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DOI
10.11646/phytotaxa.674.1.5

Publication date
2024

Document Version
Final published version

Published in
Phytotaxa

Citation (APA)
Rybak, M., Christenhusz, M. J. M., & Byng, J. (2024). Discovery of a new moss-associated diatom species, Humidophila caribaea (Bacillariophyceae: Diadesmidaceae), from terrestrial habitats of the Monts Caraïbes, Guadeloupe. *Phytotaxa*, *674*(1), 111-120. https://doi.org/10.11646/phytotaxa.674.1.5

Phytotaxa 674 (1): 111–120
https://www.mapress.com/pt/
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Article

ISSN 1179-3155 (print edition)
PHYTOTAXA
ISSN 1179-3163 (online edition)

https://doi.org/10.11646/phytotaxa.674.1.5

Discovery of a new moss-associated diatom species, *Humidophila caribaea* (Bacillariophyceae: Diadesmidaceae), from terrestrial habitats of the Monts Caraïbes, Guadeloupe

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Abstract

During the investigation of diatom diversity of terrestrial moss samples collected on Basse-Terre, Guadeloupe, French West Indies, a new species of the genus *Humidophila* (Lange-Bertalot & Werum) Lowe *et al.* was observed. The species occurred in only one sample collected from tropical, mesophytic forests in the Monts Caraïbes and could not be identified based on the literature data. Based on the set of morphological features the species is described herein as *Humidophila caribaea sp. nov.* The species is characterized by the small valve size, typical for the *Humidophila* genus, but it has a unique morphology of the areolae with small silica warts in their lumen. Additionally, a comparison with most similar taxa known worldwide, as well as ecological notes are provided.

Key words: Bacillariophyceae, bryosphere, Caribbean, taxonomy

Introduction

The genus *Humidophila* Lowe *et al.* (2014: 352) with its generitype *H. undulata* Lowe *et al.* (2014: 352) was established to accommodate taxa originally described in or transferred from the genus *Diadesmis* Kützing (1844: 109) and assigned to subgenus *Paradiadesmis* Lange-Bertalot & Le Cohu (in Rumrich *et al.* 2000: 108) (Lowe *et al.* 2014). The genus *Humidophila* includes small, biraphid diatoms with a flat valve face and a linear to elliptical valve outline, characterized by striae formed by a single areola, usually transapically elongated and internally occluded by hymenes. Live *Humidophila* cells have a single-lobed plastid (Taylor & Cocquyt 2016). Although most species in the genus are biraphid, the *Humidophila* genus also includes secondarily rapheless taxa [i.e. *H. panduriformis* Lowe *et al.* (2017: 277) or *H. cavernaphila* Lowe *et al.* (2017: 278)], as well as taxa that, depending on the environment, can be biraphid or rapheless, like *H. gallica* (W.Smith) Lowe *et al.* (2017: 281) (Cox 2006)

The genus *Humidophila* is distributed worldwide (Lowe *et al.* 2014) and is commonly reported from various subaerial habitats such as wet walls, spray zones of waterfalls, and soils (Hustedt 1962, Furey *et al.* 2020, Nikolić *et al.* 2020). High species diversity has been recorded in Europe (e.g. Werum & Lange-Bertalot 2004, Nikolić *et al.* 2020), the Maritime Antarctica (Van de Vijver *et al.* 2002; Kopalová *et al.* 2015, Zidarova *et al.* 2016), Asia (Lowe *et al.* 2017), South America (Metzeltin *et al.* 2005, Vouilloud *et al.* 2022) and Hawaii (Lowe *et al.* 2014).

Moreover, 11 mostly unidentified *Humidophila* taxa were reported from the Antillean islands (Eulin *et al.* 2014). Two other taxa, identified as *Navicula contenta* f. *undulata* Manguin in Bourrelly & Manguin (1952: 62) and *Navicula pseudocontenta* Manguin in Bourrelly & Manguin (1952: 63), possibly belonging to *Humidophila* were observed in samples collected from Guadeloupe (Bourrelly & Manguin 1952)

During a study of moss-inhabiting diatom flora of Guadeloupe, an unknown *Humidophila* taxon was observed

Accepted by Karthick Bala: 29 Oct. 2024; published: 26 Nov. 2024

in a single moss sample. Identification of this species was not possible based on the currently available literature. Detailed morphological analysis and comparison with the most similar taxa indicated that the taxon presents a unique combination of features necessitating its description as a new species.

Material and methods

Moss clumps were sampled in June 2021 during a botanical expedition to the Monts Caraïbes. Samples were, stored in labeled paper envelopes, and left to dry in the air. The collected material was used to obtain clean diatom valves and prepare filtrates for pH and conductivity analyses.

The filtrates were obtained by soaking pieces of moss in deionized water (in weight ratio 1:10) for 24 hours. The pH and electrolytic conductivity values were measured using a MARTINI pH56 pH meter and MARTINI EC59 conductivity meter.

For diatom analysis, part of the collected moss clumps was digested with sulfuric acid (H_2SO_4) and potassium dichromate ($K_2Cr_2O_7$). After dissolving all organic matter, diatom suspension was washed 3–5 times with distilled water and centrifugated at 2500 RPMfor 5 minutes. The cleaned diatom material was pipetted onto coverslips, left to dry overnight at room temperature and then mounted with Naphrax® (Brunel Microscopes Ltd, Wiltshire, U.K.).

Identification, counting and the measurements of basic morphological features of the diatoms were performed under a Carl Zeiss Axio Imager A2 light microscope (LM) equipped with a 100× Plan Apochromatic objective with differential interference contrast (DIC) for oil immersion (NA 1.4) and captured with a Zeiss AxioCamICc 5 camera.

For scanning electron microscopy (SEM) observations and areolae density measurements, part of the diatom suspension was placed on a polycarbonate membrane filter with a 3 µm pore size, attached to aluminum stubs, and sputtered with 20 nm of gold using a Quorum Q 150OT ESTurbo-Pumped Sputter Coater. Diatoms were observed using a Hitachi SU 8010 at the University of Rzeszów. Diatom terminology follows Ross *et al.* (1979), Round *et al.* (1990) and Lowe *et al.* (2014).

Results

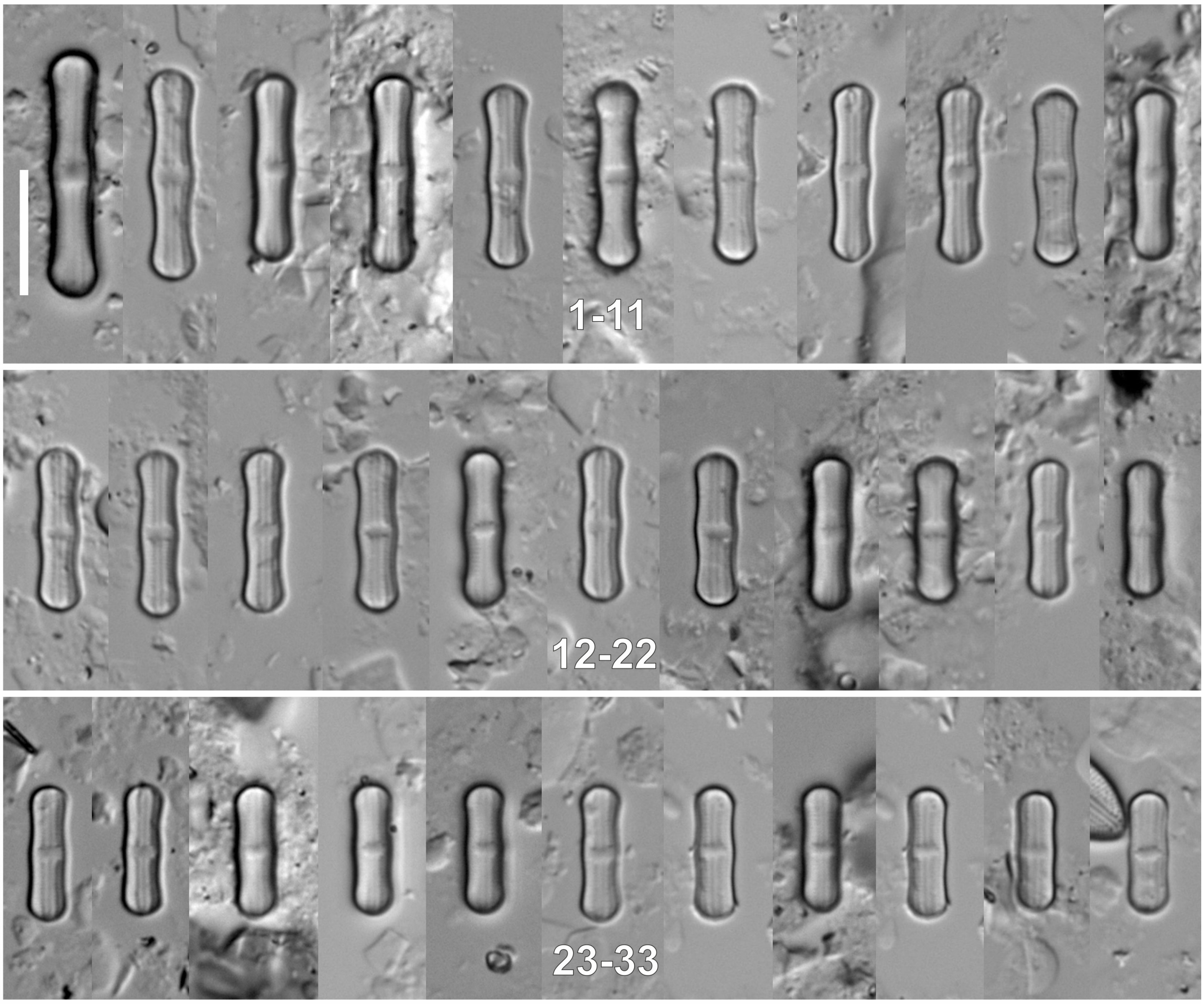
Phylum **Heterokontophyta** Moestrup, R.A.Andersen & Guiry (2023: 4)
Subphylum **Bacillariophytina** Medlin & Kaczmarska (2004: 267)
Class **Bacillariophyceae** Haeckel (1878: 95)
Subclass **Bacillariophycidae** D.G.Mann (1990: 125, 651)
Order **Naviculales** Bessey (1907: 284)
Suborder **Neidiineae** D.G.Mann (1990: 128, 657)
Family **Diadesmidaceae** D.G.Mann (1990: 660)
Genus ***Humidophila*** (Lange-Bertalot & Werum) Lowe & *et al.* 2014

Humidophila caribaea* M.Rybak, Christenh. & Byng, *sp. nov. (Figs 1–61)

LM observations (Figs 1–33):—Valves linear, slightly gibbous in the valve middle. Valve apices broadly rounded, slightly broader at the valve middle. Valve dimensions (n=40): length 9.0–19.0 µm, width 2.6–3.4 µm. Axial area narrow, linear. Central area rectangular and narrow, reduced in small specimens. Raphe straight and filiform. Proximal and distal raphe endings straight. Striae parallel, hardly discerned in LM, 34–36 in 10 µm.

SEM observations (Figs 34–61):—Externally striae composed of single, transapically elongated areola (Figs 34–43). Areolae size uniform along their entire length (Figs 34–43). A break in areole present in the central area (Figs 34–43). In some specimens short, rounded areolae, distinct in their shape and position from other areolae, occasionally present in the central area. Areolae on valve face always present with irregular silica warts in their lumen (Figs 44–46). Valve face and mantle areolae separated by large hyaline area (Figs 42, 47). Mantle areolae elongated, slit like, becoming smaller and rounded near the apices. Silica warts in mantle areolae absent. An interruption in areolae at valve apices clearly present (Figs 44, 45). External raphe branches straight. Both proximal and distal raphe endings variable even in a single valve, small elongated depressions occasionally present at the endings. Internally, raphe branches straight, proximal raphe endings straight, distal raphe endings terminating on weakly developed helictoglossae (Figs

48–51). Internally areolae covered by hymens. Girdle bands open (Fig. 47, 58–60). Pores on girdle bands present as single row, along valve margins pores strongly elongated with thickened edges (Figs 58–60), becoming smaller and rounded at the apices (Figs 60, 61). No signs of a Voigt discontinuity both in the external and internal view.



FIGURES 1–33. LM microphotographs of *Humidophila caribaea sp. nov.* holotype population in size diminution series. Scale bar = 10μm.

Type:—GUADELOUPE, the upper slope of Morne Cadet, Trace de Vent Soufflé, Monts Caraïbes, coordinates: 15°58’20.1”N 61°41’24.7”W, ca 680 m a.s.l, coll. date. 3 June 2021, *leg: M. Christenhusz & J. Byng, s.n.* Holotype slide no. PC0677386 and unmounted material with the same number at the Muséum National d’Histoire Naturelle, Paris, France.

Isotype 1 no. SZCZ28977! and unmounted material with the same number at the Szczecin Diatom Collection (University of Szczecin, Poland).

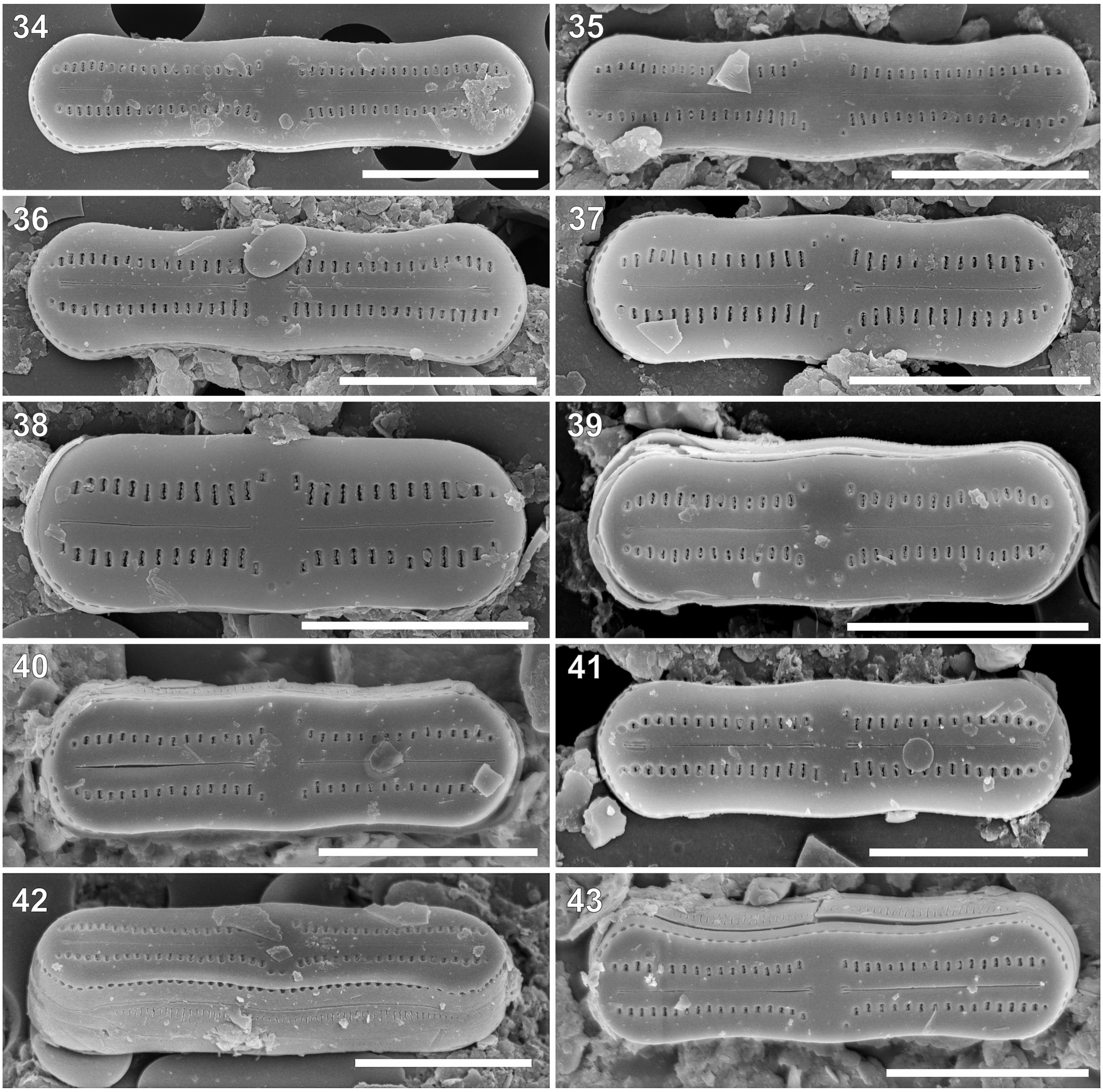
Isotype 2 no. slide no. 2021/29 and unmounted material with the same number at the University of Rzeszów, Poland.

The holotype population is presented in figs 1–51.

Etymology:—The species epithet refers to the type locality of the new species.

Distribution:—So far the species is only known from the type locality.

Ecology and associated diatom flora:—The sample was collected from tropical, mesophytic forests on volcanic, pozzolan soil. It was found among terrestrial mosses, sampled during a general botanical expedition to these hills.

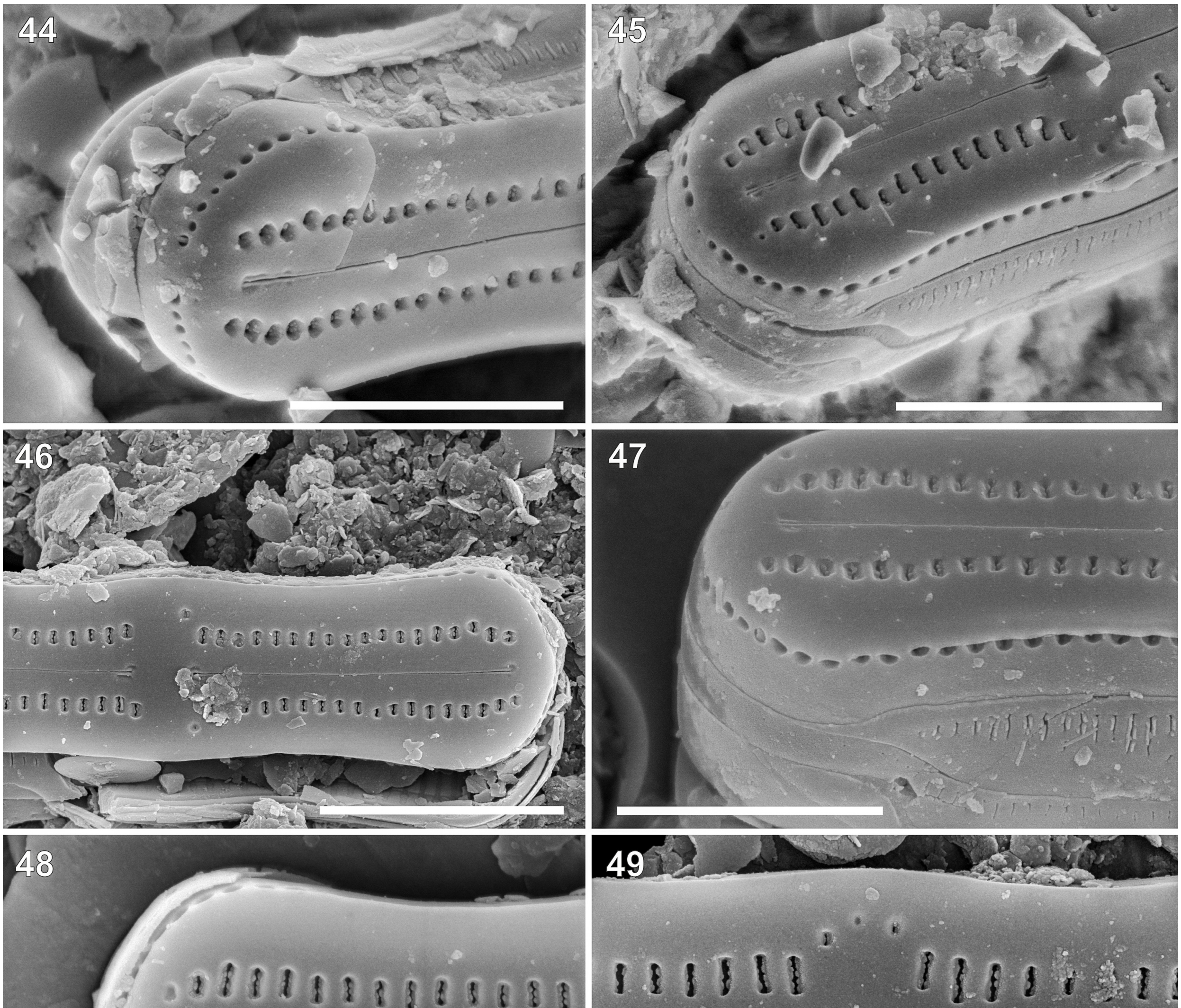


FIGURES 34–43. SEM microphotographs of *Humidophila caribaea sp. nov.* in external view. Scale bar = 5 µm (Figs 34–37, 39–43), 4 µm (Figs 38)

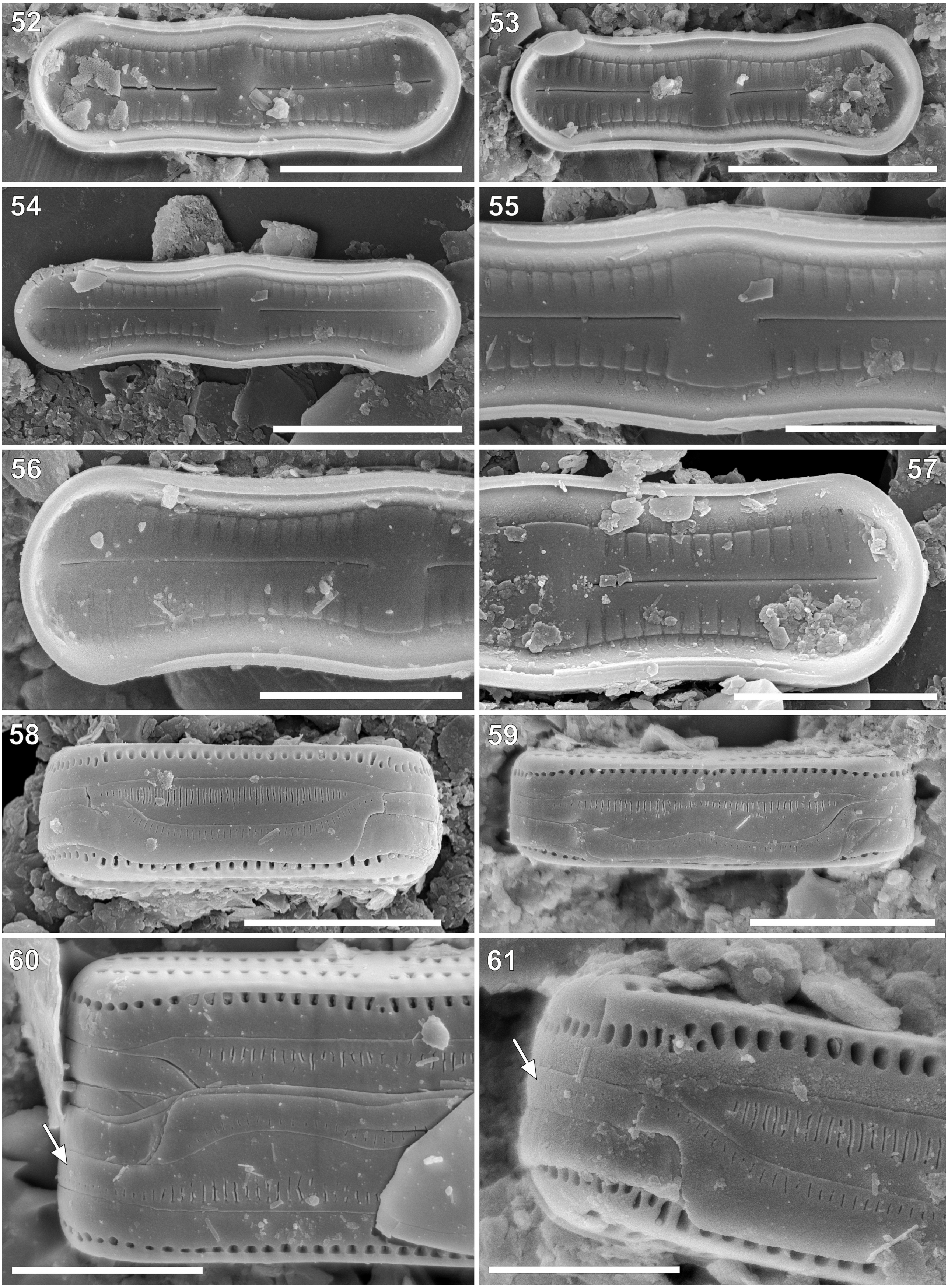
The species was observed in the sample with acidic pH (6.4) and very low conductivity (60 µS/cm). The most common co-occurred taxa included: *Angusticopula* cf. *dickei* (Thwaites) Houk, Klee & H.Tanaka (2017: 25)*, Chamaepinnularia abdita* Metzeltin & Lange-Bertalot (2007: 62), *Cosmioneis pusilla* (W.Smith) D.G.Mann & A.J.Stickle in Round *et al.* (1990: 526)*,* three unidentified *Eunotia* species*, Ferocia houkiana* Goeyers & Van de Vijver (2020: 9)*, Humidophila arcuatoides* (Lange-Bertalot) Lowe & *et al.* (2014: 357), *H. contenta* (Grunow) Lowe & al. (2014: 357), *Luticola muticoides* (Hustedt) D.G.Mann in Round *et al.* (1990: 671), *L. tomesii* Moser, Lange-Bertalot & Metzeltin (1998: 198), *Melosira* cf. *astridae* Metzeltin & Lange-Bertalot (2007: 159).

Discussion

In the current diatom taxonomy, the morphological analysis includes not only basic morphological structures, but also various fine features that can be observed using SEM, including differences in the structure of pore occlusions and other structures that seem to be constant for species (Round *et al.* 1990).



FIGURES 44–51. SEM microphotographs of *Humidophila caribaea sp. nov.* morphological detail in external view. Scale bar = 4 µm (Fig. 46) 3 µm (Figs 44, 45, 47) 2 µm (Figs 48, 49, 51), 1 µm (Fig. 50)



FIGURES 52–61. SEM microphotographs of *Humidophila caribaea sp. nov.* in internal view (Figs 52–57) and external views (Figs 58–61). Scale bar = 5 µm (Figs 52–54, 59), 4 µm (Fig. 58), 3 µm (Figs 56, 57, 60), 2 µm (Figs 55, 61), arrows indicates reduced pores on girdle bands.

The newly described species show some morphological similarity to several other *Humidophila* taxa (Table 1). However, the most important features separating *H. caribaea sp. nov.* from other species is the presence of irregular silica warts in all areolae on the valve face and a break in the striae in the middle part of the valve. These featuresare not present in any other recently described *Humidophila* taxa. The unique set of *H. caribaea* features can be easily observed using SEM, which emphasizes the importance of using SEM technique, especially for small-sized taxa.

TABLE 1. Comparison of valve dimensions between *Humidophila caribaea sp. nov.* and similar taxa.

Taxa	**length [µm]**	**width [µm]**	**striae [in 10 µm]**	**Valve outline**	**source**
H. caribaea sp. nov.	9.0–19.0	2.6–3.4	34–36	linear, slightly gibbous in the valve middle, apices broadly rounded, slightly broader than middle part of valve	this study
H. arcuata	16.0–23.0	4.0–5.5	29–31	linear, clearly gibbous in the valve middle, apices broadly rounded, slightly broader than the rest of the valve	Moser *et al.* 1998
	13.0–25.0	4.0–5.5	29–34		Zidarova *et al.* 2016
H. arcuatoides	16.0–26.0	5.0–6.0	31–33	linear with a distinct inflation in the middle, apices broadly rounded	Werum & Lange-Bertalot 2004
H. contenta	10.0–16.0	3.0	35–40	linear with distinctly inflated central part, apices weakly inflated, broadly rounded	Van de Vijver *et al.* 2022
H. costei	12.0–15.0	4.0–5.0	34–40	linear, in the valve middle slightly tumid, apices broadly rounded subcapitate	Le Cohu & Van de Vijver 2002
	19.0–23.5	3.5–4.5	34–36		Zidarova *et al.* 2016
H. eldfjallii	12.2–14.9	3.0–3.6	33.0–35.4	valves strongly triundulate	Furey *et al.* 2020
H. ingeae	8.0–18.0	2.0–4.0	31–35	linear with undulating margins and broadly rounded subcapitateapices	Van de Vijver *et al.* 2002
H. undulocontenta	7.5–10.5	2.5–3.5	40–42	triundulate	Lowe *et al.* 2017

Recent analysis of the type material of *H. contenta* (Grunow) Lowe *et al.* (2014: 357) has revealed that the general approach to this taxon should be quite different than that presented by most of the studies to date (Van de Vijver *et al.* 2022). The "true" *H. contenta*, has a triundulate valve, which makes this species similar to the *H. caribaea sp. nov.* However, *H. contenta* can be easily distinguished under LM based on the lack of a central area (Van de Vijver *et al.* 2022, figs 9–26). An additional set of morphological features visible under SEM confirms the distinctiveness of both species. Firstly, *Humidophila caribaea sp. nov.* possesses silica warts in the areolae lumen, which resemble those present in annulae in the genus *Geissleria* Lange-Bertalot & Metzeltin. The areolae of *H. contenta* are devoid of silica warts or any other silica projections in the areolae lumen (Van de Vijver *et al.* 2022, figs 27, 29, 30). Moreover, both species can be separated by the shape of areolae. *H. caribaea sp. nov.* has uniform areolae along their entire length, while in *H. contenta* areolae become wider towards the valve margins, with the shape resembling stretched teardrops (Van de Vijver *et al.*2022, figs 27, 30). The other feature separating both species is a striation arrangement in the valve center. In *H. contenta,* striation along the valve face is not interrupted (Van de Vijver *et al.* 2022 figs 27–30), whereas specimens in the new species (except for the smallest ones) have a clear break in striation in the central area. (Figs 1–33). In the smallest specimens, this break is reduced, and small areolae, often reduced to form of ghost areolae (Figs 37–42, 49, 51), can be observed in the central area. Finally, differences between the two species are also visible in the morphology of the girdle bands. *Humidophila caribaea sp. nov.* has elongated pores on all girdle bands (along margins strongly elongated with thickened margins, at the apices reduced, smaller and rounded) (Figs 60, 61), whereas *H. contenta* shows a lack of pores at the apical part of its girdle bands (Van de Vijver *et al.* 2022, figs 28–30).

Apart from *Humidophila contenta* the new species resembles other *Humidophila* species, including *H. eldfjallii, H. arcuata, H. arcuatoides, H. ingeae* and *H. undulocontenta*.

Humidophila eldfjallii Furey, Manoylov & Lowe (2020: 179) and *H. caribaea* sp. nov. overlap valve dimensions and have a similar raphe morphology (straight raphe endings with elongated depressions) (Furey *et al*., 2020: figs 8C, D). However, *H. eldfjallii* has a more gibbous valve outline (Furey *et al*., 2020: figs 8 E–H). Moreover, both taxa can be separated based on their distinct mantle areolae pattern. At the apices *Humidophila eldfjallii* has a group of areolae positioned in shallow depression (Furey *et al*., 2020: figs 8 A and C).

Humidophila arcuata (Lange-Bertalot in Moser *et al.* 1998) Lowe *et al.* (2014: 357) can be separated from *H.*

caribaea sp. nov. based on the wider valves (4.5–5.5 vs. 2.6–3.4 µm in *H. caribaea sp. nov.*) and the lower striae density (29–34 in 10 µm vs. 34–36 in 10 µm in *H. caribaea sp. nov.*) (Moser *et al.* 1998, Zidarova *et al.* 2016). Both taxa show also different morphology of raphe endings. In *H. arcuata* both the proximal and distal raphe endings are teardrop-shaped and a small silica ridge borders the raphe slit (Moser *et al.* 1998, Zidarova *et al.* 2016) while *H. caribaea sp. nov.* has simple raphe slits with straight endings, positioned in small elongated depressions (Figs 44–45).

Another species similar to *Humidophila caribaea sp. nov.* regarding its valve shape is *H. arcuatoides* (Lange-Bertalot in Werum & Lange-Bertalot, 2004) Lowe *et al.* (2014) described from Costa Rica. However, despite this similarity, *H. arcuatoides* has wider valves (5.0–6.0 *vs*. 2.6–3.4 µm) and Y-shaped distal raphe endings (Werum & Lange-Bertalot 2004: 308, fig. 7). Distal raphe endings in *H. caribaea* sp. nov are always straight.

The newly described species can be separated from *Humidophila costei* (Le Cohu & Van de Vijver, 2002) Lowe *et al.* (2014), based on slightly wider valves (3.5–5.0 *vs*. 2.6–3.4 µm) (Le Cohu & Van de Vijver, 2002). Similarly to the previous species, *H. costei* also has a different raphe morphology than *H. caribaea sp. nov.*, where both raphe endings are teardrop-shaped and do not possess any depressions (Le Cohu & Van de Vijver, 2002: figs 31, 32).

Another species with overlapping valve dimensions with *H. caribaea sp. nov.* is *H. ingeae* (Van de Vijver *et al.*, 2002) Lowe *et al.* (2014: 358). However, both taxa can be separated by the presence (in *H. caribaea sp. nov.*) or lack (in *H. ingeae*) of a striation break in the central area. Other features distinguishing both species are visible in SEM. *Humidophila ingeae* shows externally distinctly extended into teardrop-shaped proximal raphe endings (not straight with small depressions like in *H. caribaea sp. nov.*) and mantle areolae shifted onto the valve face, which gives an impression of the presence of two rows of areolae (Van de Vijver *et al.* 2002: figs 47–49).

Humidophila undulocontenta Lowe, Kociolek & Q.You (2017: 275) also resembles the new species. However it can be distinguished from *H. caribaea sp. nov.* by its smaller cell size and denser striation (see Table 1). Additionally, both species differ in the structure of their valves. *H. undulocontenta* areolae are positioned in shallow depressions (Lowe *et al.* 2017, figs 56–59). In the case of *H. caribaea sp. nov.*, the valve surface is flat (figs 34–41). Additionally, depressions at the raphe endings (if present) in *H. caribaea sp. nov.* are small and limited to the raphe endings (figs 34–41, 44–47), when in *H. undulocontenta* they are distinct and connected with depressions containing areoles (Lowe *et al.* 2017, figs 56–58).

During the studies, *Humidophila caribaea sp. nov.* was observed in only a single sample collected from Morne Cadet in the Monts Caraïbes, a mountain range in the southern end of the island of Basse-Terre, Guadeloupe, French Antilles. However, a morphologically corresponding species, named as *Diadesmis* sp. 6 (DI06), was mentioned as a rare species in a methodological guide for the implementation of the Antillean Diatom Index, but without specifying the exact locality and habitat (Eulin *et al.* 2014: planche 40). This observation may suggest that the new species may be more widely distributed throughout the Lesser Antilles, but its small size and occurrence in terrestrial environments might have been overlooked so far. Most of the taxa that co-occurred with the *Humidophila caribaea sp. nov.* are considered as typical species inhabiting terrestrial environments, often associated with bryophytes (Levkov *et al.* 2013, Lowe *et al.* 2014; Zidarova *et al.* 2016, Houk *et al.* 2017). Based on the ecological preferences of the associated diatom species, we suggest that the newly described species prefers temporarily desiccated, slightly acidic, to acidic environments with low trophic status and electrolytic conductivity. However, further investigations on the diatom diversity of the Caribbean, especially from terrestrial and semi-terrestrial habitats, are needed to fill the knowledge gap, and will most likely reveal greater diversity and uniqueness of this region.

Acknowledgements

Support for the collection expedition was granted to JB by DEAL Gaudeloupe.

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