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# The genus *Humidophila* (Bacillariophyta) in Greenland with the description of 2 new species

Charlotte Goeyers[1,2*], Koen Sabbe[2], Elie Verleyen[2], Paul B. Hamilton[3], Tyler J. Kohler[4] & Bart Van de Vijver[1,5]

[1]*Meise Botanic Garden, Research Department, Nieuwelaan 38, B–1860, Meise, Belgium; *Corresponding author e–mail: charlotte.goeyers@plantentuinmeise.be*
[2]*Ghent University, Lab Protistology and Aquatic Ecology, Department of Biology, Krijgslaan 281–S8, B–9000, Ghent, Belgium*
[3]*Canadian Museum of Nature, Research and Collections, 240 McLeod St, Ottawa, Canada*
[4]*Department of Ecology, Faculty of Science, Charles University, CZ–12844, Prague, Czechia*
[5]*University of Antwerp, Department of Biology, ECOSPHERE, Universiteitsplein 1, B–2610, Wilrijk, Belgium*

**Abstract:** During a survey of the terrestrial moss diatom flora in Greenland, two unknown *Humidophila* species were observed that could not be identified using the currently available literature. Detailed morphological analysis using both light and scanning electron microscopy revealed sufficient morphological differentiation from known species to describe these as new species: *H. helderiana* sp. nov and *H. mitosis* sp. nov. Formal descriptions are presented, each illustrated by light and scanning electron micrographs, and the new species are compared with similar *Humidophila* taxa worldwide. Additionally, eight previously described species which were also observed are discussed, and *Humidophila mochalovae* comb. nov., formerly belonging to the genus *Diadesmis*, was transferred to *Humidophila*. Of these known species, six have not been previously reported from Greenland, expanding their known geographic distributions. Our findings bring the total number of *Humidophila* species globally to 87 and contribute to a better understanding of the terrestrial Arctic diatom flora.

**Key words:** *Humidophila,* diatoms, Arctic, Greenland, morphology, new species

## Introduction

The genus *Humidophila* was established in 2014 by Lowe et al. to accommodate the taxa formerly belonging to the subgenus *Paradiadesmis* Lange–Bertalot et Le Cohu of the genus *Diadesmis* Kützing, that was originally described by Kützing (1844). The original *Diadesmis* description contained four species: one newly described, *Diadesmis confervacea* Kützing*,* whereas three others, *D. laevis* Ehrenberg*, D. sculpta* (Ehrenberg) Kützing, and *D. bacillum* (Ehrenberg) Kützing, were transferred from other genera (Kützing 1844). In 1880, Grunow transferred the members of *Diadesmis* to the genus *Navicula* Bory (Van Heurck 1880). Almost 150 years after the original description of *Diadesmis*, the genus was re–examined in Round et al. (1990), and the authors lectotypified *Diadesmis* with *Diadesmis confervacea* Kützing as the generitype (Round et al. 1990). The subgenus *Paradiadesmis* Lange–Bertalot et Le Cohu was described in 2000 based on a group of closely related *Diadesmis* species that differed from the generitype (Rumrich et al. 2000), by having striae with elongated areolae rather than rounded areolae, delimited by a hyaline zone that occupies the entire circumference of the valve and a vallum separating valve face and mantle areolae. Yet, the authors indicated that *Paradiadesmis* would likely be elevated to genus in the future when more assessments were completed. By 2014, based on detailed studies of the ultrastructure of numerous representatives of the genus *Diadesmis,* 47 existing members of *Paradiadesmis* were transferred to the new genus *Humidophila* (Lange–Bertalot et Werum) R.L.Lowe, Kociolek, Johansen, Van de Vijver, Lange–Bertalot et Kopalová, with *H. undulata* R.L.Lowe, Kociolek et Johansen as generitype (Lowe et al. 2014). The genus name is based on the typically humid, aerophilous habitat preferred by this group. More recently, molecular data has demonstrated that *Diadesmis* and *Humidophila* are phylogenetically disparate groups (Andreeva et al. 2016).

The genus *Humidophila* includes small, biraphid diatoms, characterized by linear to elliptical valves (rarely with protracted ends), a filiform raphe with simple,

drop–shaped or anchor–shaped central and terminal raphe endings, terminal raphe endings without terminal raphe fissures, and striae composed of one, usually transapically elongated, elliptical to ovoid areola, internally covered by a perforated hymen (Lowe et al. 2014). Species are generally distinguished by their valve outline and dimensions, stria density and length, striation pattern, shape of their central raphe and terminal raphe endings, size and shape of the central area, and the presence or absence of an interruption around the apices (Lowe et al. 2014; Kopalová et al. 2015; Kochman–Kędziora et al. 2016; Taylor & Cocquyt 2016; Ferreira et al. 2023). Most *Humidophila* species prefer moist habitats and are found in acidic oligotrophic waters, damp mosses, soils, and on rocks (Lowe et al. 2014; Taylor & Cocquyt 2016; Vouilloud et al. 2022; Ferreira et al. 2023).

*Humidophila* is widely distributed, with *H. contenta* (Grunow) R.L.Lowe, Kociolek, J.R.Johansen, Van de Vijver, Lange–Bertalot et Kopalová, *H. gallica* (W.Smith) R.L.Lowe, Kociolek, J.R.Johansen, Van de Vijver, Lange–Bertalot et Kopalová and *H. paracontenta* (Lange–Bertalot et Werum) R.L.Lowe, Kociolek, J.R.Johansen, Van de Vijver, Lange–Bertalot et Kopalová assumed to be cosmopolitan species (Lowe et al. 2014). However, most observations of *Humidophila* are from the Southern Hemisphere, with many recordings from Central and South America (Rumrich et al. 2000; Werum & Lange–Bertalot 2004; Metzeltin et al. 2005; Vouilloud et al. 2022), the Antarctic and Sub–Antarctic regions (e.g. Kopalová et al. 2015; Kochman–Kędziora et al. 2016; Chattová et al. 2018), and New Caledonia (Moser et al. 1998). In the Northern Hemisphere, the Guizhou Province in China has been found to be a *Humidophila* 'hotspot' (Lowe et al. 2017) together with Hawaii (Lowe et al. 2014), while new species were recently described from Yakutia, Russia (Genkal & Gabyshev 2023) and Manipur, India (Yogeshwaran et al. 2022). More 'hotspots' will likely appear when other regions are investigated in detail as well.

Little is known about the occurrence of *Humidophila* in the Arctic, especially compared to the Antarctic region. One of the first authors reporting *Humidophila* in the Arctic was Johannes Boye Petersen, who examined diatoms from aerial samples such as soil, woodwork, stones, cliffs, caves, and trees from Iceland and Greenland and described *Humidophila brekkaensis* (J.B.Petersen) R.L.Lowe, Kociolek, J.R.Johansen, Van de Vijver, Lange–Bertalot et Kopalová (as *Navicula brekkaensis* J.B.Petersen) and *H. parallela* (Petersen) Furey, Manoylov et R.L.Lowe (as *Navicula contenta* var. *parallela* J.B.Petersen) (Petersen 1928, 1935). Niels Foged later reported *H. contenta* and *H. biceps* (Grunow) Furey, Manoylov et R.L.Lowe in Spitsbergen, Greenland (Pearly Land), Iceland, and Alaska (Foged 1955, 1964, 1968, 1974), *H. perpusilla* (Grunow) R.L.Lowe, Kociolek, J.R.Johansen, Van de Vijver, Lange–Bertalot et Kopalová in Spitsbergen, Greenland, Iceland, Alaska, and Northern Norway, *H. parallela (*Petersen) Furey, Manoylov et R.L.Lowe in Greenland, Iceland, and Öland, Sweden (Foged 1955, 1974, 1980, 1989), and *H. brekkaensis* in Greenland (Foged 1989). In 1987, Denys and Beyens performed an extensive survey of the diatom flora of the Angmagssalik region of Greenland, reporting *H. contenta, H. biceps, H. parallela,* and *H. gallica* (Denys & Beyens 1987). In the Canadian Arctic Archipelago, Antoniades et al. (2008) observed *H. ingeaeformis* (P.B.Hamilton et D.Antoniades) R.L.Lowe, Kociolek, J.R.Johansen, Van de Vijver, Lange–Bertalot et Kopalová, *H. laevissima* (Cleve) R.L.Lowe, Kociolek, J.R.Johansen, Van de Vijver, Lange–Bertalot et Kopalová, *H. paracontenta,* and *H. gallica* (Antoniades et al. 2008). More recently, Buckzo et al. (2015) transferred *Navicula schmassmannii* Hustedt, a species with an Arctic–Alpine distribution, to the genus *Humidophila,* and in 2020, *H. eldfjalli* Furey, Manoylov et R.L.Lowe was described from Iceland (Furey et al. 2020).

While much progress has been made in understanding the taxonomy and biogeography of this group over the last 30 years, it is clear that much work remains to be done to adequately describe its global diversity and distribution, particularly in the Arctic region. The present paper investigates the diversity and occurrence of the genus *Humidophila* in Greenland and discusses eight previously described species that were observed during this survey. One additional species, *Humidophila mochalovae* (Potapova) Goeyers, Van de Vijver et Sabbe comb. nov. was transferred from *Diadesmis* to the genus *Humidophila.* Furthermore, two different taxa could not be identified using all currently available literature. Following detailed light and scanning electron microscopy observations, these taxa were newly described as: *H. helderiana* Goeyers et Hamilton sp. nov. and *H. mitosis* Goeyers, Van de Vijver et Kohler sp. nov. Their morphology is compared with other *Humidophila* taxa worldwide, and notes on their environmental preferences and geographic distribution are added. Our findings contribute to a better understanding of the terrestrial diatom flora found in the Arctic region, and will benefit future studies focusing on ecology, biogeography, paleoecology, and biomonitoring in this region.

## Materials and methods

A total of eight samples, collected in Greenland, was used in this study. Samples were collected in Zackenberg (74°28'N, 20°34'W), near Kangerlussuaq (67°01'N, 50°40'W), and on Disko Island (70°N, 54°W) (see Fig. 1). Zackenberg is located in central north–east Greenland and is characterized by a High Arctic polar climate. The area is underlain by continuous permafrost (Christiansen et al. 2008). Kangerlussuaq is located in the Low Arctic, in the rain shadow of the Sukertoppen Icecap, and is characterized by continuous permafrost and a hilly tundra landscape with thousands of ponds/lakes (Lindborg et al. 2016). The regional climate is relatively stable and can be regarded as continental (Engels & Helmens 2010). Disko Island (Qeqertarsuaq) is situated west of the mainland and is

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Greenland's largest island. About 20% of the area is glaciated (Humlum 1987). The island represents a transition between the High and Low Arctic, and exhibits a polar maritime climate (Abermann et al. 2021). Table 2 presents an overview of all samples together with their sampling locations, dates, elevation, and habitat characteristics.

Selected moss material was prepared for light microscopy (LM) following the method described in van der Werff (1953). Subsamples were cleaned by adding 37% $H_2O_2$ and heating to 80 °C for one hour. The reaction was then completed with the addition of saturated $KMnO_4$. After digestion and centrifugation (3 times for 10 minutes at 3700 g), the resulting cleaned material was diluted with distilled water to avoid excessive concentrations of diatom valves and mounted in Naphrax. Samples and slides are stored in the BR collection (Meise, Belgium). Slides were analyzed using an Olympus BX53 microscope at 1000× magnification (N.A. 1.30), equipped with Differential Interference Contrast (Nomarski) and a UC30 camera connected to the cellSens Standard program.

For scanning electron microscopy, stubs were prepared by filtering drops of the oxidized suspension through 5 µm pore polycarbonate membrane filters (Whatman Cyclopore PC circles, 25 mm diameter). The filters were then air–dried, and pieces were affixed to 12.7 mm aluminum stubs covered with double sided carbon stickers (Agar Carbon Tabs). The stubs were placed in a high–resolution fine sputter coater for FE–SEM (JFC–2300HR Coating Unit, JEOL) and coated with a layer of approximately 10–15 nm platinum (using Argon–gas under 0.05 mbar pressure). The SEM observations were performed using a JEOL JSM–7100FLV Field Emission SEM (at 1 kV and a working distance of 3.5–6.0 mm).

Terminology of the various structures of the siliceous cell wall is based on Ross et al. (1979, areola structure), Cox & Ross (1981, stria structure), Lowe et al. (2014, genus features for *Humidophila*), and Vouilloud et al. (2022, vallum definition, genus features for *Humidophila*). The terms 'converging' and 'diverging' are used for striae that run towards each other (see Fig. 252) or run in opposite directions (see Fig. 85).

For taxonomic comparisons, the following papers were consulted: Lange–Bertalot & Werum 2001; Antoniades et al. 2008; Lowe et al. 2017; Furey et al. 2020; Chattová et al. 2021; Van de Vijver et al. 2022; Vouilloud et al. 2022; Ferreira et al. 2023; Goeyers & Van de Vijver 2023.

For the typification of the new taxa, we chose to use entire slides as the holotype, following Article 8.2 of the International Code of Botanical Nomenclature (Turland et al. 2018). This is due to the broad morphological variability over the diatom cell cycle, which makes the choice for entire populations more appropriate. One valve was indicated to illustrate the taxon best (see Figures). All novelties are registered proactively according to Art. 42.3 (Turland et al. 2018).

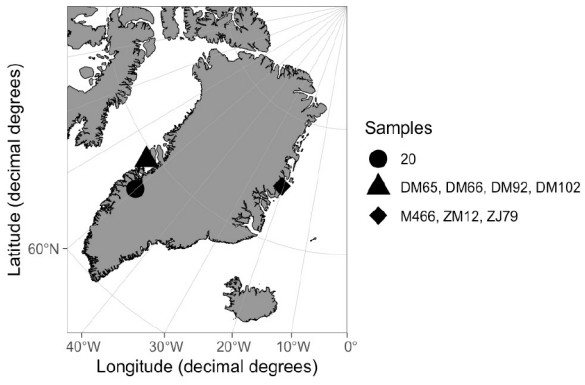


Fig. 1. Map showing the locations of the sampling sites in Greenland.

## Results

A total of 11 *Humidophila* taxa were observed during this survey. Two of them could not be identified using the currently available literature and are described as new: *H. helderiana* Goeyers et Hamilton sp. nov. and *H. mitosis* Goeyers, Van de Vijver et Kohler sp. nov. Table 1 lists all recorded *Humidophila* taxa in this study, together with a short list of other *Humidophila* taxa that are present in the Arctic as reported in the literature. The biogeographical distribution of each taxon is listed, and all taxa are discussed hereafter in alphabetical order.

***Humidophila arctica* (Lange–Bertalot et Genkal) R.L.Lowe, Kociolek, J.R.Johansen, Van de Vijver, Lange–Bertalot et Kopalová 2014 (Figs 2–23)**

**Basionym:** *Diadesmis arctica* Lange–Bertalot et Genkal 1999 in Lange–Bertalot & Genkal (1999, Iconographia Diatomologica, Vol. 6, p. 40, pl. 21, figs 8–14).

**LM (Figs 2–20):** Valves lanceolate with strictly convex margins lacking a distinctly inflated central part. Occasionally smaller valves with slightly inflated central part observed (Fig. 19). Apices not to very weakly protracted in larger valves, generally broadly rounded. Valve dimensions (n=19): length 11–20 µm, width middle 3–4 µm, width apices 2–3 µm. Axial area broad, linear. Central area rounded in appearance, visible in LM, never forming a fascia. Raphe filiform with simple, straight central endings. Terminal raphe fissures absent. Striae short, parallel, 32–34 in 10 µm. Areolae barely or not visible in LM.

**SEM (Figs 21–23):** Mantle striae composed of a single shortened, almost rounded areola forming close to the valve face/mantle junction (Fig. 21). Girdle composed of at least three open, rather broad copulae, perforated by a single row of slit–like pores (Fig. 21). Mantle striae interrupted at apices (Fig. 22). Striae of the cubiculus–type, composed of one, irregularly shortened areola (Fig. 22). Striation pattern in the central region continuous, though composed of shorter areolae. Raphe branches straight. Central raphe endings simple and weakly bent (Fig. 22). Two shallow, slit–like depressions flanking the central endings. Terminal raphe endings transverse, T–shaped (Fig. 22). Internally, well–developed, raised central nodule present, creating rounded central area view in LM (Fig. 23). Internal terminal raphe endings simple, terminating on weakly developed helictoglossae (Fig. 23). Valve face and mantle striae separated by a vallum (Fig. 23).

**Ecology and associated flora:** The largest population of *Humidophila arctica* was found in sample DM66, co–occurring with *Eunotia zackenbergensis* Goeyers et

Table 1. List of all Humidophila species present in the Arctic with their geographical distributions. Greenland is subdivided in Disko (D), Kangerlussuaq (K), and Zackenberg (Z). The literature upon which the distributions are based is listed in Supplementary Table S1 with reference to the use of LM and/or SEM to illustrate the species.

| | This study | Cosmopolitan | Northern Hemisphere | Arctic | Greenland | | |
|---|---|---|---|---|---|---|---|
| | | | | | D | K | Z |
| *H. arctica* | X | | | X | | | |
| *H. brekkaensis* | | X | | | | | |
| *H. contenta* | X | X | | | | | |
| *H. delognei* | X | | X | | | | |
| *H. eldfjallii* | X | | | X | | | |
| *H. gallica* | X | X | | | | | |
| *H. helderiana* | X | | | | | X | |
| *H. ingeaeformis* | X | | | X | | | |
| *H. laevissima* | | X | | | | | |
| *H. mitosis* | X | | | | | X | |
| *H. mochalovae* | X | | X | | X | | X |
| *H. paracontenta* | | | X | | | | |
| *H. paracontenta var. magisconcava* | X | | X | | | | |
| *H. parallela* | | X | | | | | |
| *H. perpusilla* | X | X | | | | | |
| *H. schmassmannii* | | | X | | | | |

al., *Humidophila eldfjallii*, and *H. mochalovae* (Potapova) Goeyers, Van de Vijver et Sabbe. In other samples, *H. arctica* was found together with *H. gallica, Cymbopleura tynnii* (Krammer) Krammer, *Tabellaria acidodelicata* Heudre et al., *Pinnularia subrostrata* (Cleve) A.Cleve and *P. notabilis* Krammer.

**Taxonomic remarks:** *Humidophila arctica* can hardly be confused with other *Humidophila* taxa. Based on valve outline, the most similar taxon is *Humidophila perpusilla* (see below). Van de Vijver & Goeyers (2022) studied the epitype material of the latter species and documented its morphology. Both species have an elliptic–lanceolate valve outline, although *H. perpusilla* tends to have a more rhombic–lanceolate outline, with a distinctly inflated central part, a feature not observed in *H. arctica* (see Figs 152–166). *Humidophila arctica* has typically broadly rounded, distinctly convex margins, a slightly larger size range (11–20 µm versus 9–16 µm in *H. perpusilla*), and an overall smaller width (3–4 µm versus 3.5–5.0 µm). *Humidophila arctica* has shorter, more rounded areolae and lacks the typical depressed groove observed in several *H. perpusilla* valves where the areolae are located. Additionally, the mantle striae in *H. perpusilla* are clearly situated in a depression, a feature never observed in *H. arctica*. Both species often co–occur in samples in Greenland, with *H. arctica* well–represented in Zackenberg, while *H. perpusilla* is more common on Disko Island.

### *Humidophila contenta* (Grunow) Lowe, Kociolek, J.R.Johansen, Van de Vijver, Lange–Bertalot et Kopalová 2014 (Figs 24–46, 24b–46b)

**Basionym:** *Navicula contenta* Grunow 1885, p. 109 = Grunow in Van Heurck (1880, Synopsis des Diatomées de Belgique, Atlas, Plate XIV [14], fig. 31[a], as "*Navicula trinodis* forma *minuta*" pro parte) ≡ *Diadesmis contenta* (Grunow in Van Heurck) D.G.Mann 1990 in Round et al. 1990, p. 666.

**LM (Figs 24–43, 24b–43b):** Valves triundulate, linear with slightly inflated to inflated mid–valve. Apices broadly rounded, capitate. Valve dimensions (n=20): length 8–15 µm, width 2.5–3.5 µm. Axial area relatively broad, 1/4th of total valve width. Central area formed by widening of axial area, rounded to slightly transapically elliptical, not forming a fascia. Raphe straight with simple straight central and terminal raphe endings. Striae visible in LM, 32–38 in 10 µm. Areolae barely (Figs 27, 29) or not visible in LM.

**SEM (Figs 44–46, 44b–46b):** Mantle striae composed of a single row of rounded areolae, interrupted at the apices (Fig. 44). Girdle copulae perforated by single row of slit–like pores (Fig. 44). Striae of the cubiculus–type, composed of one, transapically elongated

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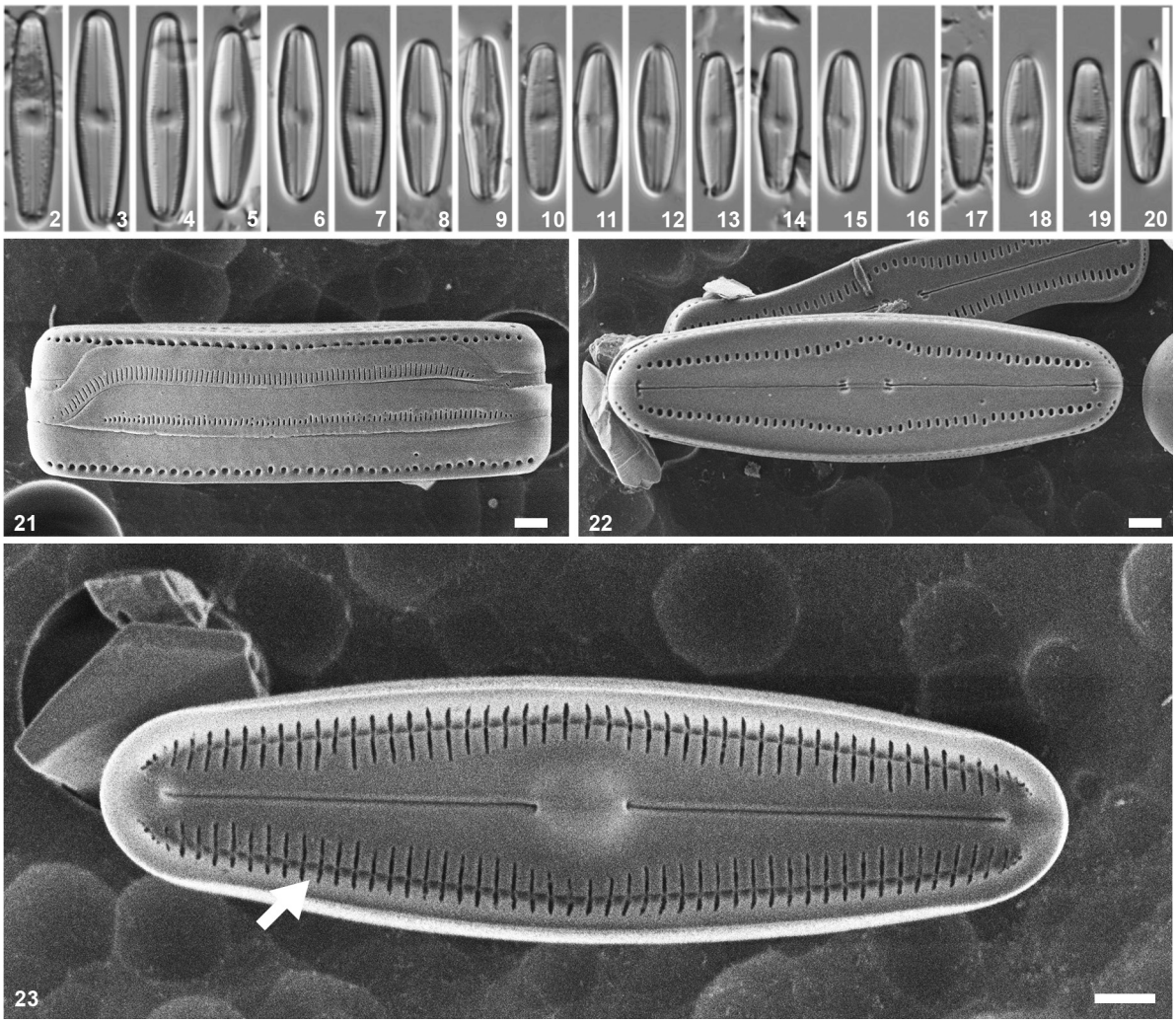
areola (Fig. 45). Striation pattern in the central area continuous, though composed of shorter areolae. Striae converging towards each other near apices (Fig. 45). Areolae elongated, of variable length, parallel to slightly convergent near the apices. Voight discordance visible (Fig. 45). Raphe branches straight. Central raphe endings bordered by distinct depressions (Fig. 45). Depressions more pronounced near central raphe endings. Terminal raphe endings Y– or T–shaped (Fig. 45). Internally, well–developed, raised central nodule present (Fig. 46). Internal terminal raphe endings simple, terminating on weakly developed helictoglossae (Fig. 46). Valve face and mantle striae separated by vallum (Fig. 46).

**Ecology and associated flora:** in sample DM66, the largest population of *H. contenta* was found, co–occurring with *Eunotia zackenbergensis*, *Humidophila arctica* and *H. mochalovae.* In other samples, *H. contenta* co–occurred with *Pinnularia borealis* var. *sublinearis* Krammer, *Eunotia bigibba* Kützing and *Eunotia fennica* (Hustedt) Lange–Bertalot.

**Taxonomic remarks:** The current concept of *H. contenta* has recently been revised based on the analysis of the original Delogne type material (Van de Vijver et al. 2022) and differs markedly from the generally accepted concept. In our analysis, two slightly aberrant populations were found. The Disko population (Figs 24–46) differs from the Kangerlussuaq population (Figs 24b–46b) in its outline and striae count. Whereas the Disko population has a triundulate outline with inflated center and a lower striae density (32–34 versus 34–38 in 10 µm in the Kangerlussuaq population), the Kangerlussuaq population has less concave valves, a less pronounced central inflation and a higher striae density. Based on valve outline, several species can be confused with the revised *H. contenta*. The most similar seems to be *H. eldfjallii*, recently described from Iceland (Furey et al. 2020). Separating both species in LM can be challenging. The apices of *H. eldfjallii* are slightly more cuneate and slightly flattened (Furey et al. 2020, figs 8E–H), while *H. contenta* has more broadly rounded, capitate apices. In SEM, differences are more pronounced. *Humidophila contenta* possesses typical slit–like markings next to both central and terminal raphe endings, whereas in *H. eldfjallii*, these markings are absent (Furey et al. 2020, fig 8A). In *H. eldfjallii*, the mantle areolae lie in distinct longitudinal depressions and near the apices running almost on the valve face, forming two distinct depressed structures on the valve face, a feature not observed in *H. contenta*. The valve face striae at the apices diverge in *H. eldfjallii* but converge in *H. contenta*, a feature which is also, though not very clearly, discernible in LM. Based on valve outline, other species that can be confused with *H. contenta* are *H. ingeaeformis* (P.B.Hamilton et D.Antoniades) R.L.Lowe, Kociolek, R.Johansen, Van de Vijver, Lange–Bertalot et Kopalová*, H. ingeae*

Table 2. Overview of all samples with the sampling location, date, coordinates, elevation, habitat characteristics, climate, and previous studies on the same material where additional environmental information on the samples can be found.

| Sample | Location | Date | Coordinates | Elevation | Habitat | Climate | Previous studies |
|---|---|---|---|---|---|---|---|
| DM65 | Disko | 23/06/2004 | 70°N, 54°W | 18 m | Moss on a hill near a waterfall. *Cassiope, Saxifraga, Phyllodoce* and *Oxyria* vegetation | Polar maritime | |
| DM66 | Disko | 23/06/2004 | 70°N, 54°W | 18 m | Moss on a hill near a waterfall. *Cassiope, Saxifraga, Phyllodoce* and *Oxyria* vegetation | Polar maritime | |
| DM92 | Disko | June 2004 | 70°N, 54°W | | | Polar maritime | |
| DM102 | Disko | June 2004 | 70°N, 54°W | | | Polar maritime | |
| M466 | Zackenberg | 01/08/1998 | 74°28'N, 20°34'W | | Moss on edge of a stony pond | High Arctic polar | Van Kerckvoorde et al. (2000) |
| ZM12 | Zackenberg | 18/08/1998 | 74°28'N, 20°34'W | | Moss in fen | High Arctic polar | Van Kerckvoorde et al. (2000) |
| ZJ79 | Zackenberg | 01/08/2000 | 74°28'N, 20°34'W | | Near river with rocky bottom and fish | High Arctic polar | |
| 20 | Near Kangerlussuaq | 6/09/2017 | 67°01'N, 50°40'W | 356 m | Ice margin, moss in rock crevice | Low Arctic continental | |




Figs 2–23. *Humidophila arctica* from sample DM66, Disko Island, Greenland: (2–20) LM of valve views; (21) SEM girdle view; (22) SEM of an entire valve (externally); (23) SEM of an entire valve (internally). Arrow indicates the vallum, separating mantle and valve face striae. Scale bar 10 µm (2–20), 1 µm (21–23).

(Van de Vijver) R.L.Lowe, Kociolek, J.R.Johansen, Van de Vijver, Lange–Bertalot et Kopalová*, H. biscutella* (Gerd Moser, Lange–Bertalot et Metzeltin) R.L.Lowe, Kociolek,.J.R.Johansen, Van de Vijver, Lange–Bertalot et Kopalová*, H. brekkaensis, H. arcuata* (Lange–Bertalot) R.L.Lowe, Kociolek, J.R.Johansen, Van de Vijver, Lange–Bertalot et Kopalová*, H. arcuatoides* (Lange–Bertalot) R.L.Lowe, Kociolek, J.R.Johansen, Van de Vijver, Lange–Bertalot et Kopalová*,* and *H. undulocontenta* R.L.Lowe, Kociolek et Q.You*.* The valves of *H. ingeaeformis* are centrally inflated as well (Antoniades et al. 2009, figs 18–21), although the valve dimensions are slightly smaller (length 10–15 µm in *H. contenta* versus 8–13 µm in *H. ingeaeformis*, width 3–3.5 µm in *H. contenta* versus 2–3 µm in *H. ingeaeformis*). The Antarctic species *H. ingeae* has less pronounced undulations and subcapitate to capitate apices (Van de Vijver et al. 2002, figs 34–45). *Humidophila biscutella,* described from New Caledonia, has a higher stria density (36–40 in 10 µm versus 32–34 in 10 µm in *H. contenta*), a weaker or not inflated mid–valve (Moser et al. 1998, pl. 28 figs 1–4), and lacks markings next to the central and terminal raphe endings. *Humidophila brekkaensis* can be separated based on its lower stria density (28–33 in 10 µm), the absence of an inflated mid–valve, and the mantle areolae are positioned on the same level as the valve face areolae, giving the impression of a double row of areolae (Chattová et al. 2018, figs 14, 16, 17). *Humidophila arcuata* also lacks a centrally inflated valve, and the striae do not converge towards the apices (see for example Kopalová et al. 2015, fig 119). The valves of *H. arcuatoides* are significantly larger (length 16–27 µm versus 10–15 µm in *H. contenta,* width 4–6 µm versus 3–3.5 µm in *H. contenta*) and the stria density is higher (38–40 in 10 µm versus 32–34 in 10 µm in *H. contenta*) (Vouilloud et al. 2022). The Chinese species *H. undulocontenta* R.L.Lowe, Kociolek et Q.You differs in the location of the striae in shallow depressions and a higher stria density (40–42 in 10 µm versus 32–34 in 10 µm in *H. contenta*). In addition, the axial area expands into a circular central area, with or without alveolae, which is not observed in *H. contenta* (Lowe et al. 2017).

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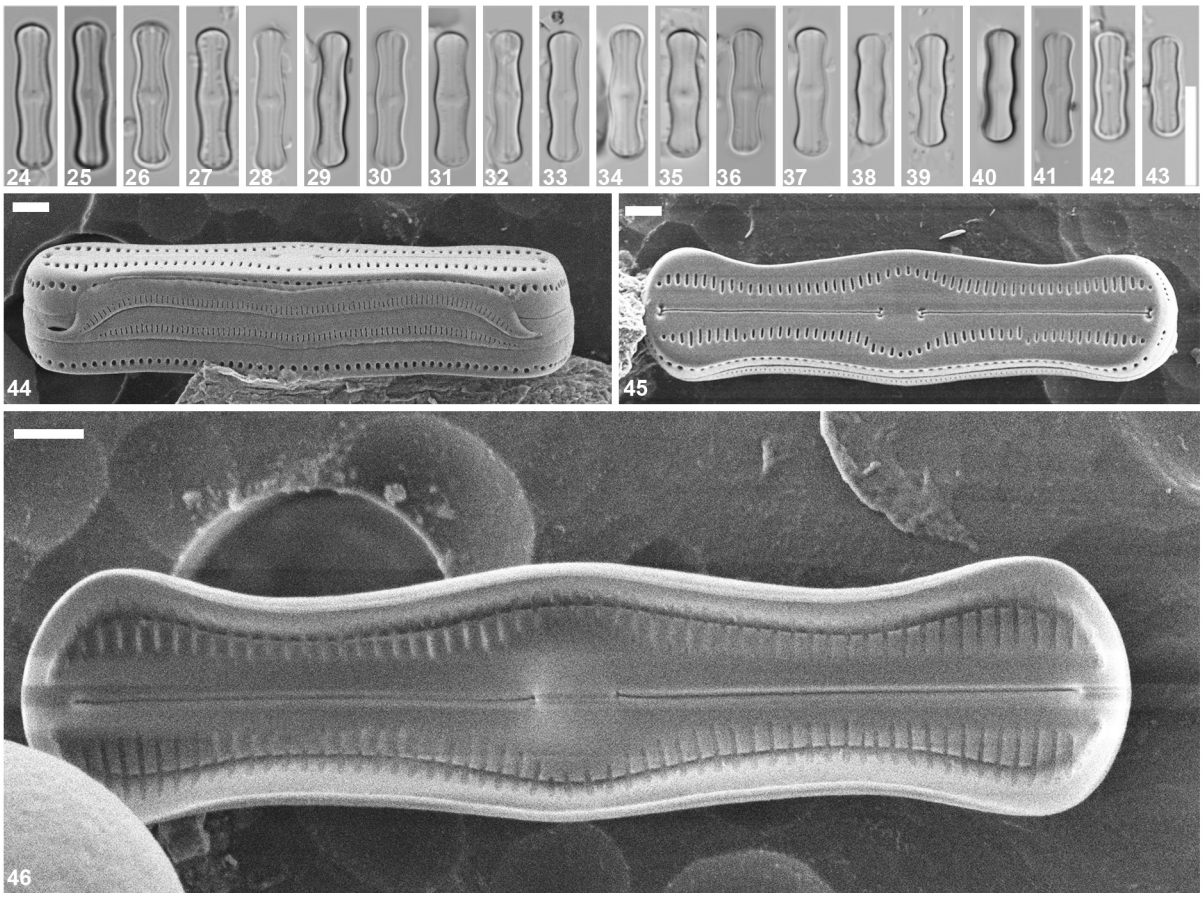



Figs 24–46. *Humidophila contenta* from sample DM66, Disko Island, Greenland: (24–43) LM of valve views; (44) SEM, girdle view; (45) SEM of an entire valve (externally); (46) SEM of an entire valve (internally). Scale bar 10 μm (24–43), 1 μm (44–46).

***Humidophila delognei* Goeyers et Van de Vijver 2023 (Figs 47–68)**

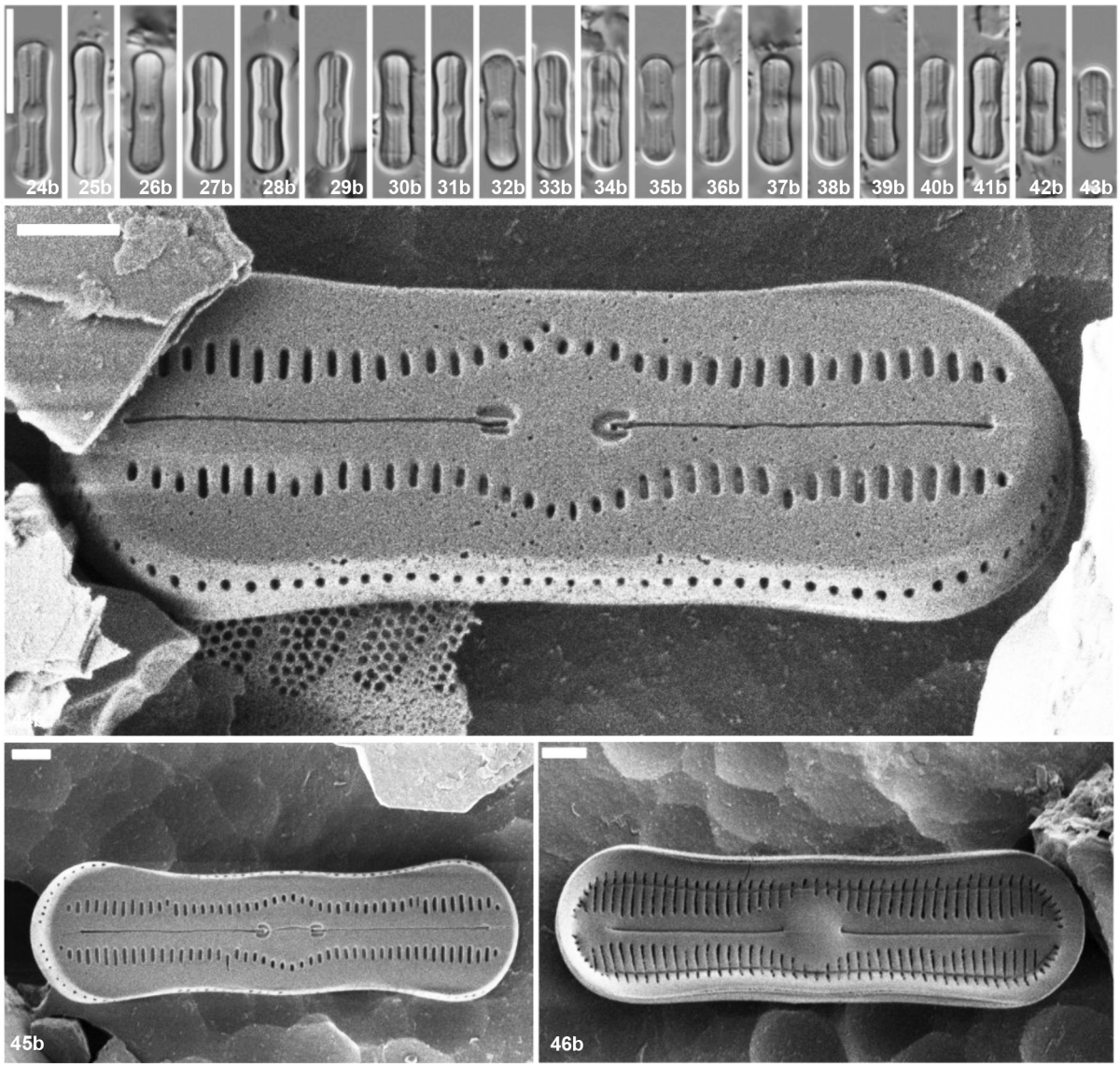
**Basionym:** *Navicula contenta* Grunow 1885, p. 109 = Grunow in Van Heurck (1880, Synopsis des Diatomées de Belgique, Atlas, Plate XIV [14], fig. 31[a], as "*Navicula trinodis* forma *minuta*" pro parte) ≡ *Diadesmis contenta* (Grunow in Van Heurck) D.G.Mann 1990 in Round et al. 1990, p. 666.

**LM (Figs 47–66):** Valves small, linear with parallel margins. Apices non–protracted, broadly rounded. Valve dimensions (n=20): length 10–14 μm, width 2–2.5 μm. Axial area linear and broad. Central area forming rectangular fascia. Raphe filiform with simple, straight central and terminal raphe endings. Striae not visible in LM.

**SEM (Figs 67–68):** Mantle striae composed of shortened areolae (Fig. 67). Girdle copulae perforated by a single row of slit–like pores (Fig. 67). Mantle striae not interrupted at apices. Striae of the cubiculus–type, composed of one irregularly shortened areola, not located in groove, ca. 40 in 10 μm (Fig. 68). Areolae interrupted around the central area, forming a rectangular fascia (Fig. 68). Raphe branches straight. Central and terminal raphe endings ending in T– or Y–shaped grooves (Fig 68).

**Ecology and associated flora:** *Humidophila delognei* was found in several bryophyte samples collected in Greenland. In the sample with the largest population, sample DM92, *H. delognei* co–occurred with *Eunotia curtagrunowii* Nörpel–Schempp et Lange–Bertalot, *Hantzschia hyperborea* (Grunow) Lange–Bertalot, *Pinnularia borealis* var. *sublinearis, Humidophila paracontenta var. magisconcava* (Lange–Bert.) R.L.Lowe, Kociolek, J.R.Johansen, Van de Vijver, Lange–Bertalot et Kopalová, and *Humidophila perpusilla.* In other samples, *Humidophila delognei* was observed co–occurring with *Staurosirella lapponica* (Grunow) D.M.Williams et Round s. l, *Meridion circulare* (Grev.) C.Agardh, *Eunotia septentrionalis* Østrup, *Nitzschia acidoclinata* Lange–Bertalot and *Pinnularia lunata* Krammer et Lange–Bertalot.

**Taxonomic remarks:** In the past, *H. delognei* has often been identified as *H. contenta.* Recent analysis of the original type material from Rochehaut (Belgium), however, indicated that the concept of *H. contenta* was incorrect (Van de Vijver et al. 2022). While the original type material shows that *H. contenta* has a distinct inflated center and lacks a fascia, the species concept changed with the discussion of the morphology and taxonomy of *Navicula contenta* in Schoeman & Archibald (1978). They suggested that *N. contenta* should be based on *Navicula trinodis* var. *biceps* (=*Diadesmis biceps* Arnott), and the illustrated valves (Schoeman & Archibald 1978, figs 46–56) show concave margins and a fascia.




Figs 24b–46b. *Humidophila contenta* from sample 20, near Kangerlussuaq, Southwest Greenland: (24b–43b) LM of valve views; (44b–45b) SEM of an entire valve (externally); (46b) SEM of an entire valve (internally). Scale bar 10 µm (24b–43b), 1 µm (44b–46b).

Confusion of *H. delognei* with this former, incorrect idea of *H. contenta* is possible. In addition, confusion is also possible with *H. simplex* (E.Reichardt) R.L.Lowe, Kociolek, J.R.Johansen, Van de Vijver, Lange–Bertalot et Kopalová, based on the pronounced rectangular fascia. Especially smaller specimens of *H. simplex* look similar to *H. delognei* (Goeyers & Van de Vijver 2023, fig 7p–t). The main difference is found in the valve outline. *Humidophila delognei* has a linear valve outline with parallel margins, whereas *H. simplex* has more concave margins. In SEM, the areolae of *H. simplex* slightly converge near the apices (Goeyers & Van de Vijver 2023, figs 7v,w,x). *Humidophila parallela,* described from Icelandic soil samples, also shows resemblance to *H. delognei*, based on the linear valves with parallel margins and broadly rounded apices (Furey et al. 2020, figs 7 M–P). The valve dimensions of *H. parallela* are however smaller (length 7.2–9.1 µm, versus 10–14 µm in *H. delognei*, width 2–3.1 µm versus 2–2.5 µm in *H. delognei*) (Furey et al. 2020) and the areolae are slightly more elongated (Furey et al. 2020 figs 7 P), whereas *H. delognei* has short, rounded, and irregularly placed areolae. *Humidophila tahitiensis* (Lange–Bertalot et Werum) R.L.Lowe, Kociolek, J.R.Johansen, Van de Vijver, Lange–Bertalot et Kopalová, a species described from Polynesia (Lowe et al. 2014), is also similar based on the parallel margins, rectangular fascia, and T–shaped raphe endings. The species differ, however, in shape of their areolae, which are elongated, regularly arranged, and thin in *H. tahitiensis* (see Lowe et al. 2014, fig 36).

***Humidophila eldfjallii* Furey, Manoylov et R.L.Lowe 2020 (Figs 69–86)**

**LM (Figs 69–83):** Valves triundulate with a distinctly inflated center. Apices inflated, broadly rounded. Valve dimensions (n=15): length 11–16 µm, width 3–4 µm.

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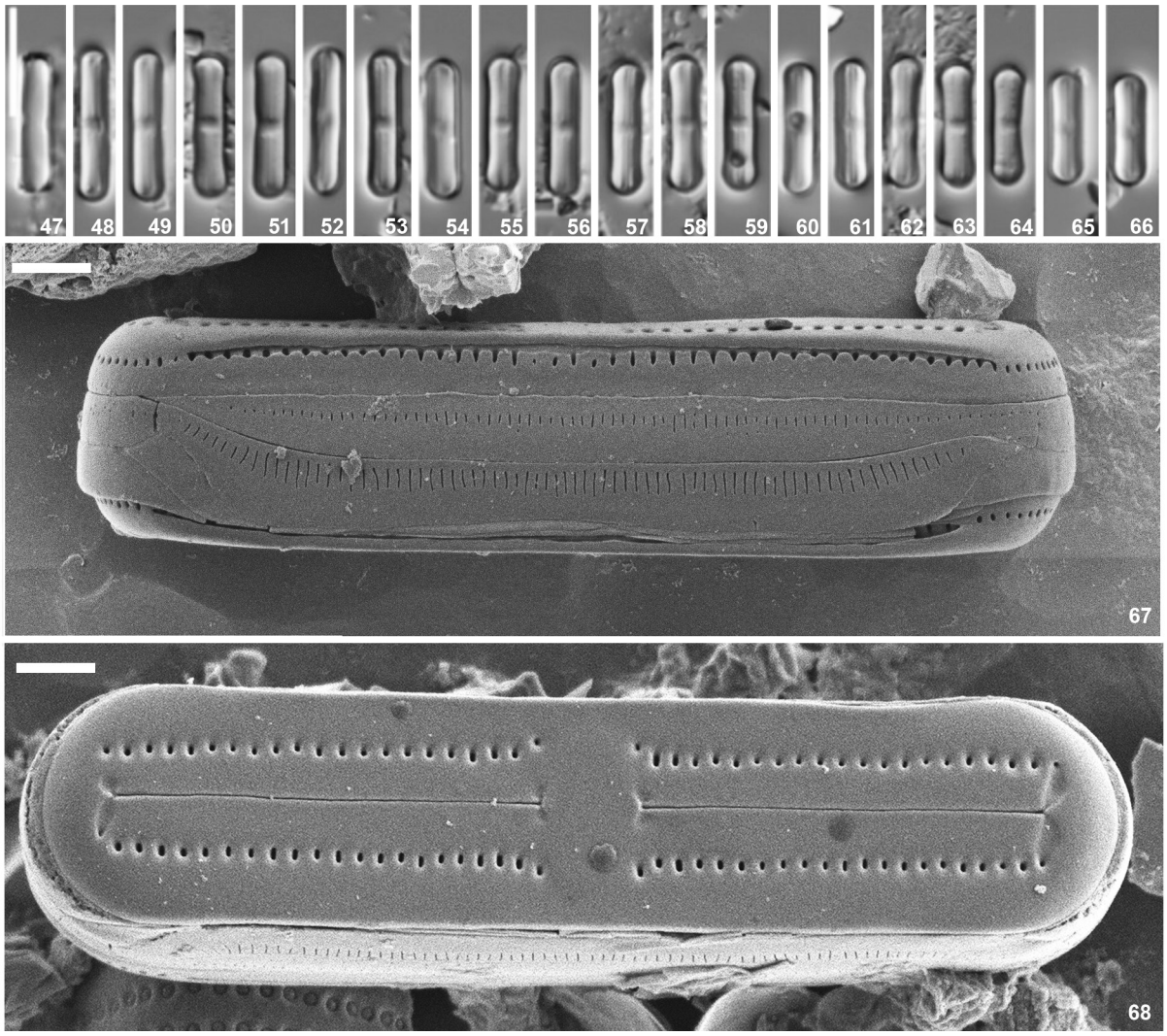


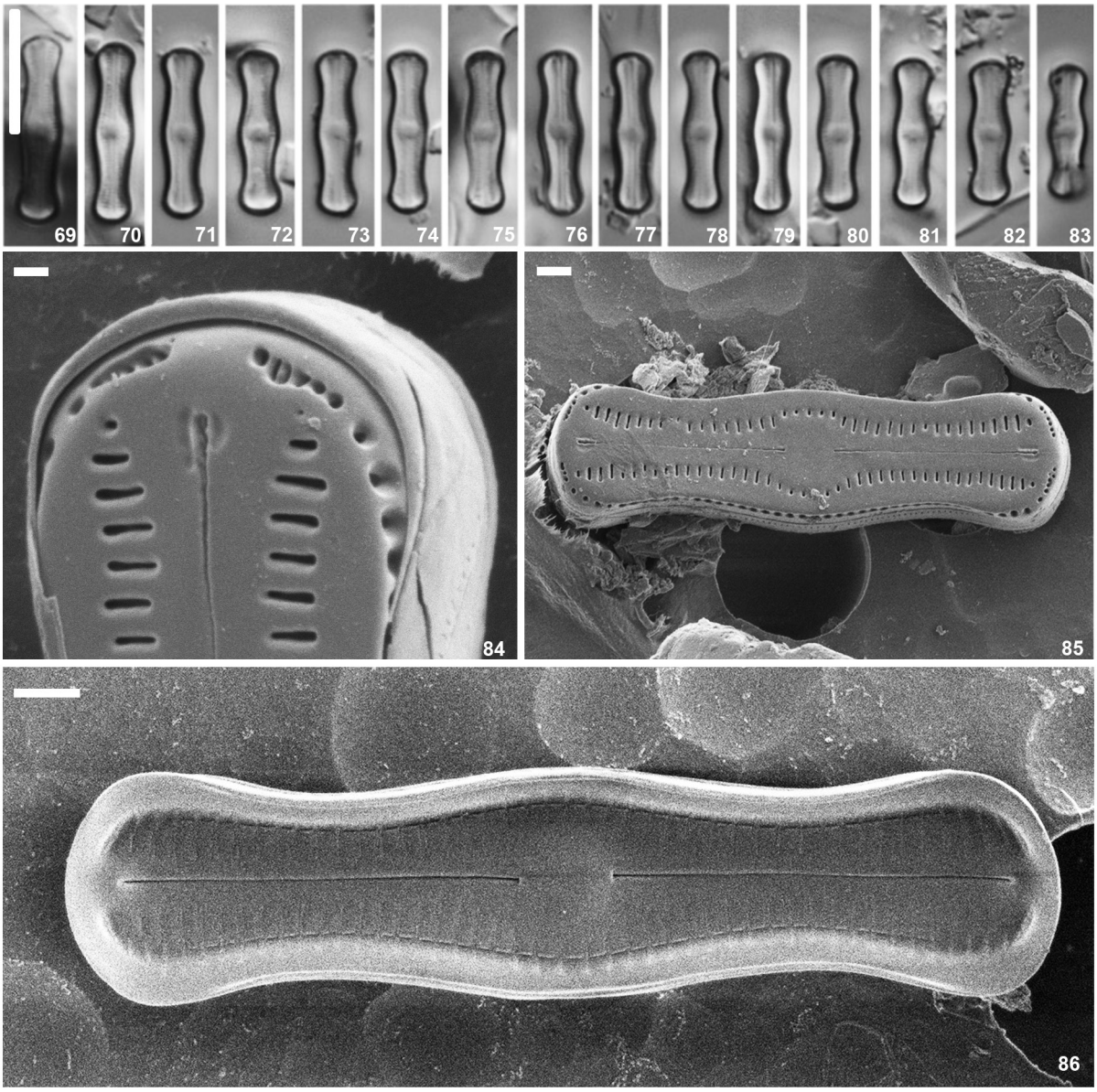

Figs 47–68. *Humidophila delognei* from sample DM92, Disko Island, Greenland: (47) LM of girdle view; (48–66) LM of valve views; (67) SEM girdle view; (68) SEM of an entire valve (externally). Scale bar 10 μm (47–66), 1 μm (67–68).

Central area rounded, no fascia present. Raphe straight with simple straight central endings. Terminal raphe endings simple. Striae present throughout entire valve, 32–34 in 10 μm, sometimes visible (Fig. 73) in LM. Areolae not visible in LM.

**SEM (Figs 84–86):** Mantle with single row of linear–elliptic to round areola, located close to valve face mantle junction at apex and interrupted at the apices (Fig. 84). Girdle copulae perforated by a single row of slit–like pores (Fig. 85). Striae of the cubiculus–type, consisting of one transapically elongated areola (Fig. 85). Striation pattern in central area continuous, though with shorter, almost rounded areolae (Fig. 85). Central raphe endings simple. Terminal raphe endings simple, bordered by shallow depressions (Fig. 85). Voight discordance visible (Fig. 85). Internally, well–developed, raised central nodule present highlighting a round central area in LM (Fig. 86). Internal terminal raphe endings simple, terminating on weakly developed helictoglossae (Fig. 86). Valve face and mantle areolae separated by vallum (Fig. 86).

**Ecology and associated flora:** In sample 20, the largest population of *Humidophila eldfjallii* was found, co–occurring with *Pinnularia borealis* var. *sublinearis, Humidophila paracontenta* var. *magisconcava* and *Caloneis* sp. [cf. *C. bacillum* (Grunow) Cleve]. In other samples, *H. eldfjallii* co–occurred with *Humidophila arctica, Eunotia zackenbergensis, Tabellaria acidodelicata* and *Eunotia fennica*.

**Taxonomic remarks:** *Humidophila eldfjallii* closely resembles *H. contenta* (see above) and *H. ingeaeformis.* Both *H. eldfjallii* and *H. ingeaeformis* have triundulate valves and a distinct inflated mid–valve, although the central part of *H. ingeaeformis* is more inflated and pronounced and *H. ingeaeformis* is more variable in length (8–18 μm versus 11–16 μm in *H. eldfjallii*). In addition, *H. ingeaeformis* has parallel to convergent striae at the poles. While *H. eldfjallii* has a relatively high abundance in Greenland, only a few specimens of *H. ingeaeformis* were found. Another similar species is *H. costei* (Le Cohu et Van de Vijver) R.L.Lowe, Kociolek,J.R.Johansen,




Figs 69–86. *Humidophila eldfjallii* from sample 20, near Kangerlussuaq, Southwest Greenland: (69–83) LM of valve views; (84) SEM of the mantle areolae, interrupted at the apices; (85) SEM of an entire valve (externally); (86) SEM of an entire valve (internally). Scale bar 10 µm (69–83), 1 µm (84–86).

Van de Vijver, Lange–Bertalot et Kopalová. Both show diverging apex striae, although the inflated center is less pronounced in *H. costei* (see Le Cohu & Van de Vijver 2002, figs 26–28). In addition, *H. costei* has a higher stria density (34–40 in 10 µm versus 32–34 in 10 µm in *H. eldfjallii*). While different in valve outline, *H. virginiana* (Lange–Bertalot) R.L.Lowe, Kociolek, J.R.Johansen, Van de Vijver, Lange–Bertalot et Kopalová is similar to *H. eldfjallii* in the pattern of mantle areolae at the apices along the valve face junction (see Werum & Lange–Bertalot 2004, plate 71, fig. 1).

### *Humidophila gallica* (W.Smith) R.L.Lowe, Kociolek, Q.You, Q.Wang et Stepanek 2017 (Figs 87–106)

**Basionym:** *Diadesmis gallica* W.Smith 1857 in W.Smith (1857, Notes on an excursion to the Pyrennees in search of Diatomaceae. Annals and Magazine of Natural History, 2nd series 19: 1–13, pls 1, 2).

**LM (Figs 87–103):** Valves rhombo–elliptic to elliptic with convex margins, lacking inflated mid–valve. Apices non–protracted, broadly rounded. Valve dimensions (n=17): length 9.5–14 µm, width at center 3–4 µm, width at apices 2–2.5 µm. Spines visible in valves without raphe. Chain–forming. Striae short, present throughout entire valve, parallel, not visible in LM.

**SEM (Figs 104–106):** Mantle with single row of round areolae, mid–way down mantle, with or without thickened rim, and continuous around the apices (Fig. 104). Girdle copulae perforated by single row of slit–like pores (Fig 104). Striae of the cubiculus–type, 32–34 in 10 µm, consisting of one transapically elongated areola (Fig. 105). Areolae approximately equal–sized, continuously around the central area, convergent near apices

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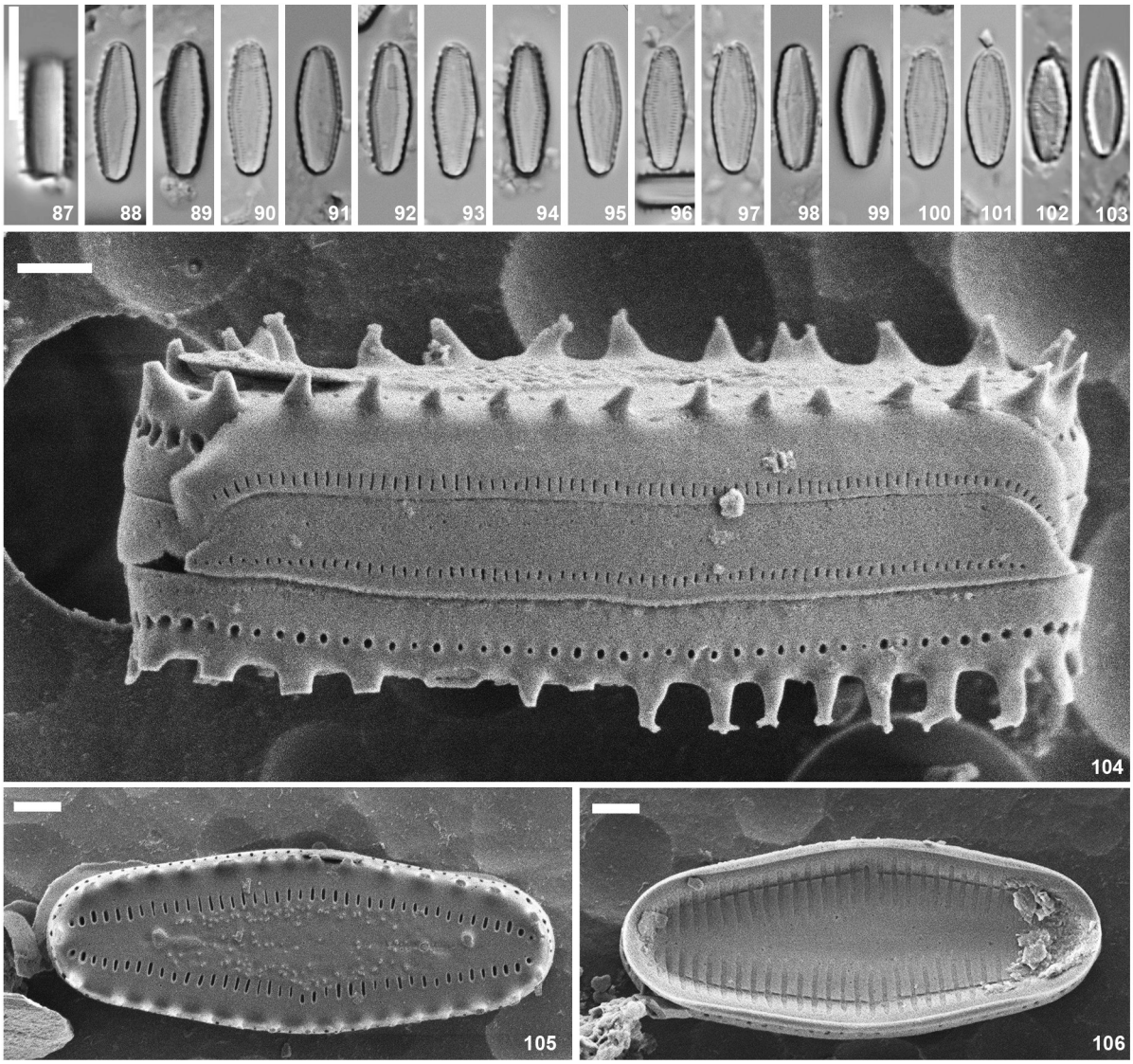
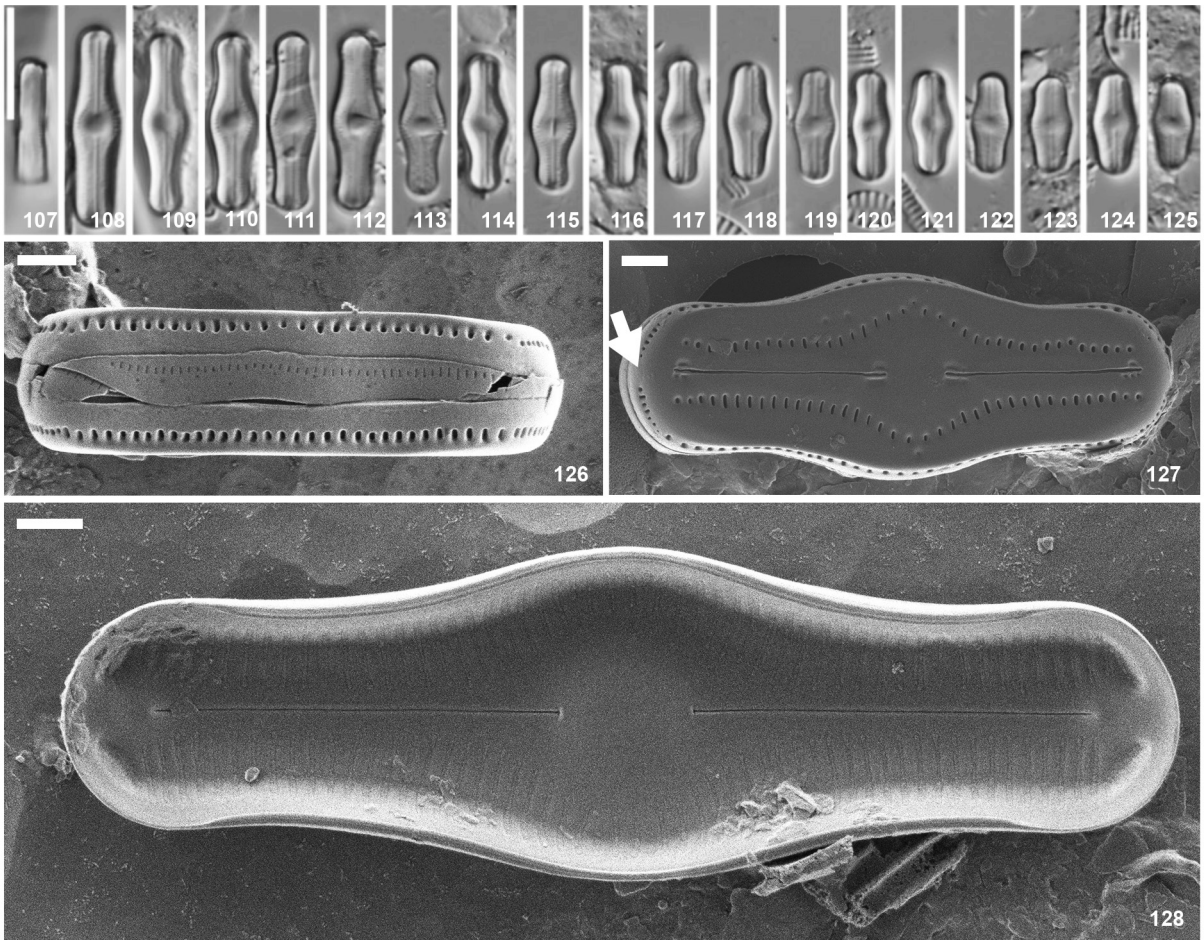



Figs 87–106. *Humidophila gallica* from sample DM65, Disko Island, Greenland: (87) LM of girdle view; (88–103) LM of valve views; (104) SEM girdle view; (105) SEM of an entire valve (externally); (106) SEM of an entire valve (internally). Scale bar 10 µm (86–103), 1 µm (104–106).

(Fig. 105). Striae internally covered by porous hymen (Fig. 106). Valve face and mantle areolae separated by a vallum (Fig. 106).

**Ecology and associated flora:** In sample DM65, *Humidophila gallica* was found together with *Humidophila arctica, H. perpusilla, Nitzschia acidoclinata, Psammothidium marginulatum* (Grunow) Bukhtiyarova et Round s.l. and *Tabellaria acidodelicata*. Other co–occurring taxa were *Orthoseira roeseana* (Rabenhorst) Pfitzer, *Psammothidium helveticum* (Hustedt) Bukhtiyarova et Round, *Meridion circulare* and *Humidophila delognei* Goeyers et Van de Vijver.

**Taxonomic remarks:** *Humidophila gallica* is one of the few *Humidophila* species that forms ribbon–like colonies (the others being *H. laevissima, H. panduriformis* R.L.Lowe, Kociolek et Q.You, and *H. cavernaphila* R.L.Lowe, Kociolek et Q.You). Similarity *H. laevissima* is mainly based on the presence of linking spines, although confusion is mostly possible with smaller specimens of *H. laevissima*. Compared to *H. gallica, H. laevissima* is larger (length 10–30 µm versus 9.5–14 µm in *H. gallica*, width 3.5–4 µm versus 3–4 µm in *H. gallica*) and has a different valve outline with capitate, protracted apices (see Goeyers & Van de Vijver 2023, fig 8). The two other colony–forming species, *Humidophila panduriformis* and *H. cavernaphila,* were described from Guizhou province, China. These presumably never produce raphe–bearing valves (Lowe et al. 2017), while *H. gallica* produces two contrasting valve morphologies with one bearing a raphe–system without spines, and one with peripheral linking spines but lacking a raphe (Cox 2006). In our analysis, we never observed raphe–bearing valves. The valves of *H. panduriformis* are, as the name indicates, panduriform, especially in larger specimens (Lowe et al. 2017, fig 61–68), and the valves of *H. cavernaphila* are inflated in the center (Lowe et al. 2017, figs 72–77),




Figs 107–128. *Humidophila ingeaeformis* from sample M466, Zackenberg, Greenland: (107) LM of girdle view; (108–125) LM of valve views; (126) SEM girdle view; (127) SEM of an entire valve (externally); (128) SEM of an entire valve (internally). Scale bar 10 µm (107–125), 1 µm (126–128). Arrow indicates interrupted areolae near apices.

whereas the valves of *H. gallica* are rhombo–elliptical with convex margins. Furthermore, *H. gallica* may also be confused with *H. perpusilla,* based on the valve outline. Both convex margins and broadly rounded apices, but *H. gallica* has spines on the rapheless valves and forms chains, unlike *H. perpusilla.* Confusion might also be possible with *H. flotowii* (Grunow) R.L.Lowe, Kociolek, J.R.Johansen, Van de Vijver, Lange–Bertalot et Kopalová, but the valves of *H. flotowii* are larger in length (12–18 µm) and lack linking spines (Goeyers & Van de Vijver 2023 figs 4 a–q).

***Humidophila ingeaeformis* (P.B.Hamilton et D.Antoniades) R.L.Lowe, Kociolek, J.R.Johansen, Van de Vijver, Lange–Bertalot et Kopalová 2014 (Figs 107–128)**

**Basionym:** *Diadesmis ingeaeformis* P.B.Hamilton & D.Antoniades 2009 in Antoniades et al. (2009, Nova Hedwigia 88(1/2): p. 60, figs 18–21, 77, 78).

**LM (Figs 107–125):** Valves weakly triundulate to linear with inflated valve center. Apices weakly protracted and broadly rounded. Valve dimensions (n=19): length 8–18 µm, width middle 3–4.5 µm, width apices 2–3 µm. Axial area linear, broad, almost ½ of total width. Central area rounded, never forming a fascia. Raphe filiform, with straight, simple central endings. Terminal raphe endings simple. Striae present throughout entire valve, short and parallel, 34–36 in 10 µm. Individual areolae not visible in LM.

**SEM (Figs 126–128):** Mantle with single row of areolae lying in a shallow groove, interrupted but shortened near apices (Fig. 127 arrow, 128). Copulae perforated by single row of slightly elongated pores (Fig. 126). Striae of the cubiculus–type, located in shallow groove (Fig. 127). Areolae with irregular lengths, continuous around the central area, although shorter in length (Fig. 127). Voight discordance sometimes visible (Fig. 127). Raphe straight, central endings bordered by distinct, elongate depressions. Terminal raphe endings straight, bordered by depressions of variable shape (Fig. 127). Central nodule raised with central raphe endings terminating at the edge of the central nodule internally (Fig. 128). Terminal raphe endings terminating on weakly developed helictoglossae. Vallum present (Fig. 128).

**Ecology and associated flora:** In sample M466, *H. ingeaeformis* co–occurs with *Tabellaria acidodelicata, Staurosirella lapponica, Cymbopleura stauroneiformis* (Lagerst.) Krammer, *Cavinula pseudoscutiformis*

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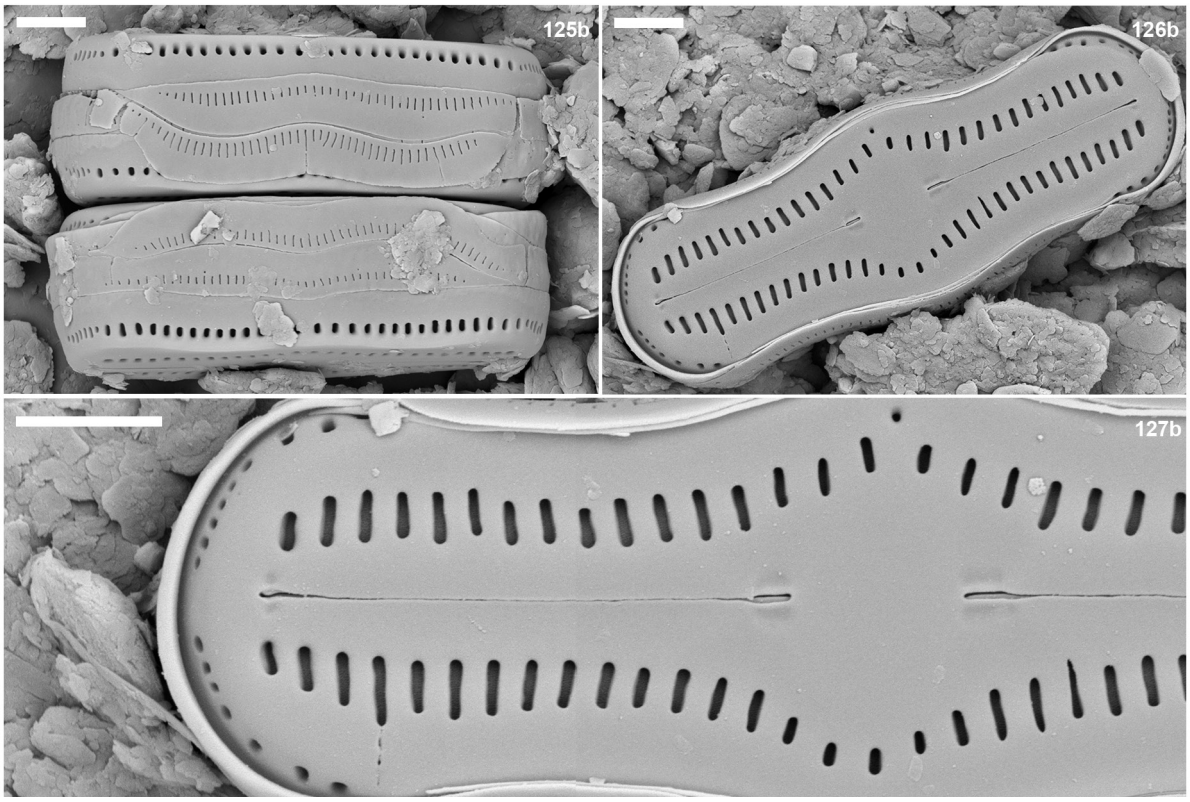
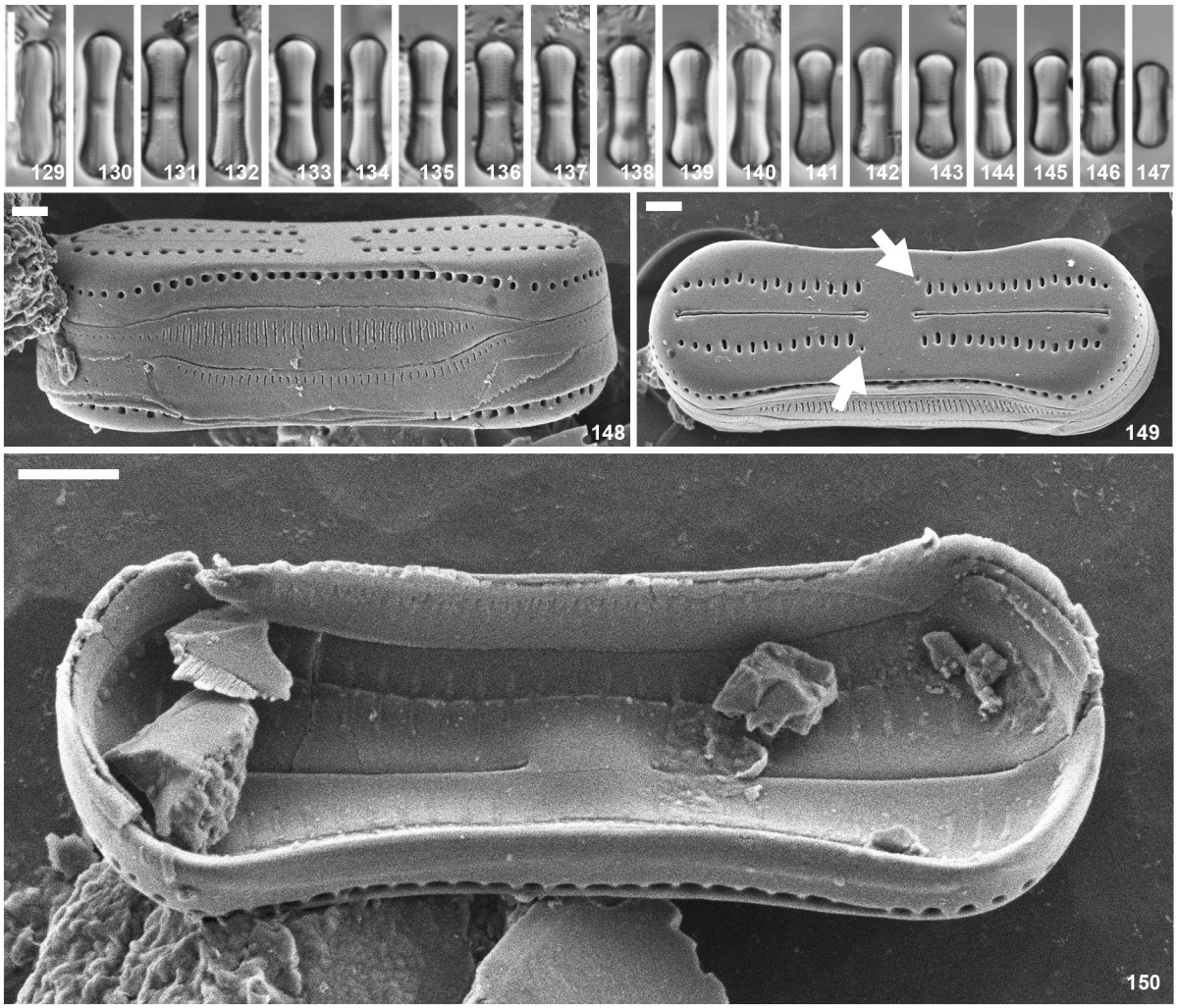



Figs 125b–127b. *Humidophila ingeaeformis* from the type sample from Pond I–O, Isachsen, Ellef Ringnes Island, Canada: (125b) SEM girdle view; (126b) SEM of an entire valve (externally); (127b) SEM of an entire valve (externally). Scale bars 1 µm (125b–127b).

(Hustedt) D.G.Mann et Stickle and *Fragilaria* sp. [cf. *F. gloiophila* (Grunow) Van de Vijver et al.]. In other samples, *H. ingeaeformis* was observed together with *Eunotia zackenbergensis, Nitzschia acidoclinata, Pinnularia subrostrata* and *Humidophila gallica.*

**Taxonomic remarks:** For comparison, SEM pictures of the type of *H. ingeaeformis* from Ellef Ringnes Island, Canada, were added (figs 125b–127b). An important difference between the type species and the Greenland species is the striation pattern. In the type, the striae converge near the apices. This difference is, however, not sufficient to separate both taxa. The most similar species is *H. perpusilla,* mainly based on the valve outline. Especially smaller specimens of *Humidophila ingeaeformis,* in which the inflated center is less pronounced, show resemblance to *H. perpusilla.* Confusion with larger specimens is less likely. In SEM, however, both species can always be distinguished based on the areolae, which are relatively longer and are distinctly radiate, also at the apices, in *H. perpusilla.* While *H. ingeaeformis* has a low abundance in Greenland, *H. perpusilla* is extremely abundant, especially on Disko Island. Another very similar species is *Humidophila australis* (Van de Vijver et Sabbe) R.L.Lowe et al., which was described from James Ross Island (Antarctic Region) in the genus *Diadesmis* (Van de Vijver et al. 2010). *Humidophila ingeaeformis* differs from *H. australis* in the slightly capitate, clearly inflated apices which are usually larger than the central part (see Van de Vijver et al. 2010, figs 46–55), and the striae that appear to converge towards each other near the apices (see Antoniades et al. 2008, figs 21–24).
Until more research is available on the complete cell diminution series of the type material of *Humidophila ingeaeformis* to objectively justify its separation from *H. australis,* we argue to keep both separated.

***Humidophila paracontenta* var. *magisconcava* (Lange–Bertalot) R.LLowe, Kociolek, J.R.Johansen, Van de Vijver, Lange–Bertalot et Kopalová 2014 (Figs 129–150)**
**Basionym:** *Diadesmis paracontenta* var. *magisconcava* Lange–Bertalot 2001 in Lange–Bertalot & Werum (2001, Diatom 17, p. 9, figs 11–14, 60–64).
**LM (Figs 129–147):** Valves small, linear with distinctly concave margins. Apices broadly rounded, non–protracted. Valve dimensions (n=19): length 8.5–14 µm, width middle 2.5–3 µm, width apices 3–4 µm. Axial area linear, broad, widening towards the apices. Fascia present, extending to valve margins. Raphe filiform, with simple, straight central endings. Terminal raphe endings simple. Striae short, parallel to slightly convergent near the apices, interrupted in center, 28–30 in 10 µm. Areolae not visible in LM.
**SEM (Figs 148–150):** Mantle with single row of rounded areola, continuous but smaller around the apices (Fig. 148). Copulae perforated by single row of slit–like




Figs 129–150. *Humidophila paracontenta* var. *magisconcava* from sample DM92, Disko Island, Greenland: (129) LM of girdle view; (130–147) LM of valve views; (148) SEM girdle view; (149) SEM of an entire valve (externally). Arrows indicate the areolae bordering the central area. (150) SEM of an entire valve (internally). Scale bar 10 µm (129–147), 1 µm (148–150).

pores (Fig. 148). Striae composed of one transapically elongated to rounded areola, usually slightly convergent near the apices (Fig. 149). Areolae with irregular lengths, interrupted by fascia in the center (Fig. 149). Central raphe endings simple, bordered by small depressions. Terminal raphe endings simple, bordered by small depressions (Fig. 149). Internally, well–developed central nodule present (Fig. 150). Areolae covered internally by porous hymenes (Fig. 150). Valve face and mantle areolae separated by vallum (Fig. 150).

**Ecology and associated flora:** *Humidophila paracontenta* var. *magisconcava* was found in several bryophyte samples collected in Greenland. In the sample with the largest population, sample DM92, *H. paracontenta* var. *magisconcava* co–occurred with *Pinnularia borealis* var. *sublinearis*, *Eunotia curtagrunowii*, *Humidophila perpusilla, Humidophila delognei* and *Hantzschia hyperborea*. In other samples, *H. paracontenta* var. *magisconcava* was observed together with *Staurosirella lapponica s.l., Pinnularia rabenhorstii* (Grunow) Krammer, *Nitzschia acidoclinata* and *Pinnularia lunata*.

**Taxonomic remarks:** based on the presence of a fascia, *Humidophila paracontenta* var. *magisconcava* might be confused with several species, such as *H. misionera* Vouilloud, J.M.Guerrero et Kociolek*, H. lagartiensis* Vouilloud, J.M.Guerrero et Kociolek*, H. delognei, H. contenta* sensu Ferreira, *H. paracontenta,* and *H. simplex.* While *H. misionera* has an almost identical valve outline (Vouilloud et al. 2022, figs 40–53), the species differ mainly in stria density (34–36 in 10 µm versus 28–30 in 10 µm in *H. paracontenta* var. *magisconcava*) and whilst *H. paracontenta* var. *magisconcava* has small areolae that border the central area, these are lacking in *H. misionera*. The apices in *H. lagartiensis* are more rounded (see Vouilloud et al. 2022, figs 28–39) and the stria density is higher (38–40 in 10 µm versus 28–30 in 10 µm in *H. paracontenta var. magisconcava*). *Humidophila delognei* can be separated based on valve outline, which is linear with parallel margins, whereas *H. paracontenta* var. *magisconcava* has distinctly concave margins. In SEM,

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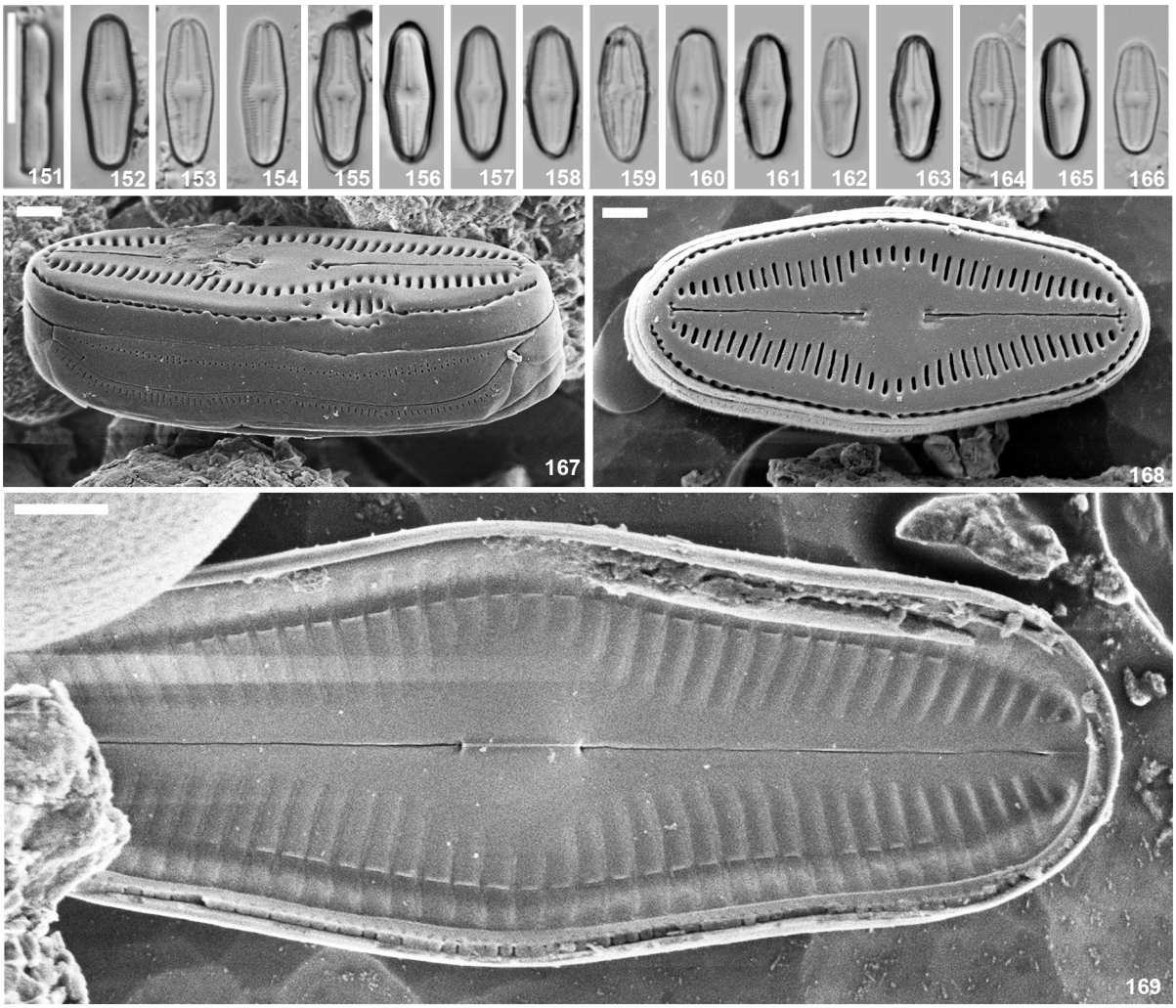



Figs 151–169. *Humidophila perpusilla* from sample DM102, Disko Island, Greenland: (151) LM of girdle view; (152–166) LM of valve views; (167) SEM of an entire valve (girdle orientation); (168) SEM external frustule, valve view; (169) SEM of an entire valve (internally). Scale bar 10 µm (151–166), 1 µm (167–169).

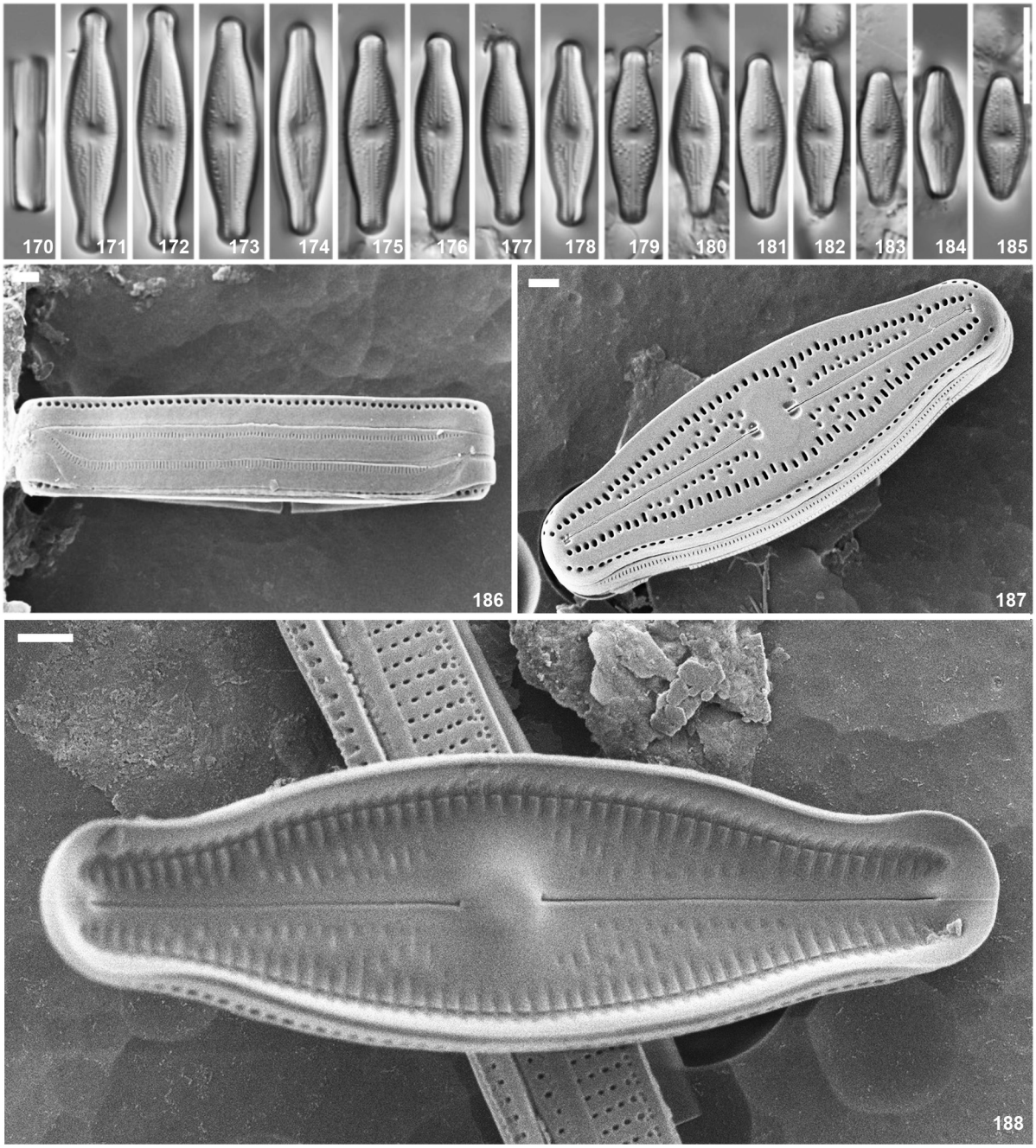
*H. delognei* shows T– or Y– shaped grooves where the raphe endings terminate, which are lacking in *H. paracontenta* var. *magisconcava.* Both species have a high abundance in Greenland, although *H. paracontenta* var. *magisconcava* has a higher occurrence in all Greenland samples we examined in this study and thus possibly less strict ecological preferences. *Humidophila contenta* sensu Ferreira et al. (2023) is similar in valve outline but can be distinguished in SEM based on the T–shaped terminal raphe endings (Ferreira et al. 2023, fig 54). *Humidophila paracontenta* var. *magisconcava* has a lower stria density (35–40 in 10 µm versus 28–30 in 10 µm in *H. paracontenta* var. *magisconcava*) (Goeyers & Van de Vijver 2023), making the striae well visible in LM, which is not seen in *H. simplex*. *Humidophila biscutella* resembles *H. paracontenta* var. *magisconcava* as well based on valve outline but lacks a fascia and is slightly smaller (length 8–12 µm versus 8.5–14 µm in *H. paracontenta* var. *magisconcava,* width 2–2.5 µm versus 2.5–3 µm in *H. paracontenta* var. *magisconcava*) (Moser et al. 1998).

***Humidophila perpusilla* (Grunow) R.L.Lowe, Kociolek, J.R.Johansen, Van de Vijver, Lange–Bertalot et Kopalová 2014 (Figs 151–169)**

**Basionym:** *Navicula perpusilla* Grunow 1860 in Grunow (1860, Verhandlungen der kaiserlich–königlichen zoologisch–botanischen Gesellschaft in Wien 10, p. 552, pl. II [2], fig. 7).

**LM (Figs 151–166):** Valves elliptical–lanceolate with central inflation. Apices non–protracted, broadly rounded. Valve dimensions (n=16): length 9–16 µm, width 3.5–5 µm. Axial area broad, widening towards central area. Central area round, no fascia present. Raphe straight, short, filiform with simple central endings. Terminal raphe endings simple. Striae ca. 32 in 10 µm, radiate throughout the valve. Individual areolae not visible.

**SEM (Figs 167–169):** Mantle with single row of elongated areolae located in a deep longitudinal groove, interrupted at apices (Fig. 168). Copulae perforated by a single row of slit–like pores (Fig. 167). Striae located in shallow groove, of the cubiculus–type, composed of one long transapically elongated areola (Fig. 168). Areolae continuous through central area but shortened (Fig.




Figs 170–188. *Humidophila mochalovae* from sample ZM12, Zackenberg, Greenland: (170) LM of girdle view; (171–185) LM of valve views; (186) SEM girdle view; (187) SEM of an entire valve (externally); (188) SEM of an entire valve (internally). Scale bar 10 µm (170–185), 1 µm (186–188).

168). Areolae continuous, shorter around central area (Fig. 168) and becoming shorter towards poles, radiate throughout (Fig. 168). Central raphe endings simple, bordered by small depressions (Fig. 168). Terminal raphe endings lying in T–shaped grooves. Internally, raised nodule present (Fig. 169). Central raphe endings simple. Terminal raphe endings simple, terminating on weakly developed helictoglossae internally (Fig. 169). Valve face and mantle areolae separated by vallum (Fig. 169).

**Ecology and associated flora:** Since the *Navicula perpusilla* type material could not be retrieved, a historic population from Scotland (i.e., Van Heurck Types du Synopsis 212) was designated as epitype in 2022 (Van de Vijver & Goeyers 2022). The epitype population shows terminal endings with inconspicuous terminal markings, whereas in our study, *H. perpusilla* has terminal markings (Fig 168). Apart from this, no other differences were found. In Goeyers & Van de Vijver (2023), both valves with (Fig 5s) and without (Fig 6r) markings are shown. The terminal markings are therefore likely a variation in morphological features related to the

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degree of valve silicification. *Humidophila perpusilla* was found in many bryophyte samples collected in Greenland. In sample DM102, the sample with the largest population, *Humidophila perpusilla* co–occurred with *Meridion circulare, Nitzschia acidoclinata, Nitzschia homburgiensis* Lange–Bertalot and *Pinnularia* sp. [cf. *P. subcapitata* var. *subrostrata* Krammer]. In other samples, *H. perpusilla* was found with *Hygropetra balfouriana* (Grunow ex Cleve) Krammer et Lange–Bert*., Tabellaria acidodelicata, Eunotia curtagrunowii, Diatomella balfouriana* (Smith) Greville and *Pinnularia obscura* Krasske.

**Taxonomic remarks:** *Humidophila perpusilla* is most similar to *H. arctica* and *H. gallica,* based on valve outline (see above). Another species showing resemblance to *H. perpusilla* is *H. flotowii,* which has long been considered as a synonym of *H. perpusilla* (Goeyers & Van de Vijver 2023). Both possess an inflated valve center and broadly rounded apices, sometimes weakly protracted in *H. flotowii* but can easily be separated based on valve outline and valve dimensions. The valve length/width ratio of *H. flotowii* is higher (3.5–4.1 versus 2.3–2.8), leading to a more elongated outline.

**Description of new combination**

***Humidophila mochalovae* (Potapova) Goeyers, Van de Vijver et Sabbe, comb. nov. (Figs 170–188)**

**Basionym:** *Diadesmis mochalovae* Potapova 2014 in Potapova (2014, Nova Hedwigia, 143, p. 89, fig. 219–224, 228–230).

**Registration for new combination:** http://phycobank.org/103969

**LM (Figs 170–185):** Valves rectangular in girdle view (Fig. 170). Valves lanceolate with distinctly convex margins, narrowing towards apices. Apices slightly protracted in smaller valves, becoming clearly protracted in larger valves, rostrate to capitate, and broadly rounded. Valve dimensions (n=16): length 12.5–25 µm, width 4.5–5.5 µm in the center to 2–3 µm at the apices. Axial area narrow, linear. Central area distinct, rectangular to elliptical, no fascia present. Raphe filiform with simple straight raphe endings. Striae slightly radiate throughout valve, 28–30 striae in 10 µm. Striae composed of 2–3 areolae, to one near the valve ends, clearly discernible in LM; areolae separated by longitudinal hyaline lines. **SEM (Figs 186–188):** Girdle composed of at least three open, relatively broad copulae, perforated by slit–like pores (Fig. 186). Mantle with single row of elongated areolae, interrupted at the apices (Fig. 186). Axial area narrow (Fig. 187). Striae composed of 2–3 transapically elongated (along valve margin) to rounded (along axial area) areolae. At apices, striae only composed of 1 areola. Raphe straight, filiform, with simple central and terminal raphe endings, both located in shallow depressions (Fig. 187). Internally, well–developed central nodule present (Fig. 188). Internal terminal raphe endings terminating on weakly developed helictoglossae. Areolae internally covered by long, porous hymenes. Valve and mantle face separated by vallum (Fig. 188).

**Ecology and associated flora:** *Humidophila mochalovae* was found in several bryophyte samples collected in Greenland. In sample ZM12, the largest population was observed. In this sample, *Humidophila mochalovae* co–occurred with *Eunotia zackenbergensis*, *Humidophila arctica, Nitzschia acidoclinata*, *Pinnularia subrostrata* and *Pinnularia* cf. *viridiformis* Krammer. *Humidophila mochalovae* was observed in other samples as well, co–occurring with *Cymbopleura tynnii, Eunotia curtagrunowii, Frustulia saxonica* Rabenhorst*, Tabellaria acidodelicata* and *Diatomella balfouriana*.

**Taxonomic remarks:** *Diadesmis mochalovae* was described by Potapova from a tundra pond on Bering Island, Russia (Potapova 2014). Some minor differences with our population are observed. In the Greenland specimens, the mantle striae at the apices are less slightly moved onto the valve face compared to the type population (see Potapova 2014, fig. 229). The terminal raphe endings are bordered by small markings, not visible in the type population (Potapova 2014, figs 228–229), and the row of areolae closest to the raphe are shorter and often split in two. However, the valves of the type population are relatively eroded and the pictures are of less quality, making characteristics less clear. In addition, we argue it is unlikely that two populations extremely similar in morphology and environment are different species. *Humidophila mochalovae* has a unique morphology that is slightly aberrant from the generic type. The generic type is composed of one areola per valve face stria and one on the mantle. In several species, such as *H. ingeae* and *H. brekkaensis*, two areolae are present on the valve face (see for instance Werum & Lange–Bertalot 2004, plate 58, figs 10–13). *Humidophila* species with multiple valve face areolae per stria on the valve face have so far not been recorded. *Humidophila mochalovae* superficially resembles representatives of *Brachysira, Nupela* Vyverman et Compère, or *Diadesmis.* However, *Brachysira* differs in raphe structure (narrow raphe sternum with straight raphe branches, simple central raphe endings and short terminal raphe endings) and typical depressions and siliceous structures on the valve face, such as longitudinal ridges bordering the axial area, marginal crests, papillae and spines (Lange–Bertalot & Moser 1994). *Nupela* species have striae with very fine, small areolae, a usually asymmetrical central area, an often monoraphid frustule structure, and long, deflected to hooked terminal raphe fissures (Vyverman & Compère 1991). *Diadesmis* has striae composed of up to 6 small, rounded areolae. Although *Humidophila mochalovae* has multi–areolate striae, in SEM, it shows the typical *Humidophila* features, such as transapically elongated to rounded areolae, internally occluded by porous hymenes, and a filiform raphe with straight, simple, drop–, T–, or anchor–shaped external raphe endings (Lowe et al. 2014). The typical vallum, separating valve and mantle face, is also discernible in SEM. There are at present no *Humidophila* species showing resemblance

to *H. mochalovae*. Confusion may arise with species in other genera such as *Sellaphora* Mereschowsky, where several species have a similar valve outline [for instance *S. lundii* C.E.Wetzel, Barragán et Ector (Wetzel et al. 2017)] but their overall morphology excludes all possible confusion.

**Description of new taxa**

***Humidophila helderiana* Goeyers et Hamilton, sp. nov. (Figs 189–209, 210–212)**

**Description**

**LM (Figs 189–209):** Valves small, linear to linear–lanceolate, with weakly convex margins, gradually narrowing towards the apices. Apices not protracted, rounded. Valve dimensions (n=21): length 8–14 µm, width 2.5–3 µm. Axial area narrow (Fig. 191) and linear to usually weakly discernible in LM. Central area small, round, no fascia present. Raphe straight, with simple raphe endings. Striae not discernible in LM.

**SEM (Figs 210–212):** Valve face almost flat. Striae uniseriate, of the cubiculus–type, composed of one transapically elongated areola, up to 36–38 in 10 µm. Areolar length variable throughout entire valve, with shortened areolae present around central area and near apices. Raphe branches straight with simple raphe endings (Fig. 210). Very thin, low longitudinal ridges present bordering raphe branches along their entire length (Fig. 210). Mantle striae composed of small, linear–elliptic areolae, seemingly interrupted at apices (Figs 210, 212). At the apices, two rows of areolae present on ledge located on valve face–mantle margin. Vallum present internally, areolae covered by hymenes (Fig. 212). Central nodule raised with central raphe endings internally terminating at the edge of central nodule (Fig. 212). Terminal raphe endings internally terminating onto weakly developed helictoglossae.

**Holotype:** BR–4833 (Meise Botanic Garden, Belgium).
**Isotype:** slide 437 (University of Antwerp, Belgium).
**Registration:** http://phycobank.org/103967.
**Type locality:** Zackenberg, Greenland, sample ZJ79 (74°29'30.5"N, 21°03'13.0"W), coll. date 01.VIII.2000, leg. Koen Trappeniers.
**Etymology:** The species is named after Mr. Schuyler Helder (Antwerp, Belgium), partner of first author Charlotte Goeyers, with thanks for never–ending support and advice during her doctoral research.
**Ecology and associated flora:** In type sample ZJ79, *Humidophila helderiana* was found together with *Pinnularia subrostrata, Tabellaria acidodelicata, Humidophila arctica* and *Neidium bisculatum* (Lagerst,) Cleve. In other samples, *H. helderiana* co–occurred with *Eunotia zackenbergensis*, *Nitzschia acidoclinata, Psammothidium helveticum* and *Staurosirella lapponica s.l.*
**Habitat:** slightly acidic (pH 6.6) habitat with low conductivity (4 $\mu S.cm^{-1}$).
**Distribution:** This species has so far only been found in the type locality.

**Taxonomic remarks:** There are only a few *Humidophila* species with isolated rows of areolae located in depressed ridges at the apices. Apart from the new species, only *H. virginiana* Lange–Bertalot et Werum, *H. fukushimae* (Lange–Bertalot, M.Werum et Broszinski) Buczkó et Kövér, and *H. flotowii* show a similar structure. *Humidophila virginiana* and *H. fukushimae* have more robust, larger valves (length 16–20 µm in *H. virginiana* and 14–21.7 µm in *H. fukushimae* versus 8–14 µm in *H. helderiana*), whereas *H. flotowii* has a different, more lanceolate to rhombic–lanceolate valve outline. Curiously enough, all four species possess the same low, very thin longitudinal ridges bordering the raphe branches (Lange–Bertalot & Werum 2001; Goeyers & Van de Vijver 2023). The latter feature is, however, not unique for these four as *Humidophila subantarctica* Le Cohu et Van de Vijver also has similar ridges but lacks a recessed ledge with circumpolar areolae at the ends (Le Cohu & Van de Vijver 2002). *Humidophila helderiana* resembles several other *Humidophila* species: *H. vojtajarosikii* Kopalová, Zidarova et Van de Vijver, *H. comperei* (Le Cohu et Van de Vijver) R.L.Lowe, Kociolek, J.R.Johansen, Van de Vijver, Lange–Bertalot et Kopalová and *H. tempiliana* (Lange–Bertalot et Rumrich) R.L.Lowe, Kociolek, Johansen, Van de Vijver, Lange–Bertalot et Kopalová. All have a similar narrow, linear valve outline, a comparable stria density (hardly discernible in LM) and non–protracted, narrowly rounded apices. But they all lack the typical rows of isolated areolae around the apices (Rumrich et al. 2000; Le Cohu & Van de Vijver 2002). *Humidophila arctica* has a slightly similar valve outline, but *H. helderiana* is distinctly smaller (max. 14 µm in length). In SEM, the areolae of *H. helderiana* are more elongated and striae are present on the valve face near the apices. Both are present in multiple locations in Greenland, although *H. arctica* is observed more frequently.

***Humidophila mitosis* Goeyers, Van de Vijver et Kohler sp. nov. (Figs 213–227, 228–230)**

**Description**

**LM (Figs 213–227):** Valves linear–lanceolate, with inflated center. Apices non–protracted and broadly rounded. Valve dimensions (n=15): length 9.5–23 µm, width 3–5 µm. Striae weakly visible in LM, ca. 28 in 10 µm (Fig. 214). Axial area very broad, 1/2 of total valve width (Fig. 213). Central area round, no fascia present. Raphe filiform, with straight endings. Siliceous markings on valve face weakly visible in LM (Fig. 224).

**SEM (Figs 228–230):** Mantle with single row of areolae just below valve face margin, interrupted at the apices. Valve face covered by siliceous thickenings, most pronounced in central area and along axial area. Distinct axial area present. Central area rounded to bow–shaped. Striae uniseriate, of the cubiculus–type, composed of one areola. Areolae elongated, of variable length, shortening near central area and apices. Near apices, striae converge. Raphe straight, with simple and straight central raphe endings, and terminal endings bordered by small

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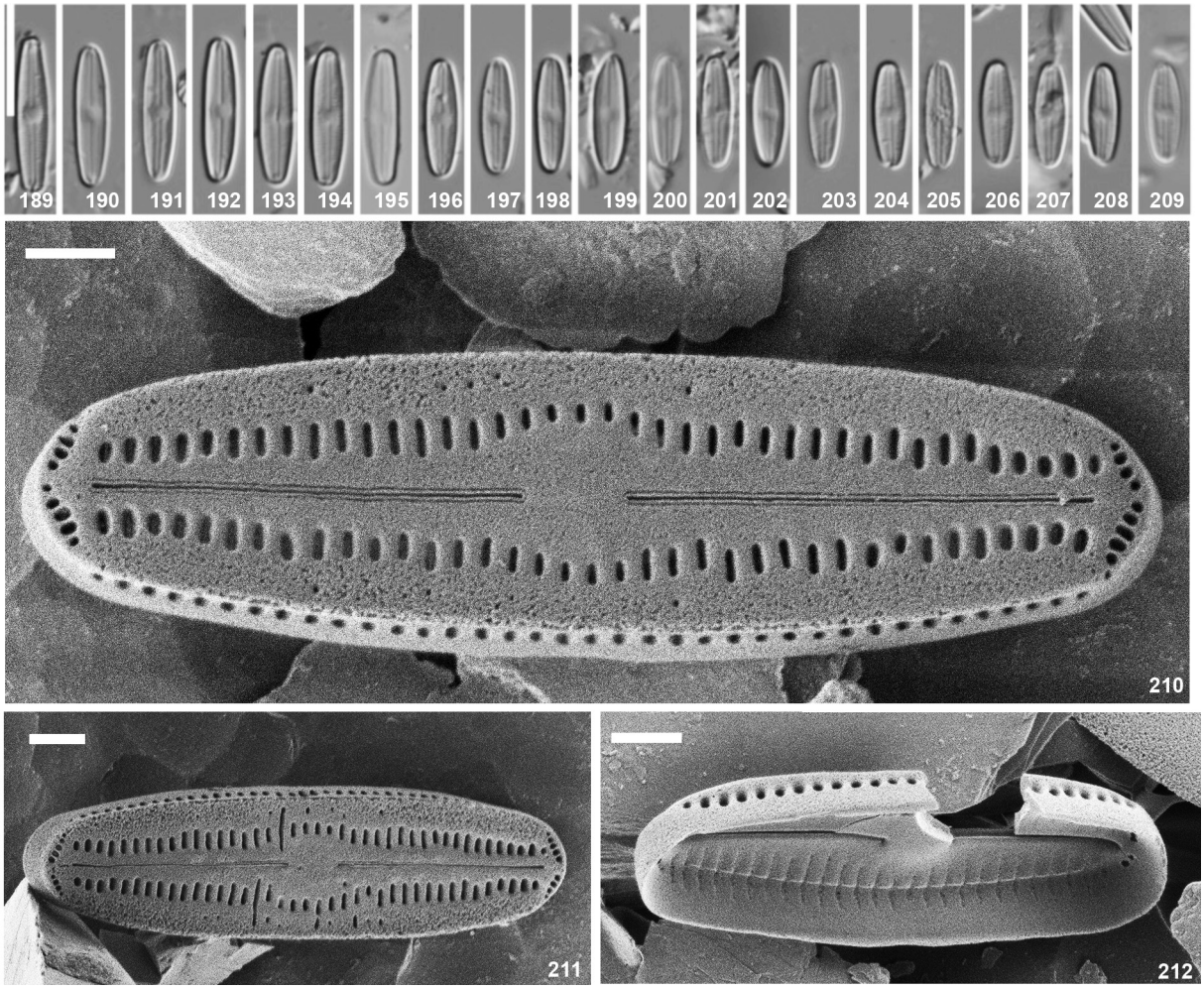


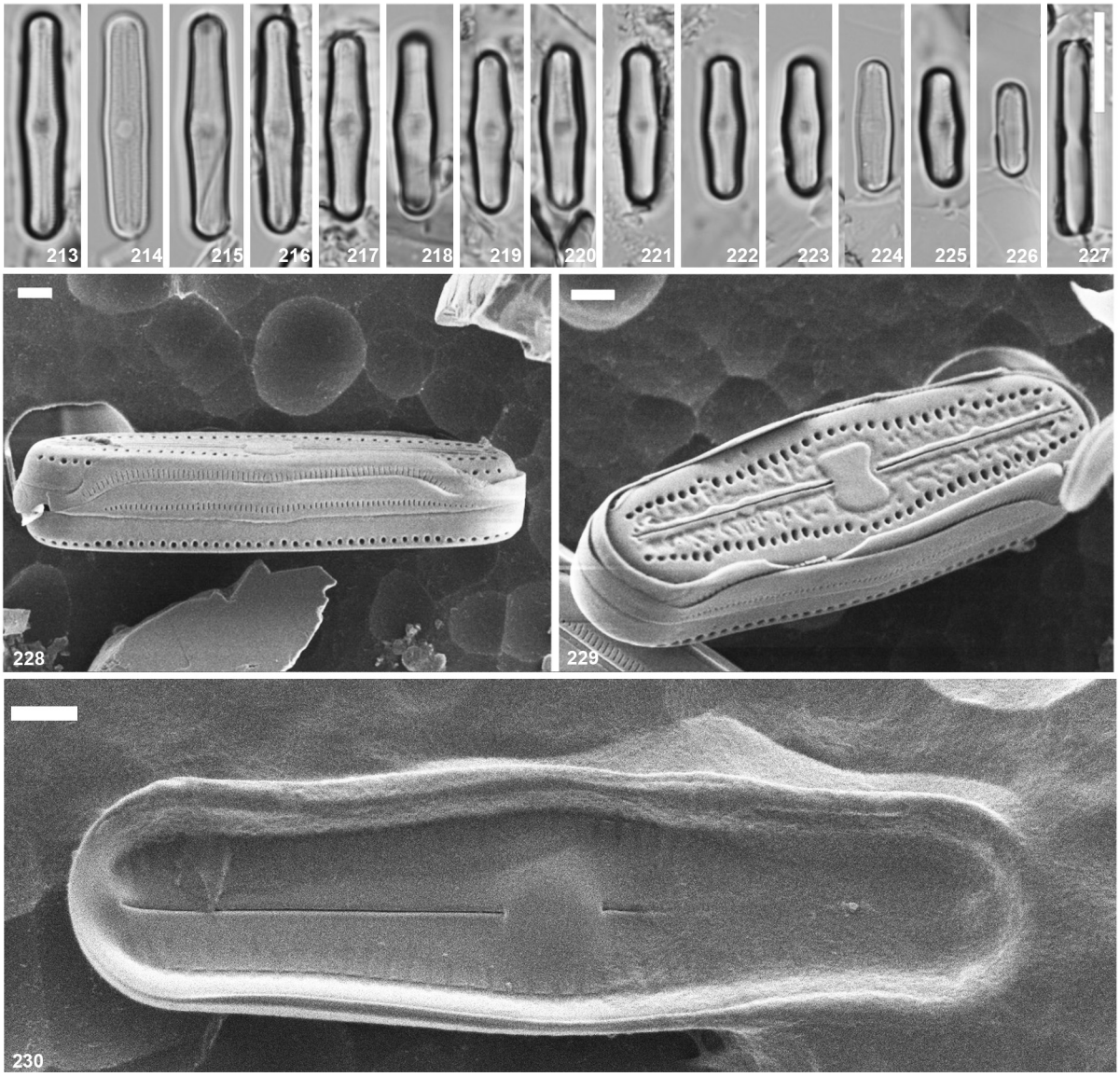

Figs 189–212. *Humidophila helderiana* from sample ZJ79, Zackenberg, Greenland: (189–209) LM of valve views; (210) SEM of an entire valve (externally) with mantle areolae visible; (211) of an entire valve (externally); (212) SEM of an entire valve (internally). Scale bar 10 µm (189–209), 1 µm (210–212).

depressions. Well–developed central nodule internally. Internal terminal raphe endings terminating on weakly developed helictoglossae. Areolae covered internally with hymenes. Vallum present. Girdle copulae perforated by a single row of slit–like pores.

**Holotype:** BR–4834 (Meise Botanic Garden, Belgium).
**Isotype:** slide 438 (University of Antwerp, Belgium).
**Registration:** http://phycobank.org/103968.
**Type locality:** Near Kangerlussuaq, Greenland, sample 20, (W050.10232, N67.14743). Collected on 6 September 2017 by Tyler J. Kohler.
**Etymology:** the epithet '*mitosis*' refers to the appearance of the bow–shaped thickening in the central area, which looks like a dividing cell.
**Ecology and associated flora:** In type sample 20, *Humidophila mitosis* co–occurred with *Pinnularia borealis* var. *sublinearis, Humidophila eldfjallii* and *H. paracontenta* var. *magisconcava.* In other samples, *Humidophila mitosis* co–occurred with *Cavinula pseudoscutiformis*, *Encyonema fogedii*, *Encyonopsis stafsholtii*, *Nitzschia acidoclinata* and *Tabellaria acidodelicata.*

**Habitat:** found in habitat with high moisture level, near an ice margin, on high elevation (356 m).
**Distribution:** This species has so far only been observed in the type locality.

**Taxonomic remarks:** *Humidophila mitosis* shows resemblance to *H. brekkaensis* in general valve outline. In SEM, both species can be distinguished based on the mantle areolae that are positioned on the same level as the valve face areolae in *H. brekkaensis,* a feature that is lacking in *H. mitosis.* Additionally, *H. mitosis* can be recognized by its siliceous thickenings on the valve face. Other similar species are *H. bigibba* (Hustedt) R.L.Lowe, Kociolek, J.R.Johansen, Van de Vijver, Lange–Bertalot et Kopalová, *Humidophila* sp. Lowe et al. (2017), *H. lacunosa* (Gerd Moser, Lange–Bertalot et Metzeltin) R.L.Lowe, Kociolek, J.R.Johansen, Van de Vijver, Lange–Bertalot et Kopalová*, H. potapovae* R.L.Lowe, Kociolek et Q.You*, H. undulocontenta,* and *H. platensis* (Metzeltin, Lange–Bertalot et Garcia–Rodriguez) R.L.Lowe, Kociolek, J.R.Johansen, Van de Vijver, Lange–Bertalot et Kopalová*. Humidophila bigibba* and




Figs 213–230. *Humidophila mitosis* from sample 20, near Kangerlussuaq, Southwest Greenland: (213–226) LM of valve views; (227) LM of girdle view; (228) SEM girdle view; (229) SEM of an entire valve (externally) with mantle visible; (230) SEM of an entire valve (internally). Scale bar 10 µm (213–227), 1 µm (228–230).

*H. mitosis* both have depressions on their external valve face but are easily distinguishable in LM based on their valve outline. While *H. mitosis* has linear–lanceolate valves, *H. bigibba* has biundulate valves with a deep constriction in the middle (Yogeshwaran et al. 2022, figs 19–28). The areolae of *H. bigibba* continue around the apices but are interrupted in *H. mitosis.* In addition, both *H. mitosis* and *H. lacunosa* share a similar central area, but the apices of *H. lacunosa* are more cuneate rather than broadly rounded, and the mantle striae are not interrupted around the apices in *H. lacunosa* (Moser et al. 1998, pl. 29, figs 1–3). Based on the external thickening in the central area, *H. potapovae* and *H. mitosis* are similar, although *H. potapovae* is longer (length 15.5–27 µm compared to 9.5–23 µm in *H. mitosis*, width 3–3.5 µm compared to 3–5 µm in *H. mitosis*), the raphe of *H. mitosis* terminates at the end of the apices whereas in *H. potapovae* the raphe terminates sooner, and the mantle areolae are interrupted in *H. mitosis,* while uninterrupted in *H. potapovae* (Lowe et al. 2017). Another species with a similar central area is presented in Lowe et al. (2017) as *Humidophila* sp.*,* but this taxon has a different valve outline and valve dimensions (length 26–48 µm compared to 9.5–23 µm in *H. mitosis*, width 3.4–3.8 µm compared to 3–5 µm in *H. mitosis*) (Lowe et al. 2017).

## Discussion

The objective of this study was to explore and describe the diversity of the genus *Humidophila* in Greenland using a fine–grained morphological approach based on detailed LM and SEM observations. In total, we

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recorded 11 *Humidophila* species, two of which are new to science, and one was transferred from *Diadesmis* to *Humidophila*. These new descriptions bring the total number of species in the genus *Humidophila* globally to 87 (Guiry & Guiry 2023). Other reported species–rich regions include Argentina with 17 species (Vouilloud et al. 2022), New Caledonia with 14 species (Moser et al. 1998), the sub– and Maritime Antarctic regions with more than 10 species for both (Van de Vijver et al. 2002; Zidarova et al. 2016), and the Guizhou province in China with 8 species (Lowe et al. 2017). Because few studies on moss–inhabiting diatoms in the Arctic exist, and since *Humidophila* is a typical terrestrial diatom genus likely to be found in moss habitats, the number of *Humidophila* taxa for the circumpolar Arctic will undoubtedly increase in the future.

Due to historical force–fitting and the now outdated paradigm for microorganisms that 'everything is everywhere but the environment selects' (Baas Becking 1934), knowledge on the biogeography of *Humidophila* and other diatom genera remains inadequate. While this study confirms that *Humidophila contenta* and *H. gallica* are indeed globally distributed species, recent efforts (together with our results) show that the distribution of many *Humidophila* is more restricted, often to the Arctic and harsh Antarctic environment (Van de Vijver et al. 2002; Kopalová et al. 2015; Furey et al. 2020). For example, *H. delognei, H. mochalovae, H. paracontenta* and *H. paracontenta* var. *magisconcava* are restricted to the Northern Hemisphere, *H. arctica, H. eldfjallii, H. ingeaeformis* have an Arctic distribution, and *H. helderiana* and *H. mitosis* are (so far) exclusively found in Greenland. However, since these species may have been overlooked elsewhere, further research is needed to establish their true geographic distributions.

The only other study on moss diatoms in Greenland reported *H. contenta* (as *Diadesmis contenta), H. perpusilla* (as *Diadesmis perpusilla)* and *H. simplex* (as *Diadesmis contenta* f. *biceps)* in Zackenberg (Van Kerckvoorde et al. 2000), although the latter might possibly correspond to *H. delognei* instead of *H. simplex.* It is however not possible to examine this in detail since the paper does not include micrographs of the observed *Humidophila* species. Because of these sparse records, coupled with the new observations reported here, we argue for continued investigation into the terrestrial diatom flora of Greenland and the wider circumpolar Arctic to urgently better document its diversity in this era of rapid climate change.

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