and not open as in *Arcanodiscus*, confirming the discrimination between *Hyalodiscus* and *Arcanodiscus*. *Podosira* on the other hand has open girdle bands, similar to *Arcanodiscus*, non-bullulate areolae (as in *Arcanodiscus*) and often a flat valve face (Round *et al.* 1990). A better structural analysis of the portulae and rimoportulae in these three genera should also shed more light on the possible relationship between them, although this is outside the scope of the present paper. Therefore, an emendation of the order and family description of *Arcanodiscus* is inappropriate at the moment, as this may obscure the relationships between the three genera.

The description of three new species of *Arcanodiscus* brings the total number in this genus now to five, all of them occurring in the southern hemisphere and (for four of them) more specifically in the sub-Antarctic region. Only the generitype species, *A. plattii* Maidana & E.Morales, was described from southern Patagonia (Maidana *et al.* 2017). The three new species can be distinguished from the two previously described species of *Arcanodiscus*. Table 2 highlights the main morphological features of

Table 2. Comparison of all species belonging to the genus *Arcanodiscus* E.Morales & Maidana.

	A. plattii Maidana et al. (2017)	A. desmetianus Van de Vijver & Houk (2019)	A. crawfordianus sp. nov. this study	A. indistinctus sp. nov. this study	A. saundersianus sp. nov. this study
valve diameter (μm)	12.5–16	10–16	9–18.5	9–17	6–17.5
frustule height (μm)	8.5–11	7–9	ca 11	7–9	4.5–7
diameter central area (% of total diameter)	up to 80%	< 50%	up to 60%	up to 75%	50–55%
number of striae (in 10 μm)	30–50	ca 35	30–33	27–35	ca 40
number of areolae (in 10 μm)	30–50	???	ca 40	ca 45	ca 45
valve mantle	narrow mantle edge	very broad mantle edge	narrow mantle edge bordered by deep groove	narrow mantle edge	mantle edge indistinct
silica mantle rings	series (up to 5) of parallel undulations	series (up to 4) of parallel undulations	only one mantle undulation present	series (up to 4) of parallel narrow undulations	series of up to 3 parallel, narrow undulations, occasionally lacking forming flat, broad mantle
areolae	in regular rows, but concentrically forming a quincunx arrangement	mantle areolae gradually changing from small, rounded to slit-like near valve face/mantle junction	in regular rows, rounded throughout entire valve	mantle areolae small and rounded, valve face areolae slit-like to almost rounded (when eroded)	rounded to slit-like on valve face, strictly rounded on mantle
spines	absent	absent	large, solid, acute, arranged in irregular ring near central area	absent	absent
granules	absent	absent	dense pattern present in central area	absent	absent
portulae	several, irregularly organised in submarginal ring	irregularly scattered on mantle, never organised in submarginal ring	irregularly scattered on mantle, never organised in submarginal ring	absent	irregularly scattered on mantle, never organised in submarginal ring

each species. Based on valve diameter or frustule height, it is impossible to separate the five species as they all show overlapping dimensions (roughly between 6 and 20 µm in diameter). The combination of morphological features is however unique for each of the five species. *Arcanodiscus crawfordianus* sp. nov. differs from all other 4 taxa in possessing distinct spines, organized in an irregular ring bordering the central area. Moreover, the entire central area, extending between the spines, is covered by a dense pattern of small granules. Additionally, only one marginal ring (undulation as stated in the genus description) is present and a clear groove borders the thickened mantle edge. None of the other four species show any of these two features, justifying the separation of *A. crawfordianus* sp. nov. as a distinct species. *Arcanodiscus indistinctus* sp. nov. does not possess the typical portulae that can be seen in the other four species. Although a large number of valves have been investigated, portulae were never observed. The new species also present a very large hyaline central area, up to 75% of the total valve diameter. Only *A. plattii* shows an even larger central area (up to 80%) whereas the other two taxa have a hyaline central area that never exceeds 60% of the total valve diameter. The areolae in *A. indistinctus* sp. nov. are not arranged in a regular striation pattern, contrary to *A. plattii*. Additionally, even the largest specimens of each of the new species only have 3, rarely 4, marginal rings whereas *A. plattii* has up to 5 rings. Finally, *A. saundersianus* sp. nov. has an indistinct mantle edge, occasionally lacking marginal rings, scattered portulae, never arranged in a submarginal ring as in *A. plattii*, and a less gently sloping valve face margin, compared to *A. desmetianus* (Maidana *et al.* 2017; Van de Vijver & Houk 2019). *Arcanodiscus saundersianus* sp. nov. also shows the highest stria (up to 40) and areola (up to 45) density, higher than any of the other four species.

The recently described genus *Angusticopula* contains seven species, slightly more than in either *Ferocia* or *Angusticopula*. Table 3 shows the features of all species of *Angusticopula* known so far. One of them, *A. chilensis*, was only known from the original drawing by Grunow and several LM illustrations in Houk *et al.* (2017: pl. 63, figs 1–5). A search for original, unmounted material remained without result (A. Igersheim, Grunow collection, Vienna). The population found on Campbell Island (and also similar populations on the Prince Edward Islands and Iles Kerguelen; Van de Vijver, unpubl. res.) shows a very high resemblance to the type specimens as depicted in Houk *et al.* (2017). The presence of the rimoportula on the margin, clearly visible in LM, is very obvious and not observed in any other species of *Angusticopula*. The most similar species might be *A. dickiei*, but the latter possesses rimoportulae that are located close to the mantle edge and not on the valve face/mantle junction as is the case in *A. chilensis*. *Angusticopula chilensis* was described from Chile although neither the slide (Houk *et al.* 2017: pl. 63, fig. 7) nor the drawing in Van Heurck (1885: pl. 90, fig. 13) provide a more detailed indication of the correct locality. The presence of a diatom described from Chile on Campbell Island is, however, not surprising given the presence of more species originally described from southern South America on the island such as *Adlafia tenuis* Van de Vijver & Goeyers (Van de Vijver *et al.* 2019a) and *Planothidium aueri* (Krasske) Lange-Bert. (Goeyers & Van de Vijver, unpubl. res.). The only difference between the type population of *A. chilensis* and the Campbell Island population can be noticed in the valve dimensions. For the type material, a valve diameter and a mantle height of 10 µm was indicated by Houk *et al.* (2017). The Campbell Island population shows larger valves (diameter 8–25 µm, mantle height 4.5–11 µm). However, the populations investigated on Campbell Island were much larger than the illustrated type population.

The second species of *Angusticopula*, the newly described *A. cosmica* sp. nov., possesses several very distinct features that were not observed so far in the other species of *Angusticopula* such as the dense pattern of very small granules covering the entire valve face and the ring of submarginal rimoportulae. *Angusticopula tanakae* Houk, Klee & H.Tanaka, *A. robusta* Houk, Klee & H.Tanaka and *A. rowlingiana* Van de Vijver, Wilfert, D.M.John & Houk all show the presence of a marginal zone of granules but these are always larger and more robust and confined to the marginal zones of the valve face, never occurring in the central area (Houk *et al.* 2017; Van de Vijver *et al.* 2019b). Only *A. robusta* and *A. ruttneri* show

Table 3. Comparison of all species belonging to the genus *Angusticopula* Houk et al.

	A. dickiei Houk et al. (2017)	*A. scheffleri* Houk et al. (2017)	*A. tanakae* Houk et al. (2017)	*A. chilensis* Houk et al. (2017), this study	*A. robusta* Houk et al. (2017)	*A. ruttneri* Houk et al. (2017)	*A. rowlingeana* Van de Vijver et al. (2019b)	*A. cosmica* sp. nov. this study
valve diameter (μm)	10–20	10–15	10–15	10 // 8–25	12–45	10–60	11–15	18–45
mantle height (μm)	7–10	ca 5	5–10	10 // 4.5–11	7–9	15–20	5.5–6.5	ca 8
valve face	flat	flat	clearly domed	flat	clearly domed	flat	flat to weakly domed	flat with weakly raised central area
central area	hyaline, not differentiated from rest of valve face	very small, bordered by dense pattern of areolae	small, bordered by dense pattern of granules	hyaline, not differentiated from rest of valve face	small, hyaline central area	raised, dominated by crown of irregular ridges	relatively large, hyaline, bordered by marginal striae	large, weakly raised
areolae	very small, rounded	large, rounded	very small, rounded	very small, rounded	moderately large, rounded	very small, rounded	very small, rounded	very small, rounded
rimoportulae	irregular ring near mantle edge	???	irregular ring on mantle	irregular ring on valve face/mantle junction	irregular ring near mantle edge	numerous, irregular ring on valve face/ mantle junction + scattered on valve face	irregular ring on valve face/mantle junction	ring of submarginal rimoportulae
spines	absent	absent	absent	absent	small, conical spines scattered over entire valve face	absent	absent	absent
granules	absent	absent	dense pattern of thick, large granules on valve margin, never on the central area	absent	irregularly formed granules	dense pattern on valve mantle	dense pattern of small granules on valve margin, never on the central area	dense pattern of small granules on entire valve face

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Table 4. Comparison of all species belonging to the genus *Ferocia* Van de Vijver & Houk.

	F. setosa Van de Vijver et al. (2017)	*F. ninae* Van de Vijver et al. (2017)	*F. subantarctica* Van de Vijver & Houk (2019)	*F. houkiana* sp. nov. this study
valve diameter (μm)	5.5–22	4.5–19	5–14	4–11
valve height (μm)	4.0–8.5	4–6	3–5	4.0–5.5
valve shape	clearly dome-shaped	dome-shaped	dome-shaped	almost flat
central area	small, rounded, hyaline	small, irregular, with scattered rounded areolae	small, rounded, hyaline	large, dominated by central crown of spines
Müller step	often very large	often very large	often very large	only occasionally present
spines	linking spines very large, irregularly shaped, often plate-like with sharp, acute endings, scattered smaller spines and granules present in between	several concentric rings of large, acute, almost never plate-like, linking spines	arranged at valve face/mantle margin + irregularly scattered spines on valve face, spines acute	central crown of blunt, wedge-shaped spines, spines often reduced
areolae	slit-like, never rounded	slit-like throughout but rounded in the central area	small, rounded	relatively rounded, almost always rounded
rimoportulae	ring of slit-like rimoportulae present near the mantle edge, never equidistant, never on valve face	ring of slit-like rimoportulae present near the mantle edge, never equidistant, never on valve face	ring of slit-like, equidistantly placed rimoportulae present near the valve face/mantle junction, never on valve face	irregularly scattered areolae on mantle + 1 areola present near valve center on valve face

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similar high valve diameters (up to 60 μm) whereas all other taxa have a maximal valve diameter never exceeding 20–25 μm. The largest valves in *A. cosmica* sp. nov. reach up to 45 μm. Finally, the weakly, but visibly raised central area in *A. cosmica* sp. nov. was not observed in any of the other seven species. The combination of these distinct features justify the separation of *A. cosmica* sp. nov. as a separate species.

The final species, *Ferocia houkiana* sp. nov., shows features of both the genera *Angusticopula* and *Ferocia* such as the narrow copulae and the scattered rimoportulae (Houk *et al.* 2017; Van de Vijver *et al.* 2017). The presence of the large central spines and the structure of the areolae, especially visible on the valve interior show more resemblance with *Ferocia* than with *Angusticopula* and therefore the species is placed within the former genus. The species is, however, unique within the genus *Ferocia* in having a distinct central ring of linking spines (Table 4). The other three *Ferocia* species lack spines in the central area but have instead often very large, acute or plate-like spines in the marginal zones of the valve face. The central rimoportula, at the edge of the central area, was not observed in the other three species of *Ferocia* (Van de Vijver *et al.* 2017; Van de Vijver & Houk 2019).

The description of the five new species almost doubles the number of melosiroid taxa in the sub-Antarctic region. Apart from these melosiroid species, the centric non-marine diatom flora in the entire Antarctic realm is rather limited. Recently, a new species of *Melosira*, *M. jeanbertrandiana* Van de Vijver & Crawford (2019) was published, found on the Îles Crozet in the southern Indian Ocean. The genus *Aulacoseira* is represented by two species (*A. principissa* Van de Vijver (2012) and *A. glubokoyensis* Oaquim *et al.* (2017)), *Orthoseira* is also present with two species (*O.* cf. *roeseana* (Rabenh.) Pfitser (Houk *et al.* 2017) and *O. biportulata* Van de Vijver & Beyens in Van de Vijver *et al.* (2002)) while a third species of *Orthoseira* was recently transferred to the genus *Guarreraea* (*O. limnopolarensis* (Van de Vijver & Crawford) Kociolek & Van de Vijver in Guerrero *et al.* (2018)). *Cavernosa kapitiana* Stidolph is present on the Iles Crozet and on Campbell Island (Goeyers & Van de Vijver, unpubl. res.) (Van de Vijver *et al.* 2002; Cremer *et al.* 2011). Only one species of *Cyclotella*, *C. deceusteriana* Van de Vijver & Dessein (2018) was observed whereas the genera *Stephanodiscus*, *Lindavia*, *Pantocsiella* and *Cyclostephanos* are entirely absent. Possible records of species belonging to these genera (or formerly placed in *Cyclotella*) should be considered as erroneous identifications or the result of contamination or force-fitting (Kellogg & Kellogg 2002). The almost complete absence of members of the latter five genera is most likely the result of the quasi-total absence of freshwater diatom plankton in Antarctica, a phenomenon that has up to now not been fully explained (Jones 1996; Van de Vijver & Beyens 1999). On the other hand, the melosiroid diatom flora seems to be overrepresented with 12 species, although only species belongs to *Melosira* s. str. The genera *Ferocia*, *Angusticopula* and *Arcanodiscus* are most likely composed of species typical of more aerophilic conditions influenced by seaspray and animals such as living on mosses, in soils exposed in cliffs, near waterfalls or near bird colonies (Cremer *et al.* 2011; Van de Vijver *et al.* 2017; Van de Vijver & Houk 2019). The observation of the five new species also highlights the diversity within the sub-Antarctic non-marine diatoms and, despite the taxonomic efforts of the past 15 years, the gap in our knowledge and the need of a continuous effort in documenting the biodiversity of these unique flora.

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