Polar Biology (2023) 46:759–772
https://doi.org/10.1007/s00300-023-03160-6

ORIGINAL PAPER

New observations on the Antarctic *Asteromphalus darwinii/hookeri* diatom species-complex (*Asterolampraceae*)

Gustaaf M. Hallegraeff[1] · **Karine Leblanc**[2]

Received: 14 October 2022 / Revised: 30 April 2023 / Accepted: 6 June 2023 / Published online: 21 June 2023

Abstract
Antarctic diatom populations of *Asteromphalus hookeri* and related species such as *A. hyalinus* and *A. parvulus* exhibit a highly variable number of hyaline rays ranging from 3 broad + 1 narrow (3 + 1) in the smallest valves, with 4 + 1 (27%) and 5 + 1 rays (35%) most common, and 6 + 1, 7 + 1, and rarely 8 + 1 rays only in larger cells. During December 1959 to April 1960 in the southern sector of the Atlantic Ocean, 6% of valves occurred as "double forms" with epitheca and hypotheca of the same cell exhibiting 4 + 1/3 + 1, 5 + 1/4 + 1, 6 + 1/5 + 1 and 7 + 1/6 + 1 ray combinations. Smaller cells (3 + 1, 4 + 1) always exhibited jagged separating lines in the central area, but larger cells (7 + 1, 8 + 1) had mostly smooth lines, and either jagged or smooth separating lines occurred in intermediate 5 + 1 and 6 + 1 forms, respectively. Epitheca and hypotheca of one and the same cell always exhibited jagged or smooth separating lines, but never mixtures. Observations of silica deposition during October to November 2011 around the Kerguelen Island plateau using the PDMPO fluorescent marker suggest that *Asteromphalus* separating lines play a key role in silica cell wall development. We discuss implications for taxonomy of what we designate as two highly variable and often confused and overlapping cold-water diatom taxa, *A. darwinii* (jagged separating lines; synonyms *A. beaumontii, A. hyalinus, A. leboimei*, *A. parvulus, A. rossii*) and *A. hookeri* (smooth separating lines; synonyms *A. antarcticus, A. buchii*).

Keywords Antarctic diatoms · *Asteromphalus hookeri* · *Asteromphalus darwinii*

Introduction

The centric diatom genus *Asteromphalus* Ehrenberg (*Astero* = star; *omphalos* = navel; "Strahlenschild" sensu Ehrenberg 1844) comprises discoid valves strikingly ornamented by a variable number of hollow tubes (hyaline rays, now termed ordinary rays), supplemented by a single narrow ray (now singular ray), both alternating with areolate sectors to form a bilaterally symmetrical spider-like pattern. We here use the designation 4 + 1 to indicate a valve with 4 ordinary and 1 singular rays, as distinct from the radially symmetrical genus *Asterolampra* Ehrenberg where all rays are equal. Ehrenberg (1844) simultaneously described and illustrated from Antarctic plankton samples, provided to him by Hooker and Darwin, seven new species *A. darwinii, A. rossii, A. hookeri, A. buchii, A. beaumontii, A. humboldtii* and *A. cuvierii*, which differed in valve diameter, number of rays (4 + 1 to 8 + 1), and branching of the separating ("umbilical") lines of the central area (zig-zag in *A. beaumontii, A. rossii, A. darwinii*; straight in the others). While originally spelled as *hookerii,* according to the International Code of Nomenclature (Turland et al. 2018; rule 60.8.a), when a species name is taken from the name of a man (Hooker), it should be formed by adding *ii*, except when the name ends in *-er* when *i* is added. The latter applies and the spelling *A. hookeri* is also adopted by AlgaeBase (Guiry and Guiry 2021). Van Landingham (1967) previously considered that only three of Ehrenberg's species were valid, *A. darwinii, A. hookeri* and *A. beaumontii*, while the other four were relegated to be synonyms. Subsequent workers, including Greville (1860) and Rattray (1889) introduced other diagnostic characters such as size of the central area compared to valve diameter, shape of the narrow singular ray within the central area, shape of the areolated sectors, and density of areolae. Later Antarctic plankton workers,

✉ Gustaaf M. Hallegraeff
gustaaf.hallegraeff@utas.edu.au

[1] Institute for Marine and Antarctic Studies, University of Tasmania, Private Bag 129, Hobart, TAS 7001, Australia

[2] Aix Marseille Université, Université de Toulon, CNRS, IRD, MIO UM 110, 13288 Marseille, France

such as Castracane (1886), Karsten (1905) and Manguin (1960) continued to describe further new Antarctic *Asteromphalus* species, such as *A. antarcticus* Castracane, *A. challengerensis* Castracane, *A. ovatus* Castracane, *A. wyvillii* Castracane, *A. hyalinus* Karsten, *A. ornithopus* Karsten, *A. parvulus* Karsten, *A. regularis* Karsten and *A. leboimei* Manguin. Boyer (1927) newly designated the chronologically first described species *A. darwinii* Ehrenberg as the lectotype, and discussed the diagnostic characters of central area and number of rays of *A. hookeri* but not of *A. darwinii.* Fryxell and Hasle (1974) produced the first scanning electron micrographs of labiate processes present at the end of all hyaline rays (illustrated for *A. hookeri* from the Weddell Sea in their Fig. 5). The application of combined light and electron microscopic characters for this diatom genus was expanded by Hernández-Becerril (1991, 1992, 1995) and Tiffany and Hernández-Becerril (2005). Hernández-Becerril (1991) newly described in *Asteromphalus* an indentation in the valve margin close to the singular ray, but absent in *Asterolampra.* Hernández-Becerril (1995) also reinstated the genus *Spatangidium* Brébisson for *A. arachne* (Brébisson) Ralfs based on the presence of 1–3 rimoportulae near the central portion of the valves, so far found only in that single taxon. Tiffany and Hernández-Becerril (2005) pointed to species-specific areolae patterns and structures of the cribra covering the loculate areolae albeit subject to maturational cell wall development, while Priddle and Fryxell (1985) emphasized branching of the separating lines as a diagnostic character.

AlgaeBase (Guiry and Guiry 2021) currently lists 85 accepted species names for the genus *Asteromphalus*, as well as 22 intraspecific names, demonstrating the uncertainties of taxonomy and understanding of species variability of this distinctive diatom genus. At present, only a single 18S SSU molecular sequence for Northern Hemisphere *Asteromphalus* sp. TN-2014 has been published (Nakov et al. 2015), with its genetically closest relatives being *Coscinodiscus* and *Stellarima* species. The genus does show up in Antarctic waters in the Tara oceans miTAG 16S 18S data base (Vernette et al. 2021) but failed to be detected in a recent Antarctic sediment DNA study (Armbrecht et al. 2022). To the best of our knowledge no culture studies on *Asteromphalus* have ever been published. While species of *Asteromphalus* are common (Ocean Biodiversity Information System OBIS lists 4770 and Global Biodiversity Information Facility GBIF lists 14,729 global records), they are rarely abundant. An opportunity to study morphological variation in prolific Antarctic populations of the *A. hookeri* complex occurred in December 1959 to March 1960 from a series of seawater pump samples collected during a voyage by the Netherlands whale-factory ship MS *Willem Barendsz*. A preliminary account of variation of diatoms in this material using light microscopy was presented by Van der Spoel et al. (1973), but in the present work *Asteromphalus* diatoms from this same material were re-examined by scanning electron microscopy and reinterpreted in view of recent developments in the taxonomy of this genus (Hernández-Becerril 1991, 1992, 1995). Complementary observations on silica deposition in Antarctic *Asteromplalus* were made during the KEOPS2 cruise in October to November 2011 around the Kerguelen Island plateau. Our main objective was to clarify the extraordinary morphological diversity of Antarctic *Asteromphalus* diatoms described in the literature, and to which extent these may represent developmental stages of only a limited number of species.

Material and methods

Plankton net samples were collected by Prof S. van der Spoel and Dr W.L. van Utrecht during a voyage of MS *Willem Barendsz* entering the Atlantic sector of the Southern Ocean in December 1959–January 1960, conducting its whaling operations throughout January and March 1960, and exiting March–April 1960 (Figs. 1a, b). Dutch whaling operations were discontinued after 1964. Samples were collected by running seawater from the ship's seawater system, pumped from about 4 m below surface and a flow rate of 13 L/min, through 40 µm plankton gauze. Samples were preserved in 5% formaldehyde, and prepared for light microscopy after potassium permanganate-hydrogen peroxide oxidation and mounting in Styrax. Some 629 *Asteromphalus* cells were examined for number of rays, cell diameter, and morphology of the central area and separating lines by oil immersion light microscopy with an Olympus microscope and later bright-field and differential interference contrast using an Axioskop 2 Plus Zeiss microscope with Zeiss Axiocam HR digital camera. Samples for scanning electron microscopy (over 150 valves examined) were thoroughly rinsed with distilled water, mounted on nucleopore filters on aluminium stubs, coated with platinum-palladium (5–20 nm layer thickness) and examined with a Hitachi SU70 scanning microscope (SEM) at 1.5–25 kV. SEM observations focussed on details of areolation, cribra, rimoportulae and the nature of the separating lines. The original *Willem Barendsz* plankton collections and Styrax slide mounts have been deposited at the Institute of Systematics and Population Biology and Zoological Museum of the University of Amsterdam, Netherlands.

Complementary observations on silica deposition in Antarctic *Asteromphalus* cells were made from 8 October to 22 November 2011 around the Kerguelen Island plateau, during KEOPS2 cruise on board the RV *Marion Dufresne* (Fig. 1C). Niskin and phytoplankton net samples were collected at various stations during the Antarctic spring diatom bloom. Samples were stained with PDMPO (LysoSensor Yellow/

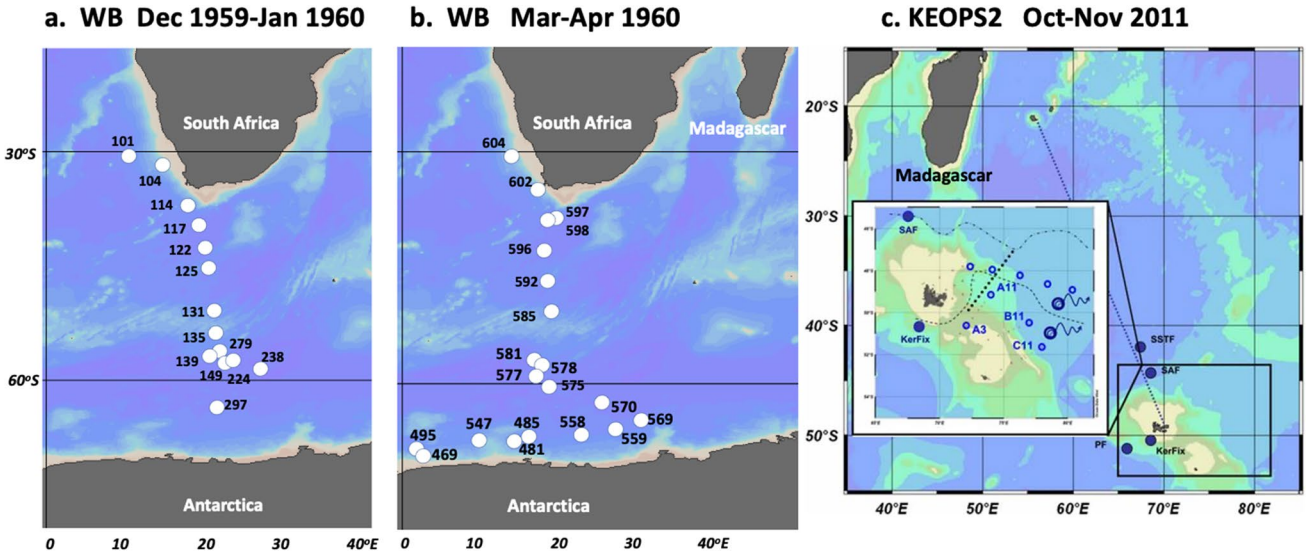


Fig. 1 Cruise tracks by MS *Willem Barendsz* entering the Atlantic sector of the Southern Ocean in (**A**) December 1959–January 1960, conducting its whaling operations throughout January and March 1960, and (**B**) exiting March–April 1960; **C** KEOPS2 cruise track by RV *Marion Dufresne* from 8 October to 22 November 2011 around the Kerguelen Island plateau

Blue DND-160), a fluorescent probe marking new Si deposition over a 24 h incubation, for epifluorescence microscopy analyses (Leblanc and Hutchins 2005). Seawater samples of 125 ml were incubated in flow-through deck incubators with a 0.125 µM final concentration PDMPO. After 24 h, a smaller volume was filtered onto black 0.8 µm polycarbonate filters depending on cell density in order to avoid cell overlap. The filters were mounted on a glass slide, covered with a drop of immersion oil, and a round coverslip and stored at − 20 °C. Filters were examined at the laboratory on an epifluorescence Nikon TE-2000 microscope equipped with a long pass DAPI filter cube (*λ*ex 330–380 nm, λdichroic 400 nm, *λ*em 435 nm) and a Nikon DS-5Mc camera.

Results

The diatom genus *Asteromphalus* was omnipresent in MS *Willem Barendsz* 1959–1960 samples and typically comprised 10–30% of total Thalassiosiraceae and Coscinodiscaceae. *Asteromphalus* abundance followed the pattern of < 1 °C surface seawater temperatures, in austral summer being mainly confined to the area south of 51°S (Fig. 2a, b; 217 valves studied), but they were more abundant in autumn (Fig. 2c, d; 412 valves studied) when their populations reached further north up to 40°S. In austral summer surface seawater temperatures < 1 °C reached northwards to 51°S (from station 131 southwards) but in austral autumn < 1 °C temperatures reached further to 50°S (from station 592 southwards). The lowest seawater temperatures recorded were − 1.4 to − 1.2 °C at stations 558, 495 and 469 near the Antarctic ice edge.

Morphology

Figures 3–14 illustrate via a combination of light and scanning electron microscopy the morphology in our Antarctic material of 8 + 1, 7 + 1, 6 + 1, 5 + 1, 4 + 1, and 3 + 1 ray forms, arranged from large to small cells. The number of hyaline rays was rarely 8 + 1 (1% of total *Asteromphalus;* SEM, Fig. 3), 7 + 1 (3%; LM, Fig. 4), or 6 + 1 (19%; SEM, Fig. 5, LM, Fig. 6) and these occurred only in larger cells (39–97 µm diameter), with 5 + 1 rays (35%; SEM, Figs. 7, 9, LM, Figs. 8, 10) and 4 + 1 (27%: SEM, Figs. 11, 12, LM, Fig. 13) the most common, and 3 + 1 representing the smallest valves (8%; 14–31 µm diameter; SEM, Fig. 14). Larger cells (6 + 1, 7 + 1, 8 + 1) always had smooth separating lines (arrowed in Fig. 4) while smaller cells (3 + 1; 4 + 1; 14–36 µm diameter) always contained jagged (zig-zag) separating lines in the central area (arrowed in Figs. 10, 13). In the intermediate size range of 5 + 1, 6 + 1 and rarely 7 + 1 ray forms, smooth separating lines occurred in larger cells (Fig. 8) but jagged spokes occurred in smaller 5 + 1 forms (Fig. 10). Similar to the variable number of rays or branched separating lines, the feature of straight rays or curved rays corresponded with cell diameter. The larger 5 + 1 to 8 + 1 ray morphs consistently had straight rays (Figs. 3–9), the smallest 3 + 1 and 4 + 1 ray morphs had curved rays (Figs. 11–14), with some overlap in smaller 5 + 1 cells (Fig. 10; slightly curved) or larger 4 + 1 cells (Fig. 11, straight). Furthermore,

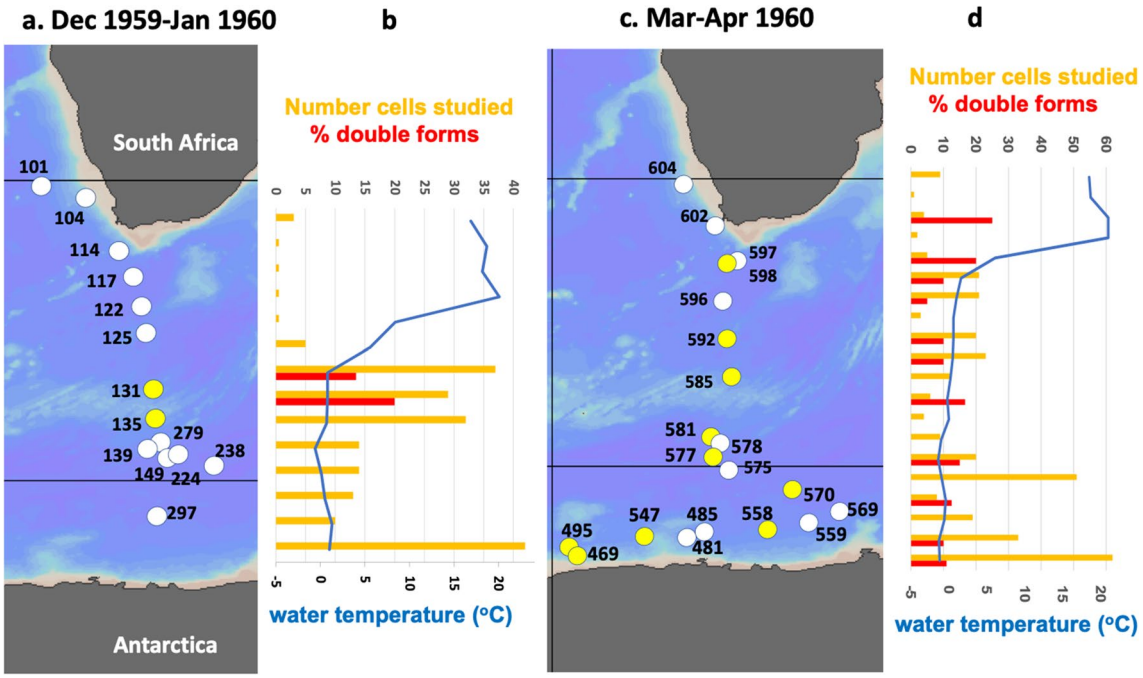


Fig. 2 Cruise track of MS *Willem Barendsz* entering the Atlantic sector of the Southern Ocean in December 1959 (**a**, **b**) and exiting March–April 1960 (**c**, **d**). Station numbers where *Asteromphalus* "double forms" were observed are indicated in yellow. Surface seawater temperatures (blue line), the total number of *Asteromphalus* cells studied (orange bars) and % "double forms" (red bars) are indicated (**b**, **d**)

the size of the central area also varied with cell diameter, being proportionally smaller in the largest 6 + 1, 7 + 1, and 8 + 1 ray forms (0.33–0.50 of diameter), larger (0.55–0.64) in the smaller 3 + 1 and 4 + 1 ray forms (e.g. Fig. 12), and intermediate in the 5 + 1 ray form (0.5–0.75). Again, with the same 4 + 1 ray morphs, larger cells had a proportionally smaller central area compared to smaller cells (compare Figs. 11 and 12).

Figures 15–33 illustrate fine structural characters used for *Asteromphalus* species discrimination as observed by scanning electron microscopy. Indentation of the valve margin was conspicuous, located to the left of the singular ray when viewed internally from the bottom of the valve (Fig. 15; arrow), but located to the right of the singular ray when viewed externally from the top of the cell (Fig. 16; arrow. The endings of the broad rays were always rounded in all ray forms (Fig. 15). Areolae occurred in rows parallel, or nearly so, to the margin, with larger areolae on the inner border of the segments (Fig. 15), 6 in 10 µm, and decreasing to 10 in 10 µm at the margin of the valves. The external (tympanum covering ray hole; Figs. 18–20) and internal rimoportulae details (flat kidney shaped labiate process; Fig. 21) of the ordinary ray holes were identical for all ray morphs. Similarly, the external (more elongate ray hole; Fig. 22) and internal (Fig. 23) rimoportulae details of the singular ray were uniform for all ray morphs. Large 8 + 1 and 7 + 1 ray morphs exhibited a quincunx cribrum structure (Hernández-Becerril 1991; Fig. 24), but mixtures of quincunx to circular cribra occurred in intermediate 6 + 1 and 5 + 1 ray morphs (Figs. 25–27), and exclusively circular cribra pore patterns were observed in 4 + 1 (Fig. 28) and 3 + 1 ray forms (Fig. 29). The nature of the separating lines was revealed to be clearly related to the partitioning of the central area into chambers. Smooth lines are demonstrated by SEM and LM, respectively, for 5 + 1 ray morphs (Figs 30, 31) and jagged lines for 4 + 1 ray morphs (Figs. 32, 33). Partially formed sibling cells (Fig. 34) or broken cells (Fig. 33) revealed that the separating lines were exclusively located in the roof of the central area (Fig. 35, arrows).

Silification deposition patterns

Samples from the KEOPS2 cruise from the Kerguelen Plateau in October—November 2011 contained abundant *Asteromphalus* cells represented by mostly 8 + 1 and more rarely 7 + 1 and 6 + 1 ray forms (Figs. 36–41). The use of the fluorescence probe PDMPO allowed us to identify cellular regions of active Si deposition. Active Si deposition in *Asteromphalus* was consistently associated with the central separating lines (Figs. 36, 37, arrows), which were smooth in large 8 + 1 ray forms, but in the case of jagged separating

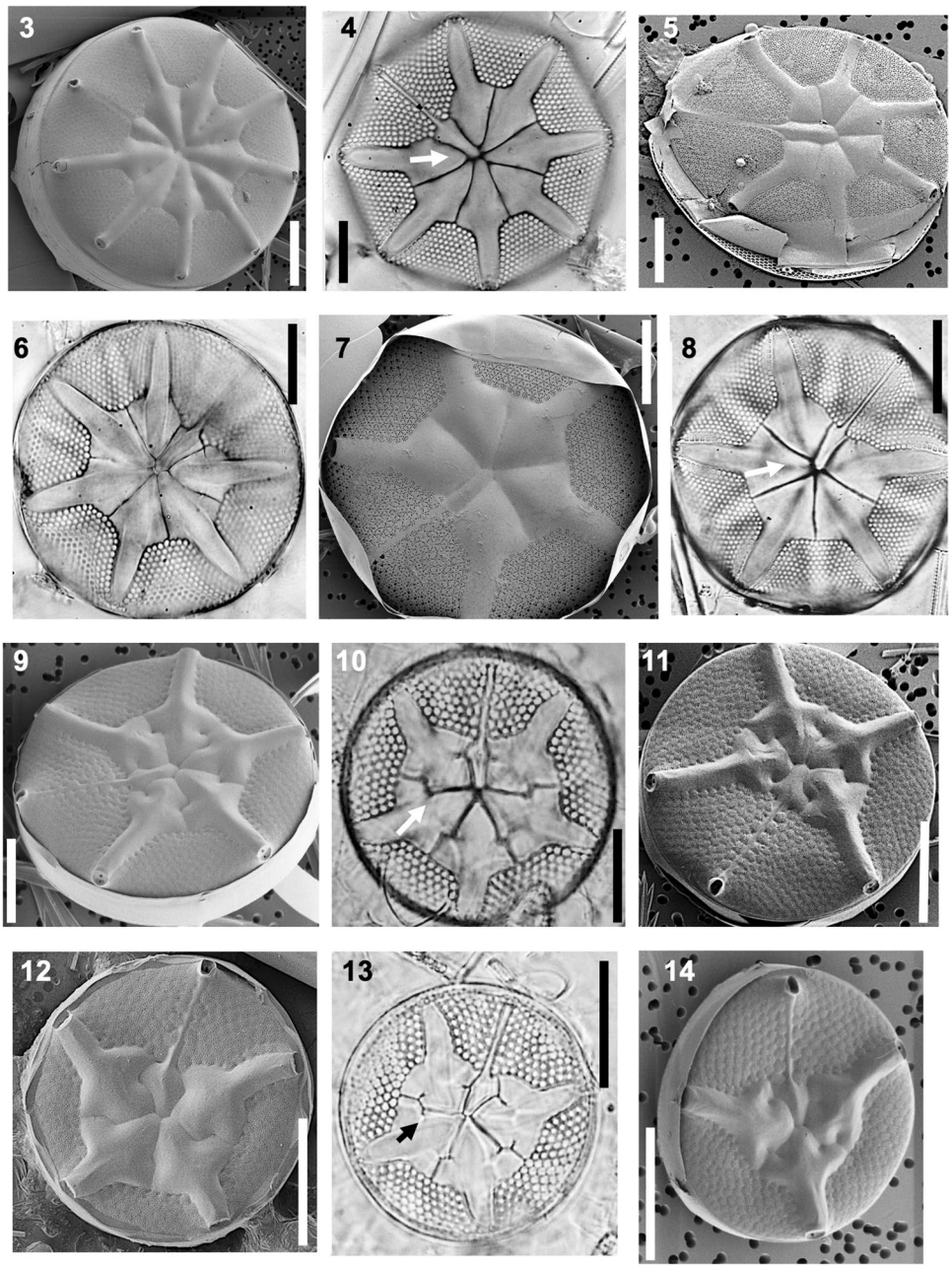
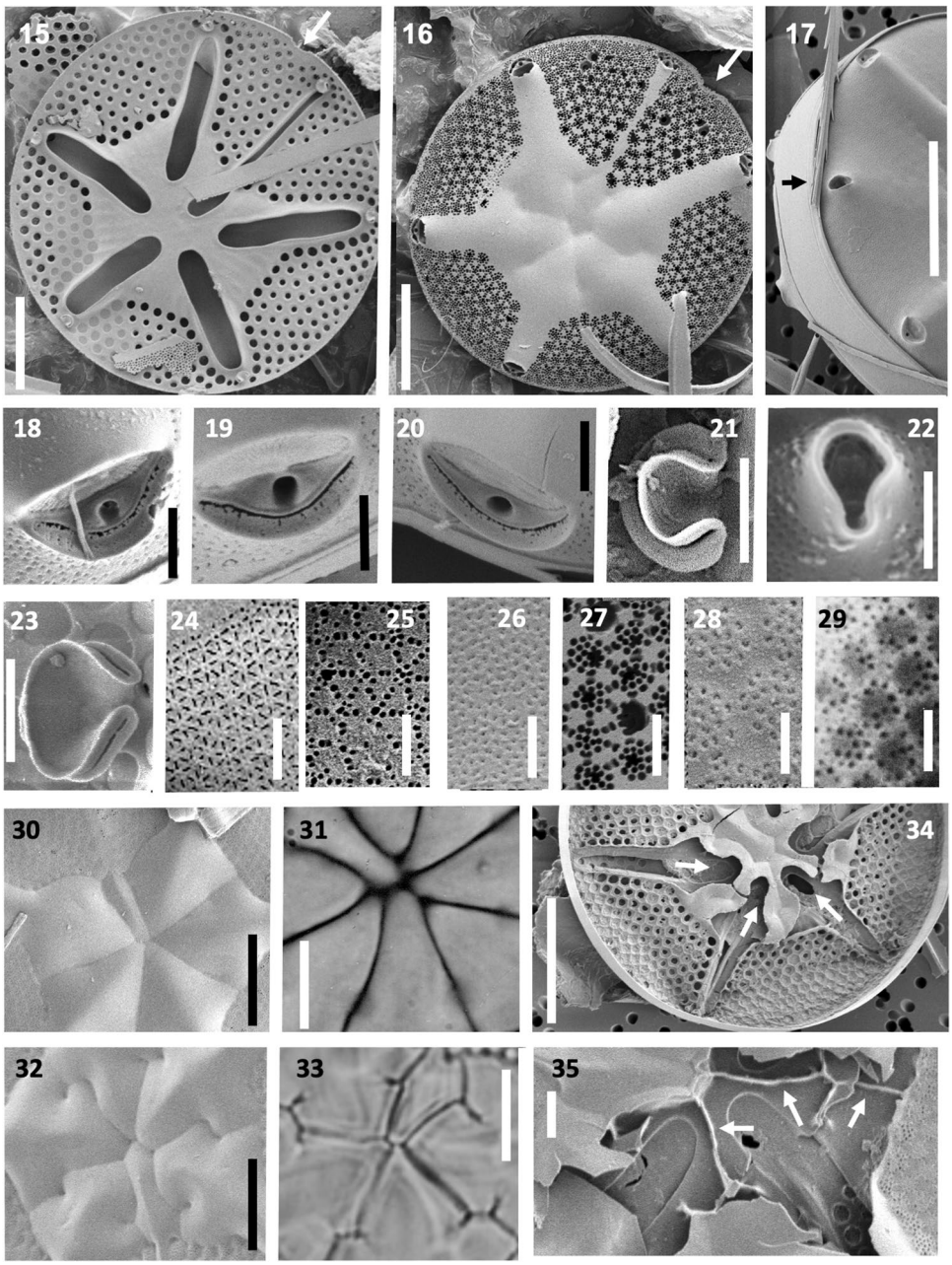


Fig. 3–14 Light and scanning electron micrographs of 8 + 1 (Fig. **3**), 7 + 1 (Fig. **4**), 6 + 1 (Figs. **5**, **6**), 5 + 1 (Figs. **7**–**10**), 4 + 1 (Figs. **11**–**13**), and 3 + 1 (Fig. **14**) ray morphs of *A. humboldtii*/ *A. hookeri*/ *darwinii*, arranged from large to small forms. The highly variable 5 + 1 forms include cells with smooth (Figs. **7**, **8**) and with jagged separating lines (white and black arrows; Figs. **9**, **10**), best visible by LM but appearing as harmonica-like folds of the central area by SEM. Both 5 + 1 and 4 + 1 forms exhibit considerable variation in the size of the central area relative to diameter (compare Figs. **7** and **9**, **11** and **12**). We identify the 8 + 1 ray morph in Fig. **3** as *A. humboldtii*, the 7 + 1, 6 + 1 and 5 + 1 ray morphs with smooth separating lines in Figs. **4**–**8** as *A. hookeri,* and the 5 + 1, 4 + 1 and 3 + 1 ray morphs with jagged separating lines in Figs. **9**–**14** as *A. darwinii*. All scale bars 10 µm

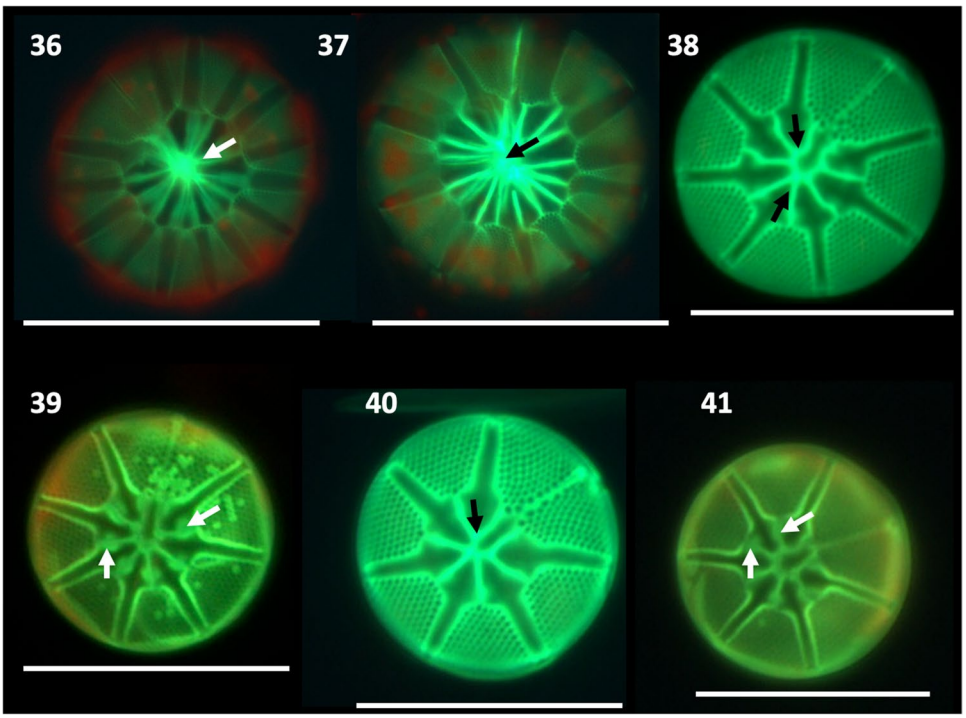
lines in 7 + 1 and 6 + 1 ray forms also associated with the swollen bend in those lines (Figs. 39, 41, arrows).

Double forms

Typically, the epitheca and hypotheca of an *Asteromphalus* valve are identical, except that the tube-shaped rays of one cell half are offset by one half of an areolated segment relative to the underlying valve. Figures 42–45 illustrate this for two recently divided, still adhering 6 + 1 rays cells comprised of four identical valves each rotated relative to the other. A surprise observation, first reported 50 years ago by Van der Spoel et al. (1973), was that of the 629 *Asteromphalus* cells studied a total of 37(6%) exhibited intervalvar variation with the designated hypotheca always having one ray less than the epitheca. Such 'double forms' were most common for the 4 + 1/3 + 1 and 5 + 1/4 + 1 ray morphs, rarer for 6 + 1/5 + 1, with only a single detection of a paired 7 + 1/6 + 1 double form, and no 8 + 1/7 + 1 couple observed. Double forms were more common and more widespread in autumn (10–20% of total cells in individual stations) than in summer when they were confined to two stations only (Fig. 2 C, D). Figures 47–50 illustrate two recently divided, still adhering cells, in the sequence 7 + 1/6 + 1; 7 + 1/6 + 1 rays, that is a double form generating a replica double



Figs. 15–35 Fine structure of *A. hookeri/ darwinii* valves. Fig. **15**. *A. darwinii*. Internal view of 5 + 1 ray morph showing the rounded ends of the broad rays (hollow tubes) and the linear singular ray. The marginal indentation (arrow) is located to the left of the singular ray. Tangential lines of areolae with internal foramina are shown, with slightly larger areolae surrounding the central area; Fig. **16**. *A. darwinii*. External view of an immature 5 + 1 sibling valve with external cribrum in various stages of development. The marginal indentation (arrow) is located to the right of the singular ray; Fig. **17**. *A. darwinii*. Detail of valve margin of a 4 + 1 ray morph showing the keyhole shaped external opening of the rimoportulae of the singular ray (arrow) flanked by external openings of the rimoportulae of the broad rays; Figs. **18**–**20**. Details of the external opening (ray hole) of rimoportulae of the broad rays of the 6 + 1, 5 + 1 and 4 + 1 ray morphs, respectively; Fig. **21** Internal lip-shaped rimoportula (labiate process) of a broad ray; Fig. **22**. Key-hole shaped external ray hole of singular ray; Fig. **23**. Internal lip-shaped rimoportula (labiate process) of a singular ray, Figs. **24**–**29**. Detail of areolation. Fig. **24**. *A. hookeri.* Quincunx external cribrum of mature valve (6 + 1 ray form in Fig. 5, smooth separating lines); Fig. **25**. *A. hookeri.* External cribrum of immature sibling cell 5 + 1 ray form in **7**, smooth separating lines; Fig. **26**. *A. darwinii*. Poroid ribrum of 6 + 1 ray form with jagged separating lines; Fig. **27**. *A. darwinii*. External cribrum of immature sibling cell 5 + 1 ray form in 16 (jagged separating lines); poroid star-shaped patterns. Fig. **28**. *A. darwinii.* Poroid cribrum of 4 + 1 ray form; Fig. **29**. *A. darwinii.* Poroid cribrum of 3 + 1 ray form. Figs. **30–33**. Details of separating lines. Figs. **30–31**. *A. hookeri.* Smooth lines of 5 + 1 ray morph by SEM (Fig. **30)** and LM (Fig. **31)**, respectively Figs. **32–33**. *A. darwinii*. Jagged lines of 4 + 1 ray morph by SEM (Fig. **32)** and LM (Fig. **33)**, respectively. Fig. **34**. Sibling cell with incompletely formed roof (arrows) of the central area of 5 + 1 morph. Fig. **35**. Broken roof of central area of 4 + 1 morph showing string-like separating lines (arrows), and ordinary ray pattern on bottom of the chamber. All scale bars 10 µm, except Figs. **18–29** (1 µm)



Figs. 36–41 PDMPO fluorochrome stained *Asteromphalus* cells from the Kerguelen Plateau in October–November 2011 represented by 8 + 1 (Figs. **36**–**37**), 7 + 1 (Figs. **38**–**39**) and 6 + 1 ray forms (Figs. **40**–**41**). Active Si deposition was associated with the central separating lines (Figs. 36, 37, arrows), which were smooth in large 8 + 1 ray forms designated as *A. humboldtii*, but in the case of jagged separating lines in 7 + 1 and 6 + 1 ray forms (*A. darwinii*) also associated with the swollen bend in those lines (Figs. 39, 41, arrows)

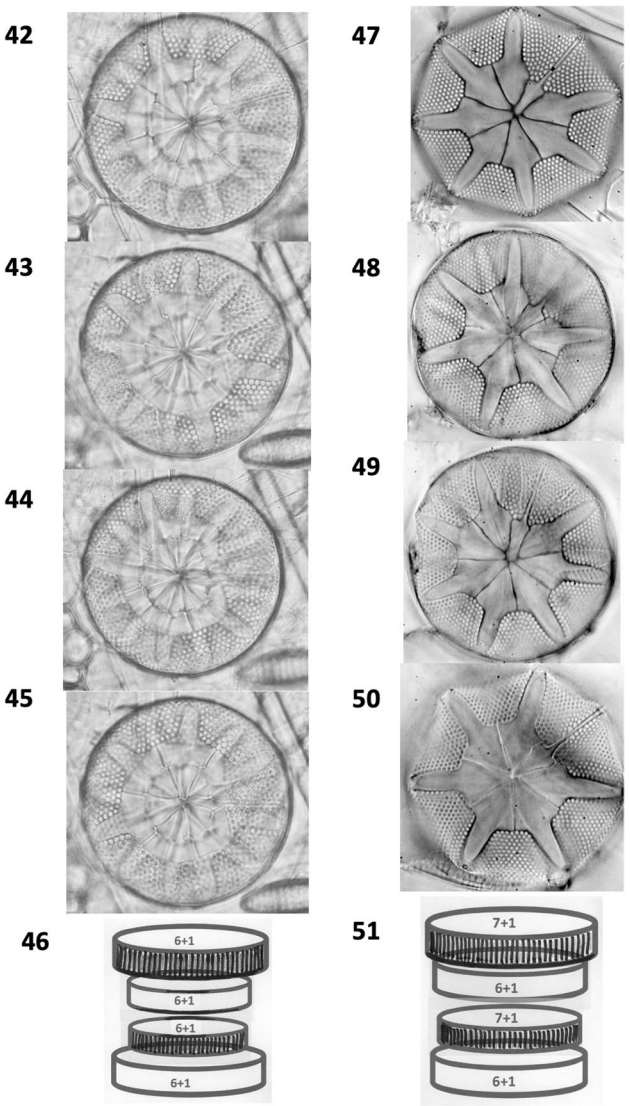
form. All ray morphs always exhibited identical arrangements of jagged (Figs. 42–45) or smooth separating lines (Figs. 47–50) between epitheca and hypotheca of the same cell and between parent and sibling cells.

Figure 52 summarises the total number of *Asteromphalus* cells studied from summer and autumn samples and their partitioning into the 8 + 1, 7 + 1, 6 + 1, 5 + 1, 4 + 1, and 3 + 1 ray forms, indicating the widespread occurrence of "double forms". The relationship between cell diameter and ray forms and the disappearance of jagged separating lines in large cells are indicated. The *Willem Barendsz* Antarctic material of 629 valves examined by oil immersion light microscopy and over 150 valves studied by scanning electron microscopy exhibited a gradient of ray morphs with no clear discontinuities discernible except for intermediate 5 + 1 and 6 + 1 ray forms where overlapping patterns of separating lines and cribra structure were evident.

Discussion

The nature of the "double forms"

The incidence in our material of 4 + 1/3 + 1, 5 + 1/4 + 1, 6 + 1/5 + 1, and 7 + 1/6 + 1 "double forms" provides strong circumstantial evidence that the ray morphs form part of the life cycle of one or more highly variable species. One possibility is that they could be a form of endogenous resting spore, resulting from unequal cell divisions and with some resting spores known to be heterovalvate (Johansen et al. 1985; McQuoid and Hobson 1996). The fact that the internal valves had identical fine structure and were not heavily silicified argues against this. The clear correlation between ray number and cell size (Fig. 52) makes it more likely that they form part of the normal process of vegetative cell division and result from MacDonald-Pfitzer cycle of size reduction (MacDonald 1869; Pfitzer 1869). The cycle would start with the largest sized 8 + 1 and 7 + 1 forms, gradually decreasing in diameter down to the smallest 3 + 1 forms. The finding of sibling cells with incompletely formed cribra (Fig. 16) supports that these are cell division stages. The largest number of 4 + 1/3 + 1 double forms coincided with the highest population density of 4 + 1 forms, largest number of 5 + 1/4 + 1 forms with 5 + 1, and 6 + 1/5 + 1 forms with high 6 + 1 population density (Fig. 52). Castracane (1886, Plate 9, his Fig. 2) previously illustrated from Antarctic material a teratological malformation (forma "*monstrosa*") of a dividing cell of *A. challengerensis* Castracane, comprising of 8 + 1 rays on the left and 5 + 1 rays on the right. He stated that "if this admitted (a frustule with a smaller number of radii than the other) then it is clear that no importance should be placed on the number of radii in specific determinations ". Priddle and Fryxell (1985) also suggested this monstrosity to be a synonym of *A. hookeri*. An anomalous form with two incompletely formed ordinary rays of the *A. hookeri* 5 + 1 ray form was illustrated by Hustedt (1958; his Plate 8, Fig. 90). A malformed cell of *Spatangidium (Asteromphalus) arachne* with 3 + 1 instead of 4 + 1 rays has also been reported (Tiffany and Hernández-Becerril 2005, Plate 26, their Fig. 2). The closest observation to our double forms, was made



Figs. 42–51 Various scenarios of *Asteromphalus* cell division stages. Figs. **42–46**. *A. darwinii.* Four 6 + 1 ray morph valves in a parent epitheca/sibling hypotheca/sibling epitheca/parent hypotheca arrangement, diagrammatically summarised in Fig. **46**; Figs. **47–51**. *A. hookeri*. "Double form" arrangement of 7 + 1 parent epitheca/6 + 1 sibling hypotheca/7 + 1 sibling epitheca/6 + 1 parent hypotheca arrangement, diagrammatically summarised in Fig. **51**. Note that all ray morphs exhibit identical arrangements of jagged (Figs. **42–45**; *A. darwinii*) or smooth separating lines (Figs. **47–50**; *A. hookeri*) between parent and sibling cells

by Wood (1959) who illustrated from Antarctic samples a "peculiar diatom", observed on two occasions in the same sample, with an *Asteromphalus* 8 + 1 rays epitheca combined with, what he believed to be, a *Coscinodiscus* hypotheca, and suggested to be mutations or crosses between two genera. We suggest that, alternatively, this could have been an *Asteromphalus* valve in the process of formation. At present, we have no knowledge of any such mechanism of hybridisation between different diatom species. Hence, we avoided the use of the term hybrid cells and instead refer to them as "double forms" until their precise status has been clarified. Except for the infrequent observation of teratological *Asteromphalus* cells, it remains surprising that no other reports of "double forms" are available for other *Asteromphalus* taxa. No double forms were found during the KEOPS2 cruise which featured predominantly 8 + 1 ray morphs, consistently with smooth separating lines, and more rarely 6 + 1 and 7 + 1 forms, the latter with jagged separating lines.

PDMPO Si uptake labeling

PDMPO fluorochrome labeling allowed for visualization of the process of sequential Si deposition in live diatoms, as previously demonstrated for Delaware Bay plankton (Leblanc and Hutchins 2005) and in the present work explored for Antarctic communities (see also Lafond et al. 2020). Similar to earlier observations, asynchronous division was evident in Antarctic diatom communities with cells of the same species within the same water sample or even same colony not always depositing biogenic silica simultaneously. In the present study, we newly point to the importance of the separating lines in silica uptake in *Asteromphalus* (Figs. 36–41). Such application of PDMPO labeling for gaining insights into diatom valve morphogenesis has not previously been conducted on any other global *Asteromphalus* populations, nor has this technique been used to determine diagnostic characters. While the number of hyaline rays was highly variable in an as yet unexplained manner, even between epitheca and hypotheca of sibling cells (Figs. 42–51), the feature of jagged versus smooth central separating lines appeared consistent also between epitheca and hypotheca of sibling cells. We thus conclude the character of morphology of separating lines to be of diagnostic value and not a simple valve developmental variation.

Species taxonomy

Figure 53 summarises type illustrations of Antarctic *Asteromphalus* taxa described by Ehrenberg (1844), Castracane (1886), Karsten (1905) and Manguin (1960). Table 1 compiles morphometric data used by various workers to discriminate Antarctic species of the *Asteromphalus darwinii /hookeri* species-complex. Species have been arranged according to the presence of jagged (*darwinii, rossii, beaumontii, parvulus, hyalinus, leboimei)* versus smooth separation lines (*hookeri, buchii, humboldtii)* and clustered according to ray morphs (3 + 1, 4 + 1, 5 + 1, 6 + 1, 7 + 1, 8 + 1) and valve diameter. Smallest valve diameters (14–36 µm) were always confined to the 3 + 1 and 4 + 1 ray morphs which also consistently have jagged separating lines and cribra with circular pore patterns. Largest valve diameters (up to 60 to 98 µm diameter) always had 7 + 1 or 8 + 1 ray morphs, smooth

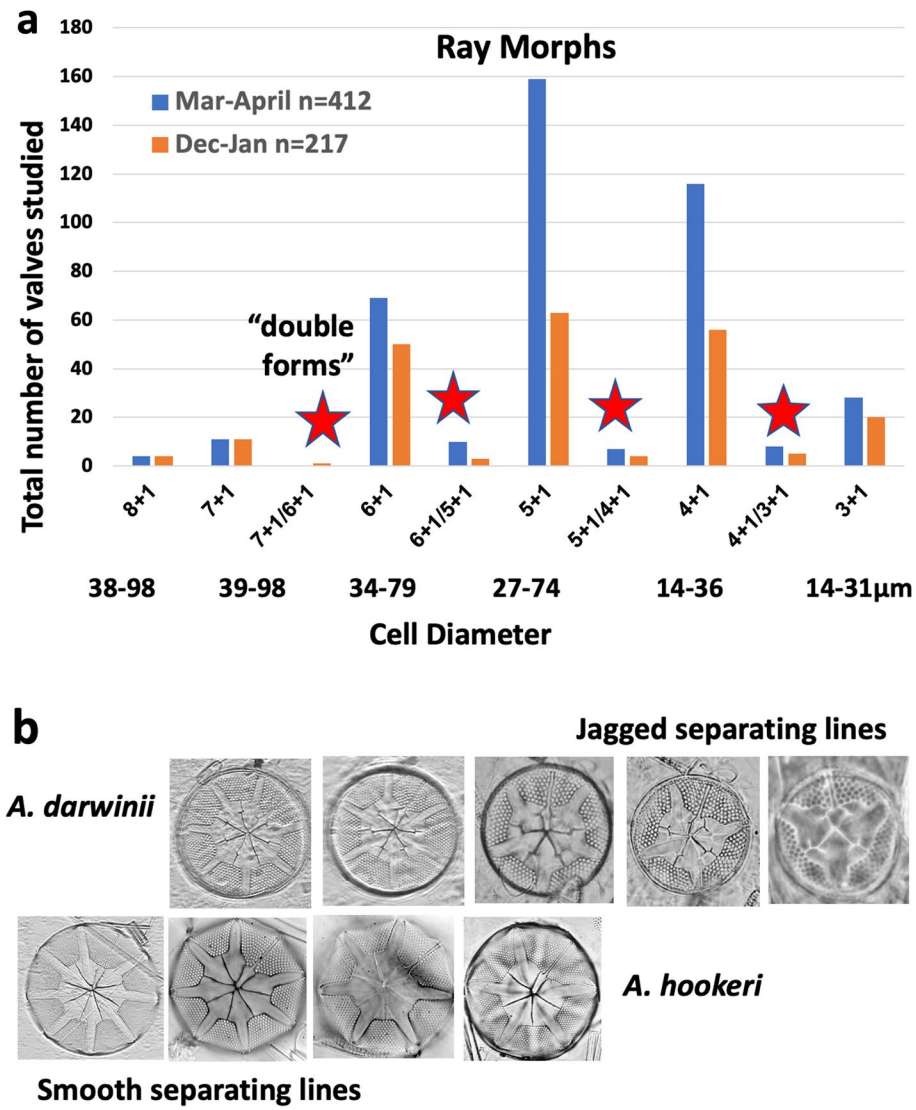


Fig. 52 a. Partitioning of the number of *Asteromphalus* cells counted from summer and autumn samples into the 8 + 1, 7 + 1, 6 + 1, 5 + 1, 4 + 1, and 3 + 1 ray forms. The number of hyaline rays varied from 3 broad + 1 narrow rays (designated 3 + 1) in the smallest valves (14–31 µm diameter), with 4 + 1 (27%) and 5 + 1 rays (35%) the most common, and 6 + 1, 7 + 1, and rarely 8 + 1 rays present only in larger cells (39–97 µm diameter); b. Smaller cells (3 + 1; 4 + 1; 14–36 µm diameter) commonly contained jagged (zig-zag) separating lines in the central area, identified as *A. darwinii*. Larger cells (6 + 1, 7 + 1, 8 + 1) most commonly had smooth separating lines, identified as *A. hookeri.* In the intermediate size 5 + 1 and 6 + 1 ray forms, both jagged and smooth separating lines can overlap and reflect two often confounded species. Similar to the variable number of rays and size of the central area, the feature of curved (3 + 1, 4 + 1) or straight rays (5 + 1 to 8 + 1) was correlated with cell diameter

separating lines and quincunx cribra patterns. Overlapping valve diameters between the two species groups occurred with the 5 + 1 and 6 + 1 ray forms. Density of areolae overlapped between the two species groups (7–10 in 10 µm) and size of the central area relative to cell diameter was strongly correlated with valve diameter (0.5–0.6 of diameter in small cells ranging to 0.3–0.4 in large cells).

The chronologically first described Antarctic species *A. darwinii* Ehrenberg 1844 (reproduced in Fig. 53i) was designated the lectotype of the genus by Boyer (1927). The only report in contemporary literature (Hernández-Becerril 1991) of *A. darwinii* relates to fossil material from Japan (Yezzo Natanai), but not from the Antarctic type locality. These Japanese cells consistently had 4 + 1 rays (not a variable number of rays), jagged separating lines and cribra of hyaline areas without poroids and flat areas with poroids. Furthermore, the Japanese cells had singular rays that were shorter than the other four rays, and not extending to the edge of the valve. This Japanese material thus does not agree with Ehrenberg's type illustration of *A. darwinii* and differs from our interpretation of this taxon. We argue that the 6 + 1 ray and 5 + 1 ray morphs with jagged separating lines, described as *A. beaumontii* Ehrenberg 1844 (Fig. 53f) and *A. rossii* Ehrenberg 1844 (Fig. 53g) are synonyms of *A. darwinii*. Hasle and Syvertsen (1997) also already raised possible conspecificity between *A. darwinii*, *A. rossii, A. parvulus* and *A. hyalinus*. The 4 + 1 form with jagged separation lines described as *A. hyalinus* (Karsten 1905; present Fig. 53j) closely resembles *A. darwinii* (4 + 1 rays), except for variations in size of the central area (0.30–0.63 of diameter) and curvature of the ordinary rays. We here argue that this constitutes part of the variability of the 4 + 1 morphs (Figs. 11–13). Hasle and Syvertsen (1997) already raised the problem that *A. parvulus* (5 + 1 and 6 + 1 forms; present Fig. 53 h) and larger specimens of *A. hyalinus* (4 + 1)

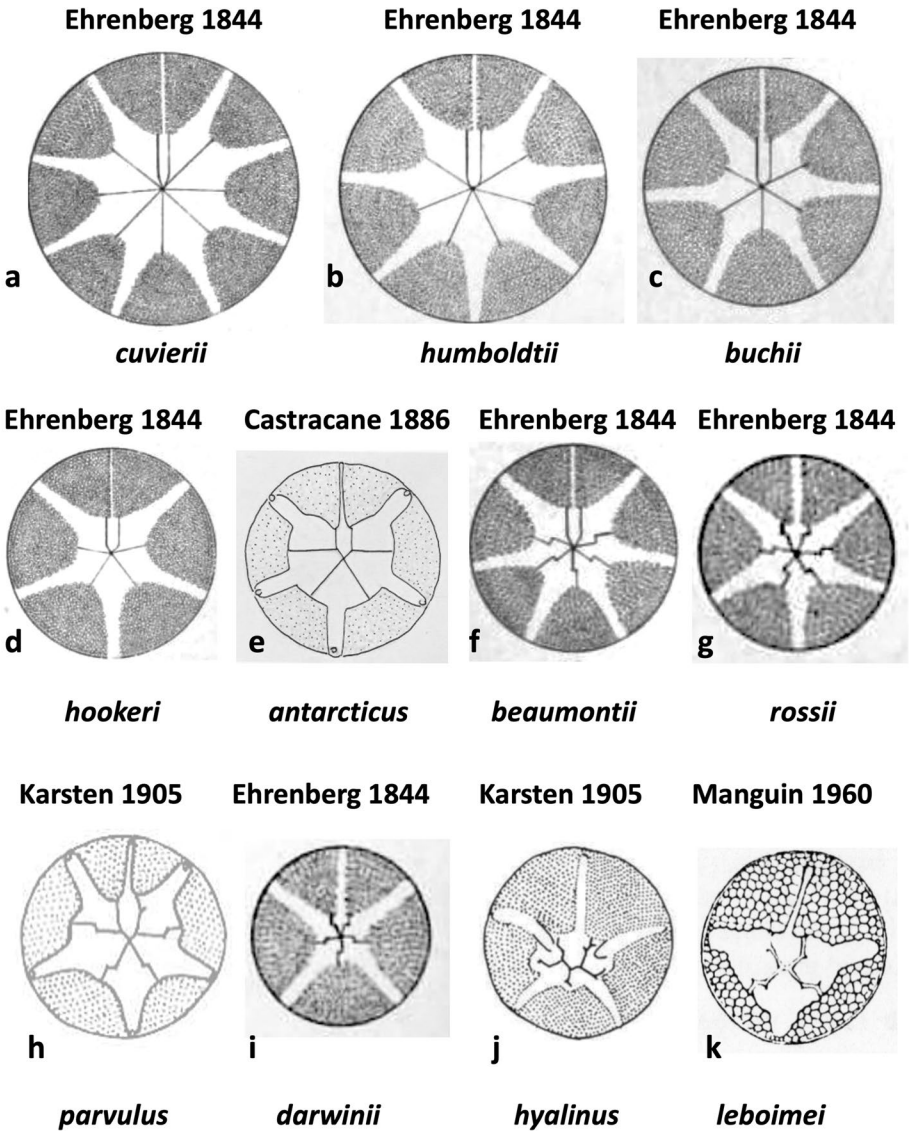


Fig. 53 Type illustrations (line drawings) of Antarctic *Asteromphalus* species reproduced from Ehrenberg 1844, Plate June, his Figs **1**–**7**; Castracane 1886, Plate 16, 11; Karsten 1905, Plate 8, 14–15; and Manguin 1960, Plate 3, his Fig. 44. Cells have been rearranged according to a sequence from 8 + 1 rays (*A. cuvierri*), 7 + 1 (*A. humboldtii*), 6 + 1 (*A. buchii),* 5 + 1 (*A. hookeri, A. antarcticus)* all with smooth separating lines; and 6 + 1 (*A. beaumontii*), 5 + 1 (*A. rossi, A. parvulus*), 4 + 1 (*A. darwinii, A. hyalinus*) to 3 + 1 rays (*A. leboimei*), all with jagged separating lines. This same sequence reflects a decrease of valve diameter from 97 down to 20 µm (compare Table 1)

could not be readily distinguished. We support this view, also reiterated by Ferrario et al. (2021). The smallest 3 + 1 form with jagged separating lines which was first illustrated by Hustedt (1958, Plate 8, his Fig. 85; as *A. hyalinus*), but described as a new species *A. leboimei* by Manguin (1960; present Fig. 53k), here also is proposed as a synonym of *A. darwinii.*

With regard to the Antarctic *Asteromphalus* with smooth separating lines, the chronologically first described species *A. hookeri* Ehrenberg 1844 (type illustration reproduced in Fig. 53d) should have priority. We argue that this 5 + 1 ray morph is synonymous with the 6 + 1 ray morph described as *A. buchii* Ehrenberg 1844 (present Fig. 53c). *Asteromphalus antarcticus* Castracane was described from a sample with numerous *A. darwinii*, and differentiated as having 5 + 1 rays but straight "umbilical lines" (Castracane 1886, Plate 16, his Fig. 3; present Fig. 53 e). We believe this species is a synonym of *A. hookeri.* We note that the *A. hookeri* cells illustrated by Hernández-Becerril (1991) include 5 + 1 and 6 + 1 ray morphs but also forms with both jagged and smooth separating lines, and a quincunx cribrum fine structure. This suggests the inclusion of two different taxa (his Figs. 24.2 vs 24.3). Priddle and Fryxell (1985) similarly mistakingly include in *A. hookeri* forms with both "smooth and bifurcate spokes". These two taxa, *A. darwinii* Ehr. (synonyms *A. beaumontii* Ehr *A. hyalinus* Karsten*, A. leboimei* Manguin, *A. parvulus* Karsten*, A. rossii* Ehr.) and *A. hookeri* Ehr. (synonyms *A. antarcticus* Castracane*, A. buchii* Ehr.) were also confused in our earlier account on the Willem Barendsz material (Van der Spoel et al. 1973).

Hernández-Becerril (1995) presented arguments that *A. humboldtii* (more robust and larger, 90–150 µm, commonly 8 + 1 up to 10 + 1 rays), always with smooth separating lines, should not be a synonym of *A. hookeri.* It remains possible

Table 1 Morphometric data of the *Asteromphalus darwinii /hookeri* species-complex from Antarctic waters as interpreted by various workers. Species have been arranged according to the presence of jagged (*darwinii, rossii, beaumontii, parvulus, hyalinus, leboimei*) versus smooth separating lines (*hookeri, buchii, antarcticus, humboldtii, cuvierii*) and clustered according to ray morphs (3 + 1, 4 + 1, 5 + 1, 6 + 1, 7 + 1, 8 + 1) and valve diameter. * estimated from published illustrations.

Species	Number of ordinary + singular rays	Valve Diameter (µm)	Size central area relative diameter	Sector areolae in 10 µm	cribrum fine structure	Shape of Separation lines	Curvature of ordinary rays	locality	Authority
darwinii	4 + 1	32	0.30*	No data		**Jagged**	Straight	Antarctic	Ehrenberg (1844), plate June, Fig. 1
rossii	5 + 1	60	0.40*	No data		Jagged	Straight	Antarctic	Ehrenberg (1844), plate June, Fig. 2
beaumontii	6 + 1	47	0.40*	No data		Jagged	Straight	Antarctic	Ehrenberg (1844), plate June, Fig. 5
parvulus	5 + 1	30–48	0.5–0.75	"Coarse"		Jagged	Straight	Antarctic	Karsten (1905), Plate 8, Fig. 14
ibid	5 + 1; 6 + 1	30–50 (55)	No data	No data		Jagged	No data	Antarctic	Priddle and Fryxell (1985)
ibid	5 + 1	22–48	0.5–0.75	8–10		"Broken"	Straight	Global	Hasle and Syvertsen (1997)
ibid	5 + 1 to 6 + 1	33.5–38.5	0.50	7–8	cribrum pores in circular pattern	Branched		Antarctic	Ferrario et al. (2021)
hyalinus	4 + 1, curved	22–32	0.5	"fine"		Jagged	Curved	Antarctic	Karsten (1905) Plate 8, Fig. 4
ibid	4 + 1	20–30	No data	6–9		Jagged	No data	Antarctic	Priddle & Fryxell (1985)
ibid	2 + 1? to 4 + 1	15–32	0.5	8–12		Genu-flexed; branched	Curved	Global	Hasle & Syvertsen (1997)
ibid	3 + 1 to 6 + 1	15.5–35.8	0.5	8–10	cribrum pores in circular pattern	Branched		Antarctic	Ferrario et al. (2021)
leboimei	3 + 1	20		10		Zigzag with hooks	Curved	Antarctic	Manguin (1960), Plate 3, Fig. 6
darwinii	5 + 1 to 6 + 1	30–38	0.50–0.56	8	Circular or star-shaped pore patterns	Jagged	Straight	Antarctic	**Present work**
darwinii	4 + 1	**14–36**	0.55–0.64	7.5–10;	cribrum pores in circular pattern	Jagged	Straight / slightly curved	Antarctic	**Present work**

Table 1 (continued)

Species	Number of ordinary + singular rays	Valve Diameter (µm)	Size central area relative diameter	Sector areolae in 10 µm	cribrum fine structure	Shape of Separation lines	Curvature of ordinary rays	locality	Authority
darwinii	3 + 1	**14–31**	0.53–0.63	9	cribrum pores in circular pattern	Jagged	Slightly curved	Antarctic	**Present work**
hookeri	5 + 1	87	0.32*	No data		**Smooth**	Straight	Antarctic	Ehrenberg (1844), plate June, Fig. 3
ibid	5 + 1 to 8 + 1	25–60	0.33–0.50	5–9?		Smooth		Global	Hasle and Syvertsen (1997)
ibid	6 + 1 to 10 + 1	No data	No data	No data		Smooth, bifurcate if > 6 + 1	No data	Antarctic	Priddle and Fryxell (1985)
ibid	5 + 1 to 8 + 1	25–60	0.33–0.50	5–9?		Smooth		Global	Hasle and Syvertsen (1997)
ibid	6 + 1 to 10 + 1	No data	No data	No data		Smooth, bifurcate if > 6 + 1	no data	Antarctic	Priddle and Fryxell (1985)
buchii	6 + 1	60	0.34*	No data		Smooth	Straight	Antarctic	Ehrenberg (1844), plate June, Fig. 4
antarcticus	5 + 1	No data	0.52*	No data		Smooth	Straight	Antarctic	Castracane (1886), plate 16, Fig. 3
hookeri	8 + 1	38–98	0.48	8		Smooth	Straight	Antarctic	**Present work**
hookeri	7 + 1	39–98	0.53	8		Smooth	Straight	Antarctic	**Present work**
hookeri	6 + 1	34–79	0.47	9	Quincunx cribrum	Smooth	Straight	Antarctic	**Present work**
hookeri	5 + 1	(22) 27–74	0.48–0.53	8–9	quincunx cribrum	Smooth in larger cells	Straight	Antarctic	**Present work**
hookeri	8 + 1	38–98	0.48	8		Smooth	Straight	Antarctic	**Present work**
humboldtii	7 + 1	82	0.44*	No data		Smooth	Straight	Antarctic	Ehrenberg (1844), plate June, Fig. 6
ibid	7 + 1 to 10 + 1	91–149	0.33	6–6.5		Smooth	Straight	Antarctic	Hernández-Becerril (1995)
ibid	5 + 1; 6 + 1	43–78; 40–73.5	0.33–0.50; 0.50	7–8; 8–10	Quincunx; cribrum of central pores surrounded by elongate pores	Angled, straight-curved	Straight or slightly curved	Antarctic	Hernández-Becerril (1991); Ferrario et al. (2021)
cuvierii	8 + 1	82	0.48*	No data		Smooth		Antarctic	Ehrenberg (1844), plate June, Fig. 7

Species have been arranged according to the presence of jagged (*darwinii, rossii, beaumontii, parvulus, hyalinus, leboimei)* versus smooth separating lines (*hookeri, buchii, antarcticus, humboldtii, cuvierii)* and clustered according to ray morphs (3 + 1, 4 + 1, 5 + 1, 6 + 1, 7 + 1, 8 + 1) and valve diameter. * estimated from published illustrations

that the larger cells in our study were not *A. humboldtii* but larger individuals of *A. hookeri.* However in our study, we never found double forms that involved 8 + 1 or larger ray morphs, and hence we similarly view *A. humboldtii* and the possible later synonym *A. cuvierii* to be distinct from *A. hookeri.* Such larger cells (with coarser areolation 6–6.5 in 10 µm, and quincunx cribra) were sparse in our material and require further study.

We hope that the present observations help to distinguish two highly variable and often confused Antarctic diatom species, *A. darwinii* (jagged separating lines, 3 + 1 to 7 + 1 ray morphs, poroid cribra) and *A. hookeri* (smooth separating lines, 5 + 1 to 8 + 1 ray morphs, quincunx cribra). For the moment, larger forms with smooth separating lines and 8 + 1 or 9 + 1 rays are best classified as *A. humboldtii.* However, molecular sequences of hand-picked cells are needed to confirm the revisions suggested here. The number of rays in these taxa is highly variable and not a suitable diagnostic character, as well demonstrated by the incidence of "double forms" with varying ray numbers in epi- and hypotheca of the same frustule. Ehrenberg did not explicitly designate types for his many taxa, nor label types in his collection which is housed at Museum für Naturkunde in Berlin (Lazarus and Jahn 1998). Future efforts may be attempted to corroborate the diagnostic characters for his numerous *Asteromphalus* species. Correct taxonomy of Antarctic diatoms is critical to document any future impacts from climate change and elucidate changes in biogeography. The validity of putative species distribution records of *A. hookeri, A. parvulus* and *A. hyalinus* in cold-water Northern Hemisphere habitats calls for further scrutiny (Hendey 1964; Hasle and Syvertsen 1997). Finally we encourage future *Asteromphalus* culture studies to elucidate the fascinating valve morphogenesis, how the hollow rays form and the active role played by the separating lines in silica uptake.

Amended diagnoses

Asteromphalus darwinii

Ehrenberg (Ehrenberg1844, pp. 198 and 200, his Fig. 1).

Synonyms: *A. beaumontii* Ehr. 1844, *A. hyalinus* Karsten 1905*, A. leboimei* Manguin 1960, *A. parvulus* Karsten 1906*, A. rossii* Ehr. 1844.

Valve outline circular, 14–60 µm diameter. The central area occupies 0.75 of valve diameter in smaller cells, but down to 0.30 of valve diameter in larger cells. Areolae 6–10 in 10 µm, with criba pores in a circular pattern. Central separating lines are jagged. Smaller cells have 3, 4 or 5 and larger cells 6, 7 or 8 ordinary rays in addition to the singular ray. Ordinary rays are straight in larger cells but slightly curved in smaller cells.

Asteromphalus hookeri

Ehrenberg (type Ehrenberg\ 1844, p. 200, his Fig. 3).

Synonyms: *A. antarcticus* Castracane 1886*, A. buchii* Ehr. 1844.

Valve outline circular, 25–98 µm diameter. The central area occupies 0.53 of valve diameter in smaller cells, but down to 0.30 of valve diameter in larger cells. Areolae 5–9 in 10 µm, with criba pores in a quincunx pattern. Central separating lines are smooth. Smaller cells have 5 or 6 and larger cells 7 or 8 ordinary rays in addition to the singular ray. Ordinary rays are straight.

Acknowledgements GMH thanks Prof. Siebrecht van der Spoel from the Institute of Taxonomic Zoology of the University of Amsterdam for providing access to his Antarctic phytoplankton samples while working as a student at the University of Amsterdam, Netherlands. Mr L. van der Laan assisted with taking the first light micrographs of double forms. The late Professors Grethe Hasle, University of Oslo, and Greta Fryxell, Texas A&M University, provided constructive criticism on an earlier 1973 account on *Asteromphalus*. Drs Karsten Goemann and Sandrin Feig offered expert technical assistance with electron microscopy at the University of Tasmania. The KEOPS work was supported by the French Research program of INSU-CNRS LEFE−CYBER (Les enveloppes fluides et l'environnement – Cycles biogéochimiques, environnement et ressources); the French ANR (Agence Nationale de la Recherche, SIMI-6 program); the French CNES (Centre National d'Études Spatiales); the French Polar Institute IPEV (Institut Polaire Paul−Emile Victor). KL thanks project's PI and chief scientist on board Pr. Stéphane Blain and Pr. Bernard Quéguiner.

Author contributions GMH wrote the main text and prepared the figures. KLB contributed the PDMPO images. Both authors reviewed the manuscript.

Funding Open Access funding enabled and organized by CAUL and its Member Institutions. The KEOPS work was supported by the French Research program of INSU-CNRS LEFE − CYBER (Les enveloppes fluides et l'environnement – Cycles biogéochimiques, environnement et ressources); the French ANR (Agence Nationale de la Recherche, SIMI-6 program); the French CNES (Centre National d'Études Spatiales); the French Polar Institute IPEV (Institut Polaire Paul − Emile Victor).

Declarations

Conflict of interest The authors have no competing interest to declare that are relevant to the content of this article.

References

Armbrecht L, Weber ME, Raymo ME, Peck VL, Williams T, Warnock J et al (2022) Ancient marine sediment DNA reveals diatom transition in Antarctica. Nat Commun 13:5787. https://doi.org/10.1038/s41467-022-33494-4

Boyer CS (1927) Synopsis of North American Diatomaceae. Part I. Coscinodiscatae, Rhizosolenatae, Biddulphiatae, Fragilariatae. Proc Acad Natl Sci Phila 78:1–228

Castracane CAF (1886) Report on the *Diatomaceae* collected by HMS challenger during the years 1873–76 Report on the scientific results of the Voyage of HMS challenger during the years 1873–76. Botany 2:1–178

Ehrenberg CG (1844) Einige vorläufige Resultate seiner Untersuchungen der ihm von der Südpolreise des Captain Ross, so wie von den Herren Schayer und Darwin zugekommenen Materialien über das Verhalten des kleinsten Lebens in den Oceanen und den grössten bisher zugänglichen Tiefen des Weltmeeres. Bericht über die zur Bekanntmachung Geeigneten Verhandlungen Der Königl. Preuss Akademie Der Wissenschaften Zu Berlin 1884:182–207

Ferrario ME, Cefarelli AO, Fernándes LF, Castaños C, Hernandez-Becerril DU (2021) Morphology and taxonomy of marine planktonic diatoms of the genus *Asteromphalus* (Bacillariophyceae) in Antarctic waters and the Southwestern Atlantic Ocean. Beihefte Zur Nova Hedwigia 151:183–204

Fryxell GA, Hasle GR (1974) Coscinodiscineae: some consistent patterns in diatom morphology. Beihefte Zur Nova Hedwigia 45:69–84

Greville RK (1860) A monograph of the genus *Asterolampra*, including *Asteromphalus* and *Spatangidium*. Transactions Microscopical Society of London New Series 8:102–124

Guiry MD, Guiry GM (2021) Algaebase. World-wide electronic publication, National University of Ireland, Galway. https://www.algaebase.org. Accessed 09 Aug 2021.

Hasle GR, Syvertsen EE (1997) Marine Diatoms. In: Tomas CR (ed) Identifying marine phytoplankton. Academic Press, San Diego, USA, pp 5–385

Hendey NI (1964) An Introductory Account of the Smaller Algae of British Coastal Waters. Part V. Bacillariophyceae (Diatoms). Ministry of Agriculture, Fisheries and Food, Fishery Investigations, Series 4, 317 pp. Her Majesty's Stationery Office, London, UK

Hernández-Becerril DU (1991) The morphology and taxonomy of species of the diatom genus *Asteromphalus* Ehr. Bibl Diatomol 23:1–57

Hernández-Becerril DU (1992) Reinstatement of the diatom genus *Spatangidium* (Bacillariophyceae): the type species *S. arachne*. Phycologia 31:278–284

Hernández-Becerril DU (1995) The genus *Asteromphalus*: further studies of some little-known species and comments on its taxonomy. In: Kociolek JP, Sullivan MJ (eds) A century of diatom research in North America: a tribute to the distinguished careers of Charles W. Reimer and Ruth Patrick. Koeltz Scientific Books, Champaign, ILL, USA

Hustedt F (1958) Diatomeen aus der Antarktis und dem Südatlantik. Deutsche Antarktischen Expedition 1938–1939(2):103–191

Johansen JR, Doucette GJ, Fryxell GA (1985) The genus *Thalassiosira* (Bacillariophyceae): Morphology of heterovalvate resting spores of *T. scotia*. Am J Botany 72:1861–1870

Karsten G (1905) Das Phytoplankton des Antarktischen Meeres nach dem Material der deutschen Tiefsee-Expedition 1898–1899. Wissenschaftliche Ergebnisse Der Deutschen Tiefsee-Expedition Auf Dem Dampfer 'valdivia' II 2:1–136

Lafond A, Leblanc K, Legras J, Cornet V, Quéguiner B (2020) The structure of diatom communities constrains biogeochemical properties in surface waters of the Southern Ocean (Kerguelen Plateau). J Mar Syst 212:103456

Lazarus D, Jahn R (1998) Using the Ehrenberg collection. Diatom Res 13:273–291

Leblanc K, Hutchins DA (2005) New applications of a biogenic silica deposition fluorophore in the study of oceanic diatoms. Limnol Oceanography-Methods 3:462–476

MacDonald JD (1869) On the structure of the diatomaceous frustule, and its genetic cycle. Annales Magaz Nat History, Ser 4:1–8

Manguin E (1960) Les Diatomées de la Terre Adélie. Campagne du Commandant Charcot 1949–1950. Annales Des Sci Naturelles, Botanique, Série 12:223–363

McQuoid MR, Hobson LA (1996) Diatom resting stages. J Phycol 32:889–902

Nakov T, Ashworth M, Theriot EC (2015) Comparative analysis of the interaction between habitat and growth form in diatoms. ISME J 9:246–255

Ocean Biogeographic Information System OBIS. https://www.obis.org. Accessed 1 Aug 2021.

Pfitzer E (1869) Über den Bau und die Zellteilung der Diatomeen. Botanische Zeitung 27:774–776

Priddle J, Fryxell G (1985) Handbook of the common plankton diatoms of the Southern Ocean: Centrales except the genus *Thalassiosira*. British Antarctic Survey. Natural Environment Research Council, Cambridge, UK

Rattray J (1889) A revision of the genus *Coscinodiscus* and some allied genera. Proc Royal Soc Edinburgh 16:449–692

Tiffany MA, Hernández-Becerril DU (2005) Valve development in the diatom family Asterolampraceae H. L Smith 1872. Micropaleontology 51:217–258

Turland NJ, Wiersema JH, Barrie FR, Greuter W, Hawksworth D, Herendeen PS et al (eds.) (2018) International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017. Regnum Vegetabile 159. Glashütten: Koeltz Botanical Books. https://doi.org/10.12705/Code.2018

Van der Spoel S, Hallegraeff GM, Van Soest RWM (1973) Notes on variation of diatoms and silicoflagellates in the South Atlantic Ocean. Neth J Sea Res 6:518–541

Van Landingham S (1967) Catalogue of the fossil and recent genera and species of diatoms and their synonyms. *Acanthoceras* through *Bacillaria* 1:493

Vernette C, Henry N, Lecuin J, de Vargas C, Hingamp P, Lescot M (2021) The Ocean Barcode Atlas: a web service to explore the biodiversity and biogeography of marine organisms. Molecular Ecolog Res 21:1347–1358. https://doi.org/10.1111/1755-0998.13322

Wood EJF (1959) An unusual diatom from the Antarctic. Nature 184:1962–1963