

Taxonomy and valve morphology of *Humidophila* species (Bacillariophyceae) from aerophilous habitats in northeastern Argentina, with the description of four new species

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Abstract: During a survey of the diatoms present in aerophilic microhabitats associated with waterfalls in Misiones Province (Argentina), mainly within Iguazú National Park (N.P.), seventeen taxa belonging to the genus *Humidophila* have been recorded. Previously, only six species of the genus have been reported for all of Argentina. Of the seventeen taxa considered here, four exhibit a unique combination of features and are proposed as new species. These are *H. iguazuensis* sp. nov., *H. lagartiensis* sp. nov., *H. misionera* sp. nov. and *H. sebastianii* sp. nov. An additional six previously-described species (*H. arcuatooides*, *H. contenta*, *H. nienta*, *H. parallela*, *H. platensis* and *H. subtropica*) are reported. Of these previously-described taxa, only *H. contenta* has been reported previously from Argentina, so the occurrences of the others in the region expand their known geographic distributions. One taxon has been tentatively identified (as *Humidophila* aff. *biscutella*) and the remaining six taxa observed are presumed to be new but remain unidentified at the species level because they occurred in small numbers and could not be sufficiently documented for formal description. This is currently the largest concentration of *Humidophila* taxa reported in a relatively small geographic region anywhere in the world. Morphological features among the species of the genus are discussed, and we describe the structure of the features associated with longitudinal tubes in the genus. We also present and describe the ecological and biogeographic distributions of *Humidophila* species.

Key words: diatoms, *Humidophila iguazuensis*, *Humidophila lagartiensis*, *Humidophila misionera*, *Humidophila sebastianii*, Iguazú National Park, new species, sub-aerial habitats, taxonomy, valve morphology

INTRODUCTION

The genus *Humidophila* Lowe, Kociolek, Johansen, Van de Vijver, Lange-Bertalot et Kopalová (LOWE et al. 2014, p. 352), includes small, biraphid diatoms, with linear to elliptical valves, characterized by having striae formed by a single areola that is usually transapically elongated, and internally occluded by hymenes; aligned with the striae is a row of areolae on the mantle. Most of the species were formerly included in the genus *Diademesmis* Kützing (KÜTZING 1844, p. 109) (ROUND et al. 1990; LANGE-BERTALOT & WERUM 2001; WERUM & LANGE-BERTALOT 2004), but later recognized as distinct

from the generitype of *Diademesmis* and segregated into a separate subgenus (*Paradiademesmis* Lange-Bertalot et Le Cohu in RUMRICH et al. 2000, p. 108). Members of this subgenus and others were then transferred to the newly-created genus *Humidophila* (LOWE et al. 2014). Currently ca. 64 species have been assigned to the genus, many of which were described in the last two decades (KOCIOLEK et al. 2020); ANDREEVA et al. (2016) have shown with molecular data that *Diademesmis* and *Humidophila* are phylogenetically not closely related to one another.

Members of *Humidophila* tend to be more frequent in sub-aerial environments (humid soils, on moss or humid rocks), sometimes forming filamentous chains. The genus broadly speaking is widely distributed, being found in

North America, Europe, and Asia (LANGE–BERTALOT & WERUM 2001; GRUNOW in VAN HEURCK 1885; FUREY et al. 2020; LOWE et al. 2017). Most species are from Hawaii (LOWE et al. 2014) and the southern Hemisphere, with numerous species having been recorded from Central and South America (RUMRICH et al. 2000; WERUM & LANGE–BERTALOT 2004; METZELTIN et al. 2005), as well as the Antarctic and sub–Antarctic regions (e.g. KOPALOVÁ et al. 2015; CHATTOVÁ et al. 2018). Many of these species have been reported to be endemics. *Humidophila contenta* (Grunow ex Van Heurck) Lowe et al. (LOWE et al. 2014, p. 357), *H. gallica* (W. Smith) Lowe, Kociolek, Q.You, Q.Wang et Stepanek (LOWE et al. 2017, p. 281) and *H. paracontenta* (Lange–Bertalot et Werum) Lowe et al. (LOWE et al. 2014, p. 358) are considered cosmopolitan species (LOWE et al. 2014).

According to the Ministerio de Medio Ambiente de la Nación, Argentina is one of most biogeographic diverse countries in the world comprising 18 ecoregions (5 of them exclusive or semi–exclusive) (<https://www.argentina.gob.ar/parquesnacionales/educacionambiental/ecorregiones>). Despite this high environmental diversity, only six species of *Humidophila* have been recognized in Argentina so far. These have included two species with cosmopolitan distributions, such as *H. contenta* and *H. gallica*. They have been reported from High Andes and Puna, Patagonian steppe and Subantarctic Islands (VOUILLOUD 2003; FLOWER 2005; MAIDANA & SEELIGMANN 2006; GARCÍA & MAIDANA 2015, among others). There has been no previous treatment of *Humidophila* taxa from NE Argentina, especially from Iguazú National Park (N.P.) in Misiones Province.

The geography of Misiones is characterized by a landscape mainly composed of plateaus and mountain ranges. The abundant rainfall of the area (up to 2,000 annual mm) generates numerous and relatively short fluvial courses which, in their descent to the large rivers that delimit the province, overcome the altitude differences by means of rapids and waterfalls (CRANWELL 1974). The largest of them are Iguazú Falls, located within the Iguazú N.P. on the geographic border with Brazil. The area is covered by a tropical forest known as Paranaense rain forest, a major subdivision of the Atlantic Rain Forest ecoregion of South America (DI BITETTI et al. 2003). This biome is one of the most important biodiversity hotspots in the world, hosting a high number of endemic plants and animals (AVIGLIANO et al. 2019). The falls are developed in basaltic steps across the Iguazú River, a tributary of the Upper Paraná River, and consist of 160–200 individual falls, depending on available discharge (STEVEAUX & LATRUBESSE 2010). Even though there are previous studies devoted to the diatom flora of Misiones (MAIDANA 1981, 1983, 1985), and particularly for the area of Iguazú (FRENGUELLI 1953; BARTOZEK et al. 2013; NARDELLI et al. 2016), the numerous and diverse sub–aerial microhabitats associated with the waterfalls are still rather unexplored in terms of their diatom composition.

The purpose of the present report is to consider the taxonomy and valve ultrastructure of *Humidophila* species from aerophilous habitats from northeastern Argentina, including Iguazú N.P.

MATERIALS AND METHODS

Samples examined for this study were collected at aerophilous microhabitats mainly associated with waterfalls during two expeditions carried out to Misiones Province, one in December 2017 and the other in May 2019. The samples were mostly taken from mosses and rock scrapings in sites affected by the waterfalls' spray. Sampling sites were georeferenced with a Garmin eTrex 20× GPS. Physicochemical parameters of the water (temperature, pH, conductivity, and total dissolved solids (TDS)) were measured with a Hanna HI98130 multiparameter probe.

Unpreserved samples were kept refrigerated until laboratory analyses. An aliquot of each sample was treated to eliminate organic matter following the methods described in VAN DER WERFF (1953), PRYGIEL & COSTE (2000) and the protocol outlined in www.queensu.ca/pearl/methods/diatoms.php, each for different subsets of samples. For light microscopy (LM) observations, materials were mounted in permanent slides with Naphrax®, examined with a Leica DM2500 microscope equipped with DIC optics and photographed with a Leica DFC425 digital camera (División Ficología, Museo de La Plata, Argentina). The position on the slides of the specimens designated as holotypes was recorded with a S7 England Finder slide (Graticules Pyser–SGI Ltd.). For scanning electron microscopy (SEM) observations, aliquots of the cleaned material were air–dried onto glass coverslips, attached to bronze stubs and sputter–coated with ca. 1.5 nm gold–palladium using a Jeol Fine Coat ion–sputter JFC–1100. Observations were made using a Jeol JSM–6360 LV SEM (Servicio de Microscopía Electrónica, Museo de La Plata, Argentina) and a Carl Zeiss NTS SUPRA 40 SEM (Centro de Microscopías Avanzadas, Universidad de Buenos Aires, Argentina).

Raw samples, treated subsamples and permanent slides are deposited at the Herbarium of the División Ficología “Dr. Sebastián A. Guarrera” (LPC), Museo de La Plata, Argentina. Samples studied, their geographic coordinates and main environmental features are listed in Table 1.

Terminology of frustular features follows that in LOWE et al. (2014).

RESULTS

A total of 17 *Humidophila* taxa were observed. Six of them could be assigned to previously described species and, with the exception of *H. contenta*, all species are cited for the first time for Argentina (Table S1). Four taxa could not be identified after searching the available literature and are described as new species. One taxon has been tentatively identified whereas the other six morphologies after an exhaustive analysis of the literature do not correspond to any already known taxon but since they were poorly represented in the studied samples, require further study for their description as new species.

The detailed analyses of the fine valve morphology revealed a unique structure of the valves. We propose the term cubculus to describe the stria morphology.

Table 1. Sampling sites (geographic coordinates and main environmental features) and samples collected, (nd) no data.

LPC	Site	Date	Latitude	Longitude	Altitude (m a.s.l.)	pH	Temperature (°C)	Conductivity (mS.cm ⁻¹)	TDS (g.l ⁻¹)	Type of sample
15436	Núñez waterfall	09–12–2017	–25.6838	–54.4426	135	nd	nd	nd	nd	Composite aerophil
15442	Dos Hermanas waterfall	10–12–2017	–25.68385	–54.44569	137	7.6	24.7	0.05	0.03	Composite aerophil (cave)
15444	Dos Hermanas waterfall	10–12–2017	–25.68385	–54.44569	137	7.6	24.7	0.05	0.03	Mosses and rock scrape
15446	Dos Hermanas waterfall	10–12–2017	–25.68385	–54.44569	137	7.6	24.7	0.05	0.03	Leaves of higher plants
15447	Dos Hermanas waterfall	10–12–2017	–25.68385	–54.44569	137	7.6	24.7	0.05	0.03	Algae on railing
15660	Dos Hermanas waterfall	22–05–2019	–25.68385	–54.44569	137	7.55	22.2	0.06	0.03	Mosses
15661	Dos Hermanas waterfall	22–05–2019	–25.68385	–54.44569	137	7.55	22.2	0.06	0.03	Mosses
15664	Dos Hermanas waterfall	22–05–2019	–25.68385	–54.44569	137	7.55	22.2	0.06	0.03	Mosses (cave)
15449	Chico waterfall	10–12–2017	–25.68486	–54.44563	163	7.62	24.5	0.06	0.03	Mosses and rock scrape
15459	Small stream flowing into Iguazú River	10–12–2017	–25.68829	–54.45111	158	nd	nd	nd	nd	Composite aerophil
15472	Arrechea waterfall	11–12–2017	–25.65513	–54.45715	153	7.56	20.7	0.03	0.02	Mosses and rock scrape
15473	Arrechea waterfall	11–12–2017	–25.65513	–54.45715	153	7.56	20.7	0.03	0.02	Rock scrape
15636	Arrechea waterfall	21–05–2019	–25.65513	–54.45715	153	7.42	19.4	0.04	0.02	Wood scrape
15639	Arrechea waterfall	21–05–2019	–25.65513	–54.45715	153	7.42	19.4	0.04	0.02	Dry mosses
15605	Chávez waterfall	19–05–2019	–27.27186	–54.92281	295	6.7	19.5	0.04	0.02	Mosses on dry rocks and tree
15610	El Lagarto waterfall	20–05–2019	–27.07633	–54.86871	348	6.7	20.4	0.06	0.03	Rock scrape

The cubculus is an elongated chamber that is internally covered by a plate of fine pores (hymen), and externally opens by one large, usually elongated foramen on the valve surface and another one on the valve mantle. Each cubculus is connected with a longitudinal tube that runs on the valve margin (Figs 1–2).

We also introduce the term vallum to designate the longitudinal sunken line or discontinuity that occurs internally and extends nearly the length of the valve near the margins on either side of the raphe. These lines are unilaterally flanked (towards the axial area) by silica protuberances of the virgae (Fig. 1, arrowhead).

Additionally, we use the term ‘troughs’ to describe the small indentations in the valve associated with the external central and / or terminal raphe endings present in some species.

***Humidophila arcuatooides* (Lange–Bertalot) Lowe, Kocielek, Johansen, Van de Vijver, Lange–Bertalot et Kopalová (Figs 3–13)**

Basionym: *Diadesmis arcuatooides* Lange–Bertalot in WERUM & LANGE–BERTALOT 2004, *Iconographia Diatomologica* 13, p. 134, figs 61: 1–7.

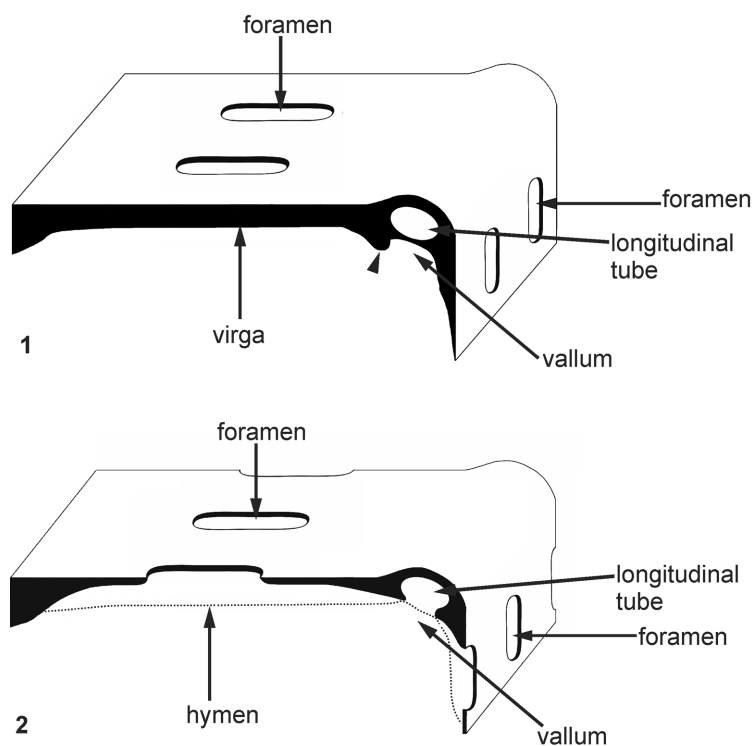
Type Locality: Bosque Nuboso, Monteverde, Puntarenas, Costa Rica. Valves are linear, with broadly rounded to subcapitate apices and strongly inflated in the central portion. Axial area is narrow, slightly widened towards the apices and expanded at mid–valve to form a circular central area. Raphe is filiform, externally with straight external central endings and external terminal endings with bifurcated troughs, not extending to the end of the valve; internally, central raphe endings are slightly laterally expanded, terminating on a small, round central nodule and terminal

raphe endings terminate in scarcely developed helictoglossae. Cubculus–type striae are discernible in LM, forming a line parallel to the valve margin, radiate about the center of the valve, becoming parallel towards the ends, composed of transapically elongated foramina, slightly shorter around the central area and internally occluded by hymenes. There is a distinct vallum running longitudinally on either side of the axial area near the margin. Mantle has small, rounded foramina. Valve face striae are continuous with mantle striae except at the poles.

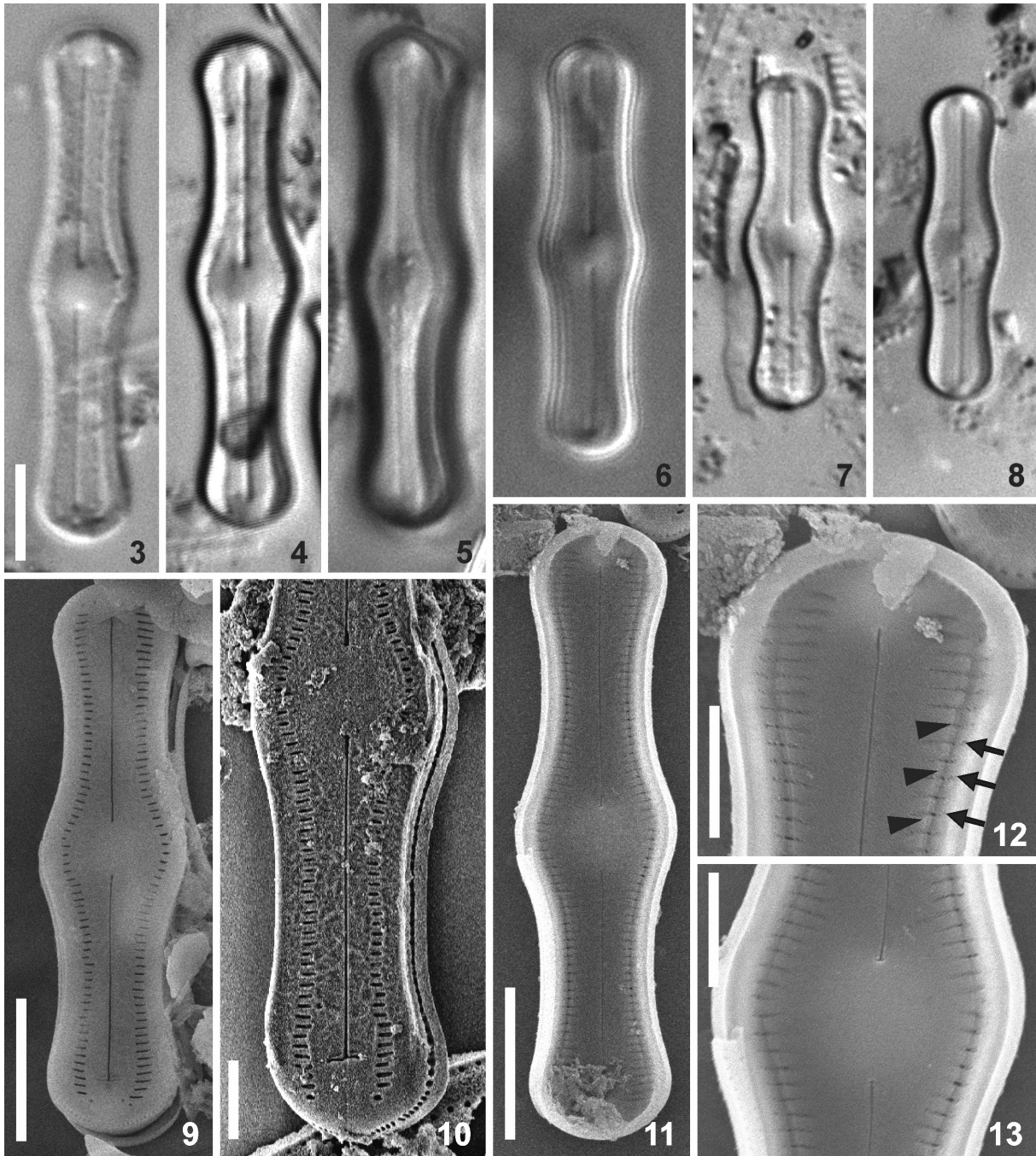
Morphometric data (n=18): length 16.0–27.0 μm , width 4.0–6.0 μm , 38–40 striae in 10 μm .

Distribution: In this study the species was found at Dos Hermanas waterfall. Previously this taxon was reported from North, Central and South America, including USA (VESELÁ 2014), Costa Rica, Ecuador and Guyana (RUMRICH et al. 2000; WERUM & LANGE–BERTALOT 2004) and Brazil (WETZEL 2011).

Comments: The identification of this species in Argentina is in agreement with the specimens reported from the type locality (WERUM & LANGE–BERTALOT 2004), except for the higher striae densities in the individuals reported herein. The specimens illustrated in RUMRICH et al. (2000, pl. 83, figs 1–3, 5–6), identified as *Diadesmis arcuata* Lange–Bertalot (MOSER et al. 1998, p. 136) may be more correctly interpreted as *H. arcuatooides*. Moreover, the SEM image in their fig. 6 shows the same individual depicted in the original publication by WERUM & LANGE–BERTALOT (2004, fig. 61: 7).



Figs 1–2. Schematic cross–sections of a *Humidophila* valve showing the main ultrastructural features: (1) cross–section at the virga level, the arrowhead indicates the silica protuberances; (2) cross–section at the cubculus–type stria level.



Figs 3–13. *Humidophila arcuatoides* (Lange–Bertalot) Lowe et al.: (3–8) LM valve views showing population variability; (9) SEM external valve view; (10) SEM external valve view detail showing the proximal and distal raphe ends and the transapically elongated foramina; (11) SEM internal valve view; (12) SEM internal valve view detail of valve apex showing the distal raphe end and helictoglossa, note the vallum (arrows) and the silica protuberances (arrowheads); (13) SEM internal valve view detail of valve center showing the central nodule and the proximal raphe ends. Scale bar 5 μm (3–9, 11), 2 μm (10, 12–13).

***Humidophila contenta* (Grunow) Lowe, Kociolek, Johansen, Van de Vijver, Lange–Bertalot et Kopalová (Figs 14–20)**

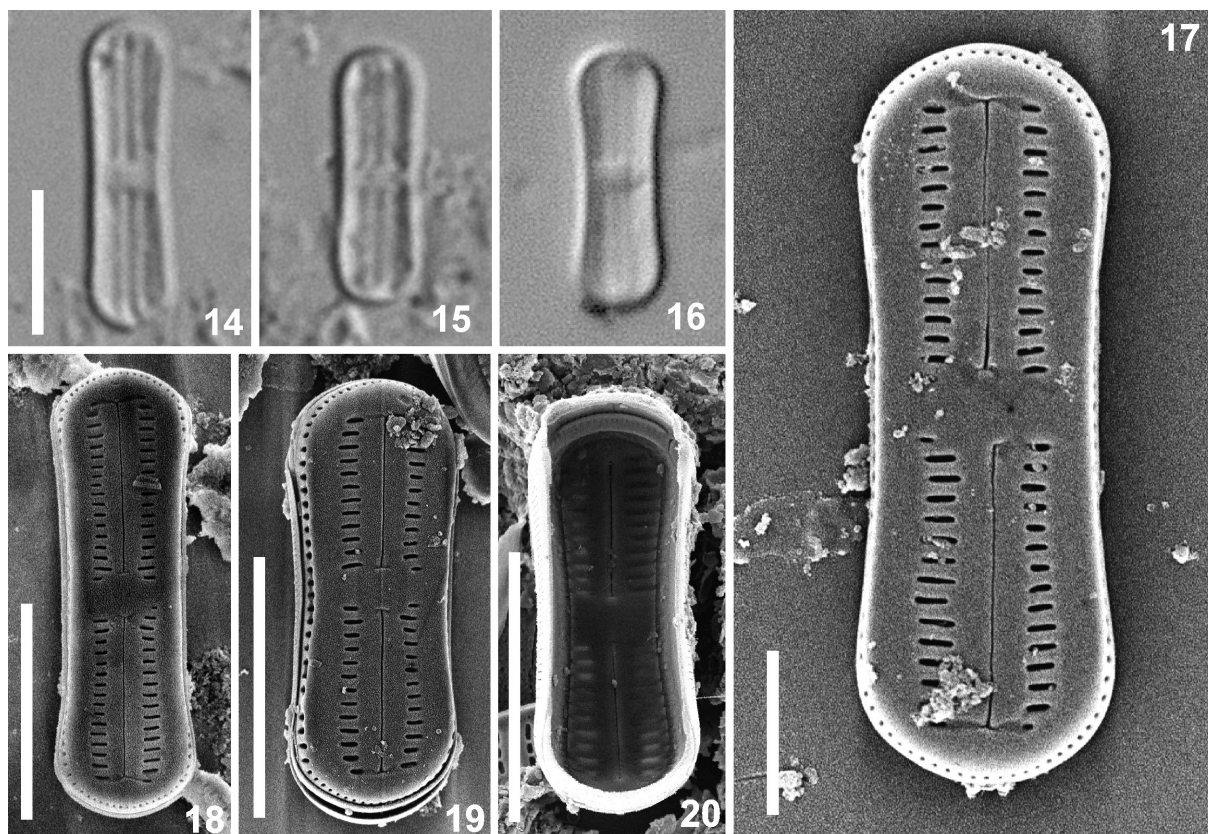
Basionym: *Navicula contenta* Grunow in VAN HEURCK 1885, Synopsis des Diatomées de Belgique, p. 109.

Synonym: *Diadsmis contenta* (Grunow) D.G. Mann

Type Locality: Rocheaut, Belgium

Valves are linear to linear–elliptical, with margins slightly constricted and broadly rounded apices. Axial area is narrow, expanded at mid–valve in a rectangular central

area. Raphe is straight, filiform, externally with bifurcated troughs at the central and terminal endings, generally intersecting the last striae; internally, there is only an indiscreet central nodule and terminal endings terminate in weakly developed helictoglossae. Cubiculus–type striae are not resolvable in LM, with parallel orientation. The vallum is distinct at the margin. Mantle has large, drop–like foramina at the lateral margins, somewhat smaller and without interruption at the apices.



Figs 14–20. *Humidophila contenta* (Grunow) Lowe et al.: (14–16) LM valve views showing population variability; (17–19) SEM external valve views showing the proximal and distal raphe ends flanked by troughs; (20) SEM internal valve view, note the vallum. Scale bar 5 μm (14–16, 18–20); 2 μm (17).

Morphometric data (n=20): length 6.5–13.0 μm , width 2.5–3.0 μm , 40–42 striae in 10 μm .

Distribution: Recorded in this study from the waterfalls Arrechea, Dos Hermanas, Chico, Chávez, Núñez and unnamed stream. Apparently cosmopolitan.

Comments: Many previous records of this species, including those for Argentina, should be viewed with caution since most of the identifications were based only on LM observations. *H. contenta* is a controversial, allegedly cosmopolitan taxon that must be critically revised to achieve a better circumscription of the species (CHATTOVÁ et al. 2018). The original description by Grunow in VAN HEURCK (1885) for a diatom from Belgium, indicated length: 7–10 μm ; width: 2.0–2.5 μm ; 36 striae in 10 μm , delicate and parallel. In the original drawing the specimen is slightly inflated and the apices are flared. Specimens from the USA are in agreement with the original description (see LOWE et al. 2014).

Specimens collected in Iguazú were identified as *H. contenta* based on the description and illustrations provided by LANGE-BERTALOT & WERUM (2001, figs 58–59), CHATTOVÁ et al. (2018, p. 31, figs 18–38), LOWE et al. 2017 (figs 1–14) and the website diatom.org (LOWE 2015). Striae densities in our specimens are somewhat higher than those mentioned in the original description (36 striae in 10 μm) although fall within the ranges given by CHATTOVÁ et al. (2018) for materials

collected on islands of the southern Indian Ocean (34–49 striae in 10 μm) and by VAN DE VIJVER et al. (2002a) for specimens from the subantarctic Île de la Possession (40–50 striae in 10 μm).

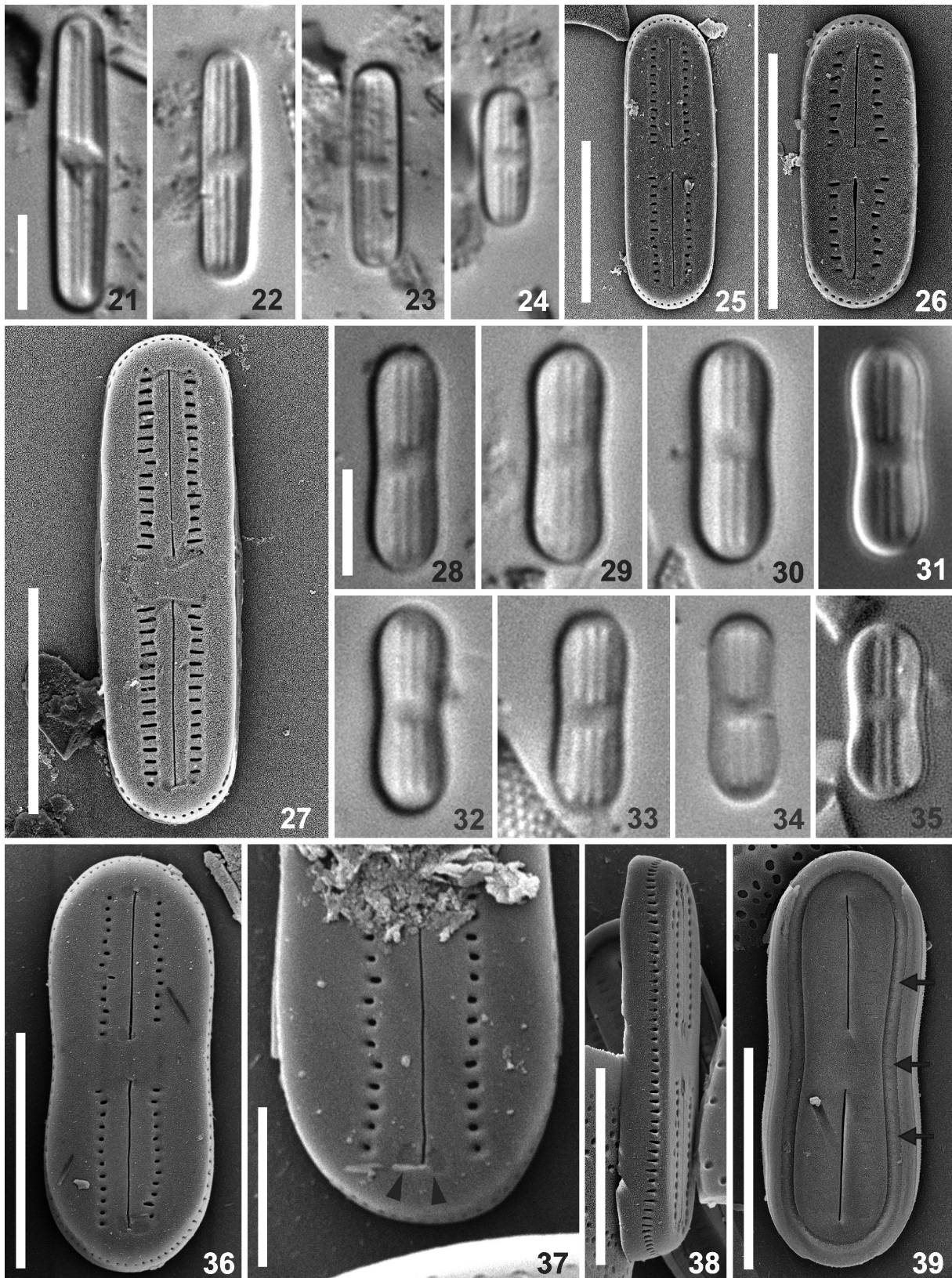
***Humidophila iguazuensis* Guerrero, Vouilloud et Sala sp. nov. (Figs 21–27)**

Description: Valves are linear with parallel sides and broadly rounded apices. The raphe is straight, filiform. Central and terminal raphe ends are simple pores, bordered by irregular troughs that expand laterally and intersect with the last striae. Axial area is moderately broad, straight; central area is orbicular or quadrangular, delimited by semicircular depressions in which variably elongated foramina are located. Striae are of cubculus-type, parallel and not resolvable in LM. Mantle with rounded foramina, continuous around the apices where they are visible in valve view.

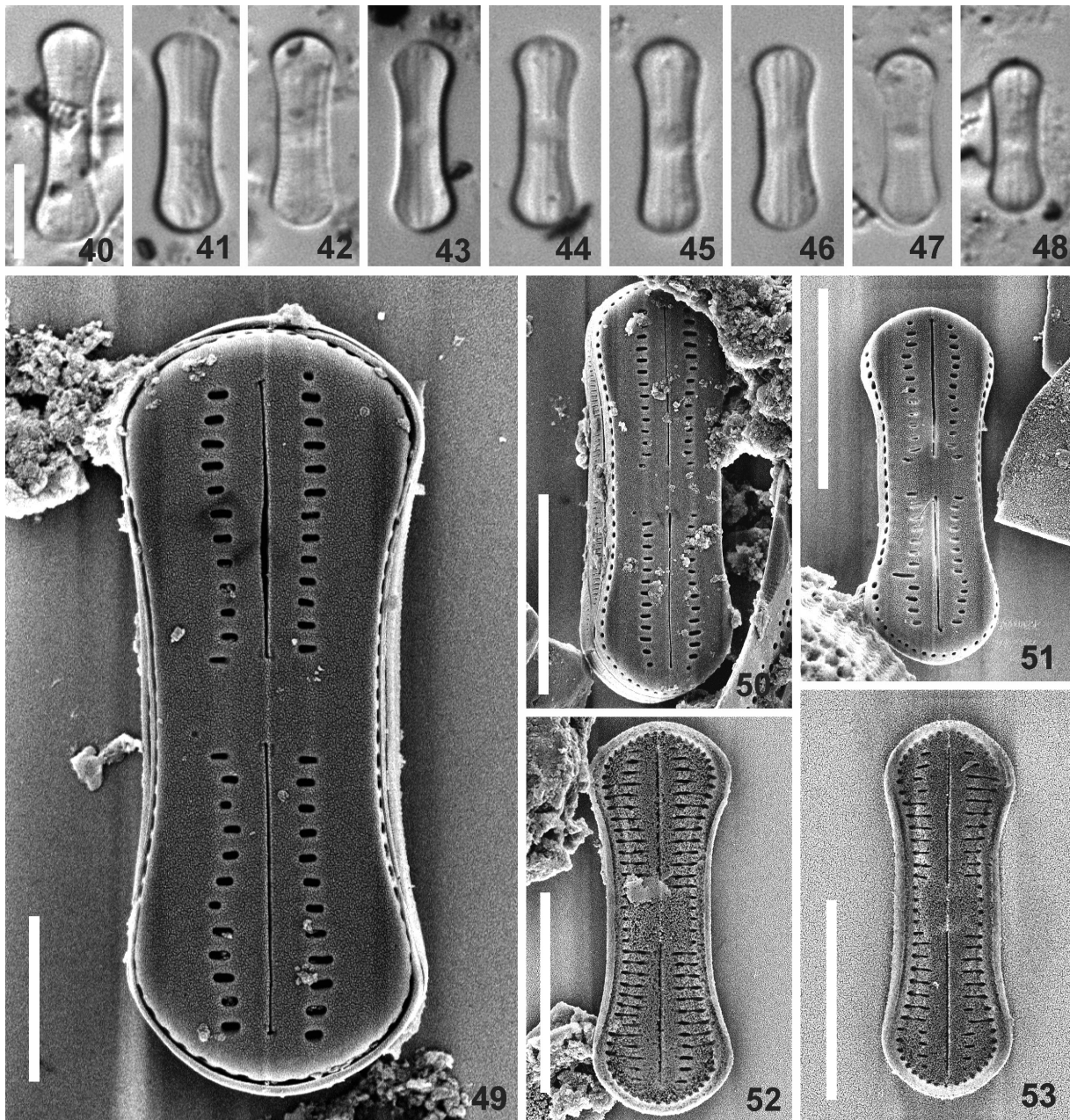
Morphometric data (n=27): length 5.5–16 μm , width 2.5–3.0 μm , 36–40 striae in 10 μm .

Type Locality: Argentina. Dos Hermanas waterfall, Misiones Province (25°41'01.9"S, 54°26'44.5"W, 137 m a.s.l.), leg. J. Simonato, May 2019.

Holotype: Slide LPC 15660(3)! (Museo de La Plata Herbarium, La Plata, Argentina, here depicted in Figs. 21–27). The holotype specimen is shown in Fig. 22 and



Figs 21–27. *Humidophila iguazuensis* Guerrero et al. sp. nov.; (21–24) LM valve views showing population variability (Fig. 22 represents the holotype); (25–27) SEM external valve views, note the striae foramina located in a longitudinal depression. Scale bar 5 μ m (14–27). Figs 28–39. *Humidophila lagartiensis* Vouilloud et al. sp. nov.; (28–35) LM valve views showing population variability (Fig. 33 represents the holotype); (36) SEM external valve view; (37) SEM external valve view detail showing distal raphe end flanked by troughs (arrowheads); (38) SEM valve in girdle view showing the row of mantle foramina; (39) SEM internal valve view, note the silica lamina covering the interior of valve and the marginal vallum (arrows). Scale bar 5 μ m (21–36, 38–39); 2 μ m (37).



Figs 40–53. *Humidophila misionera* Vouilloud et al. sp. nov.: (40–48) LM valve views showing population variability (Fig. 44 represents the holotype); (49–51) SEM external valve views, note the simple proximal ends without troughs and the irregular foramina; (52–53) SEM internal valve view, showing the lines of silica protuberances parallel to the margin and the longitudinal vallum near both margins. Scale bar 5 μm (40–48, 50–53); 2 μm (49).

is located at England Finder N36–4.

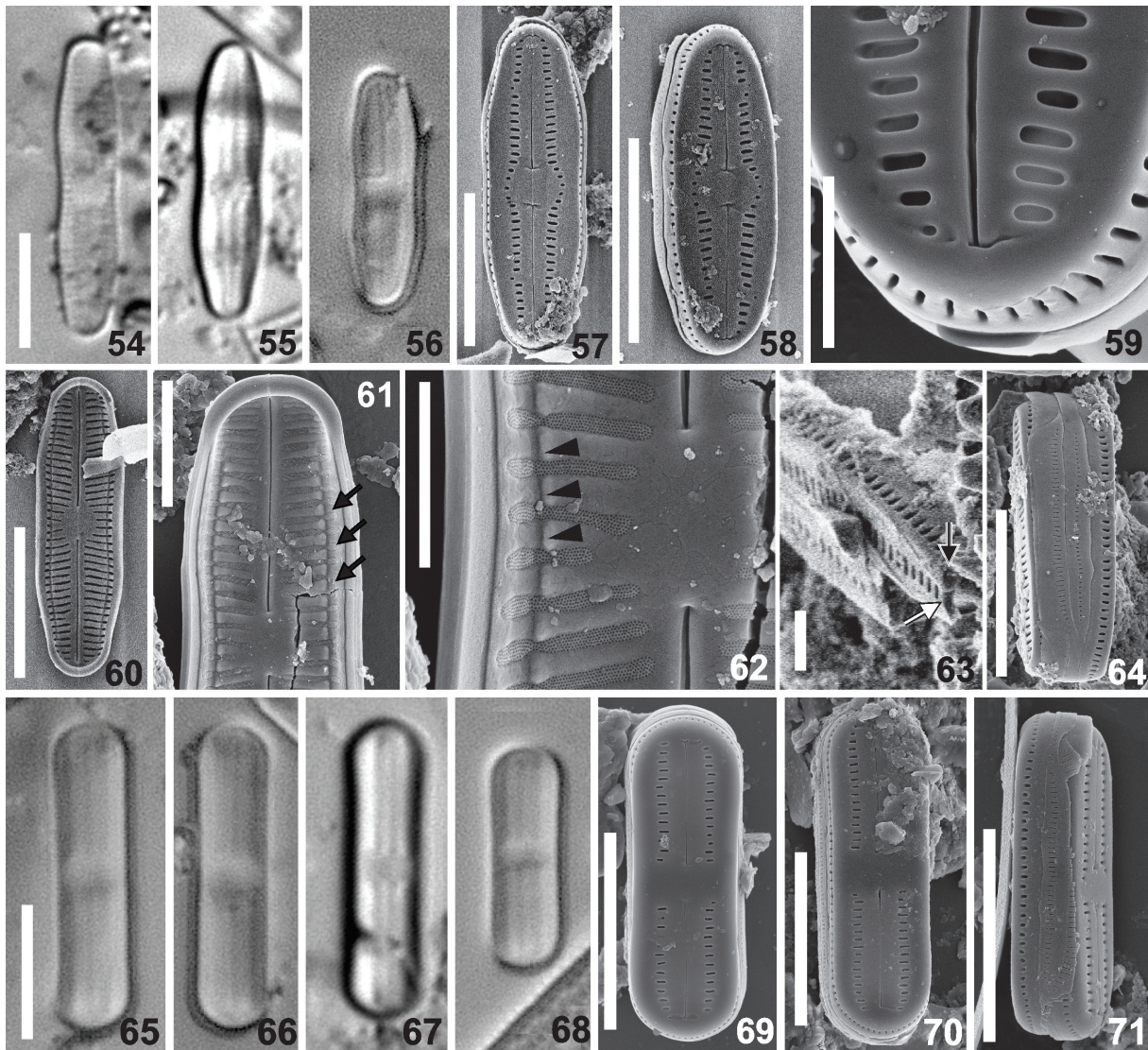
Isotype: Slide COLO 650060 (University of Colorado, Boulder, USA).

Etymology: The specific epithet refers to the name of the National Park Iguazú where the new species has been collected.

Distribution: The new species was found at the type locality and at Arrechea waterfall.

Comments: The occurrence of striae positioned in longitudinal depressions is a character shared with several other species within *Humidophila* (see Table S3). The taxon most similar to the specimens from Iguazú is

Humidophila lacunosa Moser, Lange–Bertalot et Metzeltin (LOWE et al. 2014, p. 358), originally described from New Caledonia (as a member of the genus *Diademsis*, MOSER et al. 1998); they are similar in dimensions and overall valve morphology, but the latter has cuneate rather than rounded apices, rounded central area, elongated mantle striae and proximal raphe endings are slightly deflected to the primary side. Specimens reported from Ecuador as *D. lacunosa* (RUMRICH et al. 2000) match the new species in valve outline, morphology and dimensions, and therefore they are most probably conspecific. Specimens described as *D. lacunosa* from Uruguay (METZELTIN et al.



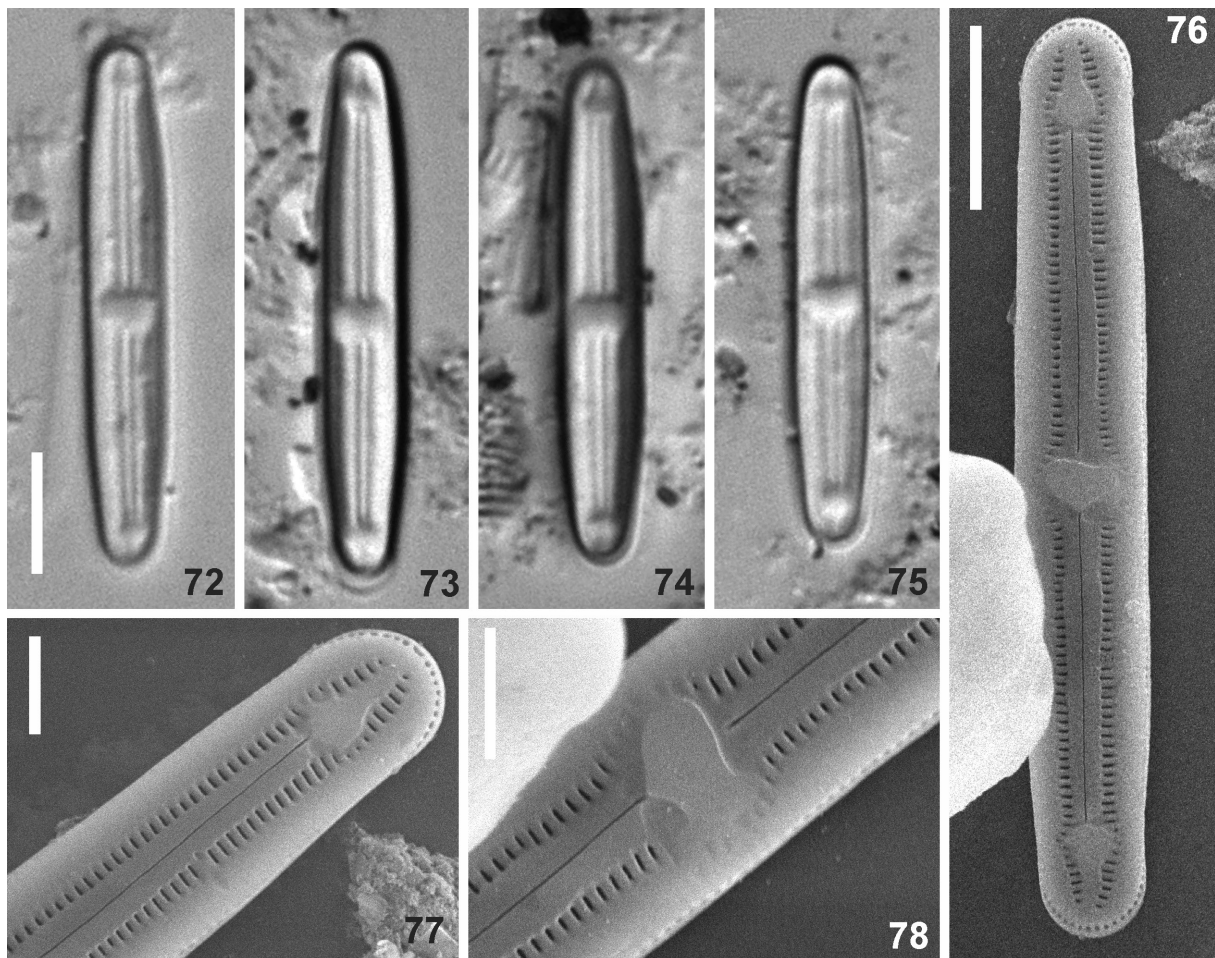
Figs 54–64. *Humidophila nienta* (Carter) Lowe et al.: (54–56) LM valve views, showing population variability; (57–58) SEM external valve view; (59) SEM external valve view detail of the valve apex, note T-shaped terminal raphe fissure; (60) SEM internal valve view; (61) SEM internal valve view detail showing the longitudinal vallum near both margins (arrows); (62) SEM internal valve view detail of the cubculus-type striae, note silica protuberances (arrowheads) and the porous hymenes continuous onto valve mantle; (63) SEM internal valve view of broken valve showing the longitudinal canal (black arrow) running beneath the vallum (white arrow); (64) SEM frustule in girdle view. Figs 65–71. *Humidophila parallella* (Petersen) Furey et al.: (65–68) LM Valve views, showing population variability; (69–70) SEM external valve views, showing the proximal and distal ends with troughs; (71) SEM tilted frustule showing the cingulum. Scale bar 5 μm (54–58, 60, 64–71); 2 μm (61); 1 μm (59, 62–63).

2005) are also very similar but they have small granules surrounding the areolae, which were not observed in our materials. *H. platensis* Metzeltin, Lange–Bertalot et García–Rodríguez (LOWE et al. 2014, p. 359) resembles the new species in its striae positioned in longitudinal depressions and a rather similar morphology of the central area but it can be clearly differentiated even under LM due to its larger, more elongated valves, and the very typical expansion of the axial area at the apices (see below). *H. keiliorum* Kopalová (KOPALOVÁ et al. 2015, p. 123; ZIDAROVÁ et al. 2016) is another species with conspicuously depressed striae and valve outline similar to *H. iguazuensis* but it differs in valve dimensions, stria density and morphological features such as

mantle areolae located in grooves and interrupted at the apices and morphology of the central area. Comparisons of the main morphometric features of the new species with those of the most similar taxa are shown in Table 2.

***Humidophila lagartiensis* Vouilloud, Guerrero et Kocielek sp. nov. (Figs 28–39)**

Description: Valves are elliptical, with a slight constriction at mid-valve and apices broadly rounded. Axial area is broad, expanded at mid-valve to form a laterally-expanded central area. Raphe is filiform and straight. Externally, central raphe endings are T-shaped and terminal raphe endings are straight. Troughs are present. Internally, the raphe is straight and terminates both



Figs 72–78. *Humidophila platensis* (Metzeltin et al.) Lowe et al.: (72–75) LM valve views showing population variability; (76) SEM external valve views; (77) SEM external valve views detail of the valve apex showing distal raphe end and ‘crayon-tip’ area; (78) SEM external valve views detail of the central area showing proximal raphe ends. Scale bar 5 μm (72–76); 2 μm (77–78).

proximally and distally in very indistinct raised areas. Raphe terminates distally away from the valve terminus. Striae are of the cubculus-type, parallel and visible in LM only near the axial area, with a single, ellipsoidal foramen, located closer to the raphe than to the margin. The entire interior is covered with a lamina, which is separated from the margin by the vallum. Central nodule is distinct, central raphe endings are simple and terminal endings terminate in weakly developed helictoglossae. Mantle is well-developed, with one row of drop-shaped foramina, shorter at mid-valve and continuous around valve apices.

Morphometric data (n= 28): length 8.0–11 μm , width 3.0–3.5 μm , 38–40 striae in 10 μm .

Type locality: Argentina. El Lagarto waterfall, Aristóbulo del Valle, Caingúas, Misiones Province (27°04'34.8"S, 54°52'07.4"W, 348 m a.s.l.), leg. J. Simonato, May 2019.

Holotype: Slide LPC 15610(6)! (Museo de La Plata Herbarium, La Plata, Argentina, here depicted in Figs 28–39). The holotype specimen is shown in Fig. 33 and is located at England Finder H47–2.

Isotype: Slide COLO 650048 (University of Colorado, Boulder, USA)

Etymology: The specific epithet refers to the name of the waterfall where the new species has been collected.

Distribution: the species was only found at the type locality.

Comments: As observed with LM the new species resembles *Humidophila tahitiensis* (Lange–Bertalot et Werum) Lowe et al., a species described from Polynesia (LOWE et al. 2014, p. 355), in valve outline, size and shape. However, the latter taxon differs in its higher stria density (45–47 in 10 μm) and in the foramina being more transapically elongated. Moreover, in *H. tahitiensis* both central and terminal raphe endings terminate in laterally expanded depressions that connect with one or two foramina. *H. lagartiensis* is also similar to *H. contenta* in valve outline and stria density but the latter can be distinguished by its typical T-shaped external central and terminal raphe endings and by the areolae, which are more transapically elongated. The species that more closely resembles *H. lagartiensis* is *H. parallela* (Petersen) Furey, Manoylov et Lowe as illustrated by FUREY et al. (2020, p. 190) from aerial diatom assemblages in Iceland, but the latter differs in the striae being less densely arranged (34.0–34.9 in 10 μm), composed

Table 2. Main morphometric features of *Humidophila iguazuensis* sp. nov. and most similar taxa.

Taxon	Length (µm)	Width (µm)	Striae density in 10 µm	Reference
<i>Humidophila iguazuensis</i>	5.5–16.0	2.5–3.0	36–40	This study
<i>Diadasmus lacunosa</i>	10.0–15.0	2.8–3.5	~ 36	MOSER et al. (1998)
	11.5–12.5*	2.5–3.0*	36–42*	RUMRICH et al. (2000)
	7.0–20.0	2.8–3.5	~ 36	METZELTIN et al. (2005)
<i>Humidophila platensis</i>	20.0–25.0	3.0–3.5	38–40	This study
<i>Humidophila keiliorum</i>	10.4–31.2	3.2–5.2	27–30	KOPALOVÁ et al. (2015)
	8.0–31.0	3.0–5.5	27–32	ZIDAROVA et al. (2016)

*Measured on figures in the text.

Table 3. Main morphometric features of *Humidophila lagartiensis* sp. nov. and most similar taxa.

Taxon	Length (µm)	Width (µm)	Striae density in 10 µm	Reference
<i>Humidophila lagartiensis</i>	8.2–10.8	2.9–3.5	38–40	This study
<i>Humidophila contenta</i>	6.0–12.1	2.4–2.6	36–38	LOWE et al. (2014)
<i>Humidophila parallela</i>	7.2–9.1	2.0–3.1	34–34.9	FUREY et al. (2020)
<i>Diadasmus tahitiensis</i>	11.2–14.0	2.9–3.8	37–42	LANGE–BERTALOT & WERUM (2001)

Table 4. Main morphometric features of *Humidophila misionera* spec. nov. and most similar taxa.

Taxon	Length (µm)	Width (µm)	Striae density in 10 µm	Reference
<i>Humidophila misionera</i>	8.8–11.7	2.3–3.0	34–36	This study
<i>Diadasmus paracontenta</i>	7–15	2.8–3.8	27–30	LANGE–BERTALOT & GENKAL (1999)
<i>Humidophila paracontenta</i> var. <i>magisconca</i>	7–13	2.0–3.3	28–30	LANGE–BERTALOT & WERUM (2001)
<i>Diadasmus discordabilis</i>	16–20	5.5–6.5	28–32	MOSER et al. (1998)

of transapically elongated foramina, and by the valve exhibiting crenulated lateral margins. Comparisons of the main morphometric features of the new species with those of the most similar taxa are shown in Table 3.

***Humidophila misionera* Vouilloud, Guerrero et Kociolek sp. nov. (Figs 40–53)**

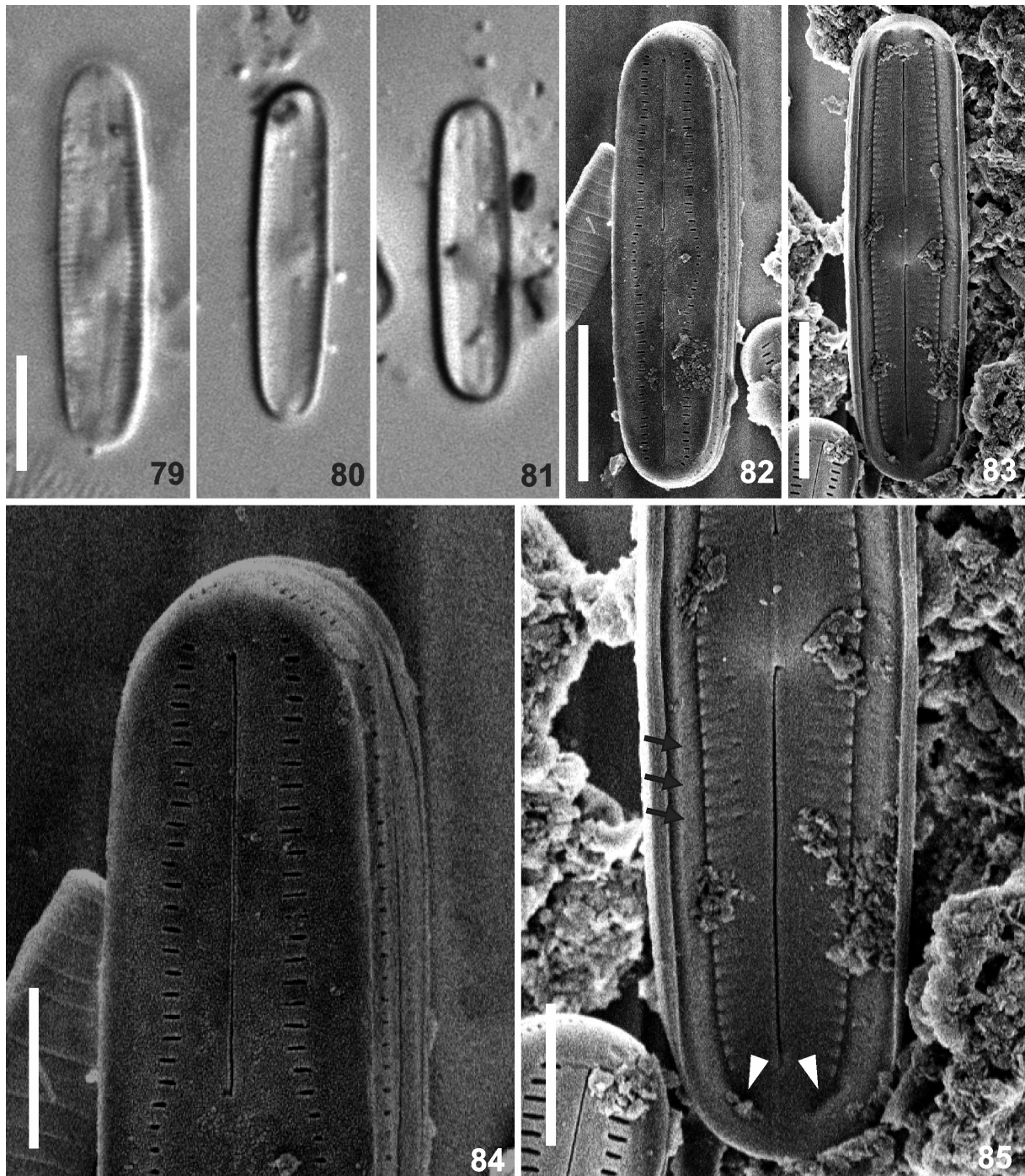
Description: Valves are linear, with inflated, broadly rounded apices, barbell-shaped. Axial area is narrow, wider towards the poles and at mid-valve expanded forming a very distinct fascia. Raphe is filiform, straight, externally central and terminal endings are simple and occasionally flanked by small, shallow depressions. Internally, central raphe endings are simple and terminal endings terminate in inconspicuous helictoglossae. Striae are of the cubculus-type, parallel and barely resolvable in LM; each is composed of a single foramen, ellipsoidal

in shape, sometimes of varying length, small, located closer to the axial area than to the margin. Internally, there is a vallum running longitudinally on either side of the axial area; the hymenes are larger than externally and reaching the valve/mantle junction, except those closer to the apices. Mantle well-developed, in right angle to the valve face, with a distinct row of foramina, continuous around valve apices.

Morphometric data (n=31): length 9.0–11.5 µm, width 2.5–3.0 µm (at mid-valve), 3.0–3.5 µm (at the apices), 34–36 striae in 10 µm.

Type locality: Argentina. Dos Hermanas waterfall, Iguazú N.P., Misiones Province (25°41'01.9"S, 54°26'44.5"W, 137 m a.s.l.), leg. J. Simonato, May 2019.

Holotype: Slide LPC 15660(1)! (Museo de La Plata Herbarium, La Plata, Argentina, here depicted in Figs



Figs 79–85. *Humidophila sebastianii* Guerrero et al. sp. nov.: (79–81) LM valve views showing population variability (Fig. 80 represents the holotype); (82) SEM external valve view, note the simple raphe ends and the small foramina; (83) SEM internal valve view showing the vallum and the silica protuberances; (84) SEM external valve view detail showing the proximal and distal raphe ends and the transapically elongated foramina; note the mantle foramina interrupted at the valve apex; (85). SEM internal valve view detail showing the longitudinal vallum near both margins (arrows), the prominent central nodule and the internal apical depressions (arrowheads). Scale bar 5 μm (79–83); 2 μm (84–85).

40–53). The holotype specimen is shown in Fig. 44 and is located at England Finder Q30–3/4.

Isotype: Slide COLO 650059 (University of Colorado, Boulder, USA).

Etymology: The specific epithet refers to the distribution of the new species in several waterfalls in the Argentinian province of Misiones.

Distribution: This species was encountered from the

following waterfalls in northeastern Argentina: Dos Hermanas, Núñez, Arrechea, Chávez and El Lagarto.

Comments: Due to its valve outline and overall appearance when observed with LM, *H. misionera* can be easily misidentified as other previously-described species. Although similarly sized, *H. paracontenta* Lange–Bertalot et Werum (Lowe et al. 2014, p. 358)

found in Siberia (LANGE–BERTALOT & GENKAL 1999) differs in valve outline, having less pronounced valve ends, and in its lower striae density (27–30 in 10 μm). The taxa that most closely resemble our new species are *H. paracontenta* var. *magisconcava* (Lange–Bertalot) Lowe et al. (LOWE et al. 2014, p. 358) described by LANGE–BERTALOT & WERUM (2001) from the United States, and *H. paracontenta* as described from specimens collected in Iceland by FUREY et al. (2020). These taxa only differ in their lower number of striae in 10 μm (28–30 in the former and 28.5–31.2 in the latter), in terms of having finer striae and the presence of small areolae bordering the central area. *H. misionera* differs from *H. discordabilis* (Moser, Lange–Bertalot et Metzeltin) Lowe et al. (LOWE et al. 2014, p. 357), described from New Caledonia (MOSER et al. 1998), in its greater valve size, shape of the central area and the raphe endings and in having finer striae. It is possible that *H. misionera* is the same as “*Diademsis* sp.” reported in RUMRICH et al. (2000, pl. 83, figs 13–14), which is larger, ranging in length from 17.7 to 19.3 μm , and is 2.5 μm in breadth, but only two specimens were represented. Comparison of *H. misionera* to most similar taxa is presented in Table 4.

***Humidophila nienta* (Carter) Lowe, Kocielek, Johansen, Van de Vijver, Lange–Bertalot et Kopalová (Figs 54–64)**

Basionym: *Navicula nienta* Carter (CARTER 1966, Nova Hedwigia 11, p. 464, pl. 3, fig. 17).

Synonyms: *Diademsis langebertalotii* Van de Vijver et Le Cohu in LE COHU & VAN DE VIJVER 2002; *Diademsis pseudolangebertalotii* Metzeltin, Lange–Bertalot et García–Rodríguez 2005

Type Locality: Gough Island, South Atlantic.

Valves are linear, with undulate margins and a central constriction; undulation is less evident in smaller valves which have almost parallel margins. Valve apices are slightly protracted, nearly rostrate. Axial area broadly expanded to form a circular central area. Raphe is straight and filiform. Externally, central and terminal raphe endings terminate in transversal depressions giving the appearance of T– or Y–shaped terminal fissures. Raphe endings, both central and terminal, have narrow troughs on both sides of the raphe opening. Internally, central raphe endings are simple pores and terminal endings terminate in barely developed helictoglossae. Cubiculus–type striae are fine, discernible in LM, parallel and at the center becoming radiate without an interruption to delimit a central area. Striae have one elongated

foramen, shortened at the central area. Hymenes are larger than foramina, reaching the valve the mantle. The vallum, running longitudinally on either side of the axial area, is positioned near the margin. Small pseudosepta are present at the apices. Mantle ornamented with large elongated, drop–like foramina, uninterrupted around the apices, where they are somewhat smaller. Girdle composed of at least three open bands ornamented with elongated, slit–like pores that become shorter and even roundish near the apices.

Morphometric data (n=28): length 7.5–16.0 μm , width 2.0–3.0 μm , 36–42 striae in 10 μm .

Distribution: This species was encountered from the following waterfalls in northeastern Argentina: Dos Hermanas, Arrechea, Núñez, Chico, Chávez and El Lagarto. Previously reported for Hawaii (LOWE et al. 2014), Crozet archipelago (as *Diademsis langebertalotii*, LE COHU & VAN DE VIJVER 2002, p. 128), South America: Uruguay–Río de la Plata (as *Diademsis pseudolangebertalotii*, METZELTIN et al. 2005, p. 45).

Comments: Specimens from Iguazú Falls match well the valve dimensions and main morphological features provided for the species by LOWE et al. (2014) from materials collected in the Hawaii archipelago, by LE COHU & VAN DE VIJVER (2002) from Crozet archipelago, by ZIDAROVA et al. (2016) from Maritime Antarctic Region and by METZELTIN et al. (2005) from Río de la Plata estuary. This species was first described (as a species of *Navicula*) from islands in the south Atlantic (CARTER 1966). Based on valve outline and metrics, this taxon would possibly include *H. bigibba* (Hustedt) Lowe et al. (LOWE et al. 2014, p. 357), as a synonym.

***Humidophila parallela* (Petersen) Furey, Manoylov et Lowe (Figs 65–71)**

Basionym: *Navicula contenta* var. *parallela* Petersen 1928, p. 15, fig. 2.

Synonym: *Diademsis contenta* var. *parallela* (Petersen 1928b, p. 15) Spaulding in SPAULDING et al. (1997, p. 410). *Diademsis contenta* var. *parallela* (Petersen) Tuji (2003, p. 66) nom. superfluous.

Type Locality: Iceland, in soil.

Valves are linear with parallel margins and broadly rounded apices. Axial area is moderately narrow, expanded at mid–valve forming a very distinct fascia. Raphe is filiform and straight. Externally raphe has central and terminal endings barely T–shaped, sometimes intersecting the last areolae, with troughs somewhat

Table 5. Main morphometric features of *Humidophila sebastianii* sp. nov. and most similar taxa.

Taxon	Length (μm)	Width (μm)	Striae density in 10 μm	Reference
<i>Humidophila sebastianii</i>	13–17	3.5–4.0	34–36	This study
<i>Humidophila komarekiana</i>	14–20	3–4	29–32	KOCHMAN–KEDZIORA et al. (2016)
<i>Diademsis subantarctica</i>	6–20	2–4	34–38	LE COHU & VAN DE VIJVER (2002)
<i>Diademsis templiniana</i>	10–18	2,6–3	27–30	RUMRICH et al. (2000)

asymmetrically developed. Striae are not resolvable in LM, parallel throughout the valve and slightly shortened towards the apices, each with one foramen. Mantle is high, ornamented with tear-shaped foramina, continuous at the valve apices.

Morphometric data (n=9): length 8.5–12.0 μm , width 2.5–3.0 μm , 46–48 striae in 10 μm .

Distribution: In this study this species was found at Núñez, Chico and Arrechea waterfalls. Previously reported in Europe (FUREY et al. 2020), Japan (TUJI 2003), Antarctica (KOCIOLEK et al. 2020) and North America (JOHANSEN 2010).

Comments: Specimens from Misiones closely resemble in overall valve morphology those of *H. parallela* reported by FUREY et al. (2020) from aerial diatom assemblages in Iceland. The latter differ, however, in their lower stria density (34.0–34.9 striae in 10 μm).

***Humidophila platensis* (Metzeltin, Lange–Bertalot et García–Rodríguez) Lowe, Kociolek, Johansen, Van de Vijver, Lange–Bertalot et Kopalová (Figs 72–78)**

Basionym: *Diademesis platensis* Metzeltin, Lange–Bertalot et García–Rodríguez 2005, Iconographia Diatomologica 15, p. 43, pl. 56, figs 1–10.
Type Locality: Río de La Plata estuary near Colonia del Sacramento (Uruguay).

Valves are linear with broadly rounded to rostrate apices. Axial area is narrow, distally expanded to form a distinct, hyaline, ‘crayon–tip’ area at each apex. Central area is very distinct, orbicular to quadrangular, delimited by smaller and silica filled foramina. Externally, raphe is straight, filiform, with simple central and terminal endings. The terminal endings not extending to the end of the valve. The raphe is contained in a central rib that is elevated slightly from the rest of the valve face. The ‘crayon tip’ structures and thickened central area are present at the apices and valve center, respectively. Cubiculus–type striae are not discernible in LM, more or less parallel, slightly radial near the central area, located in a longitudinal depression and bordered by a narrow and sinuous silica rim. Mantle areolae round, continuous at the valve apices where they are visible in valve view.

Morphometric data (n=5): length 20.0–25.0 μm , width 3.0–3.5 μm , 38–40 striae in 10 μm .

Distribution: Found in Dos Hermanas waterfall. This species is endemic to South America, previously only reported from the type locality (METZELTIN et al. 2005).

Comments: Valve dimensions and morphology of our specimens match those of the type specimens except for stria density, which are slightly lower in the latter (35–36 in 10 μm , measured on the figures since not provided in the original description).

***Humidophila sebastianii* Guerrero, Vouilloud et Sala sp. nov. (Figs 79–85)**

Description: Valves are linear with almost parallel margins and slightly convex in the valve middle, apices are broadly rounded. Axial area is linear and broad,

expanding to form a rounded central area that does not reach the valve margins. The raphe is indistinct, straight and filiform. Externally, the central and terminal endings are without troughs. Internally, the central raphe endings terminate on a round, prominent central nodule. Terminal raphe endings terminate in scarcely developed helictoglossae. Cubiculus–type striae are parallel to slightly radiate, easily discernible in LM, each with a single, small foramen. The vallum physically separates the virgae connected with the axial area from those on the mantle. Mantle with one row of small, weakly elongated foramina, interrupted at valve apices.

Morphometric data (n=6): length 13.0–17.0 μm , width 3.5–4.0 μm , 34–36 striae in 10 μm .

Type locality: Argentina. Arrechea waterfall, Iguazú N.P., Misiones Province (25°39'18.5"S, 54°27'25.7"W, 153 m a.s.l.), leg. J. Simonato, May 2019.

Holotype: Slide LPC 15639(1)! (Museo de La Plata Herbarium, La Plata, Argentina, here depicted in Figs 79–81). The holotype specimen is shown in Fig. 80 and is located at England Finder P31–4.

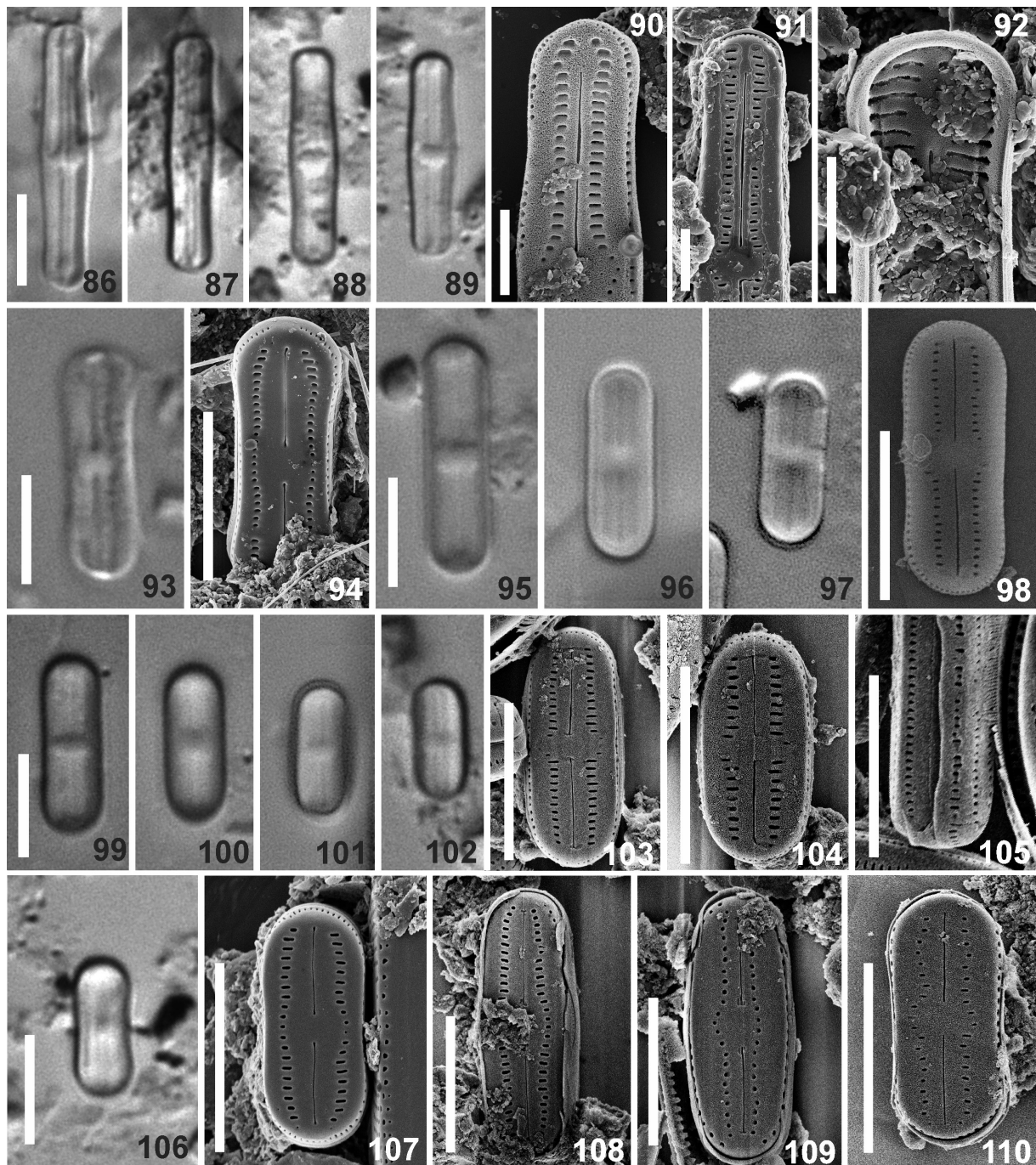
Isotype: Slide COLO 650061 (University of Colorado, Boulder, USA).

Etymology: The specific epithet refers to Dr. Sebastián A. Guarrera, a pioneer in phycological studies in Argentina and South America.

Distribution: This species was found in Arrechea and Dos Hermanas waterfalls, Iguazú N.P.

Comments: The occurrence of internal apical depressions at both sides of the sternum near the apices is an infrequent character within *Humidophila*, only previously reported in *H. fukushimae* (Lange–Bertalot et al.) Buczkó et Kövér (KÖVÉR et al. 2015, p. 247) (see Table S3).

Humidophila sebastianii was compared with *H. komarekiana* Kochman–Kedziora, Noga, Zidarova, Kopalová et Van de Vijver (KOCHMAN–KEDZIORA et al. 2016, p.186), described from King George Island, Antarctica, with *H. subantarctica* (Le Cohu et Van de Vijver) Lowe, Kociolek, Johansen, Van de Vijver, Lange–Bertalot et Kopalová (LOWE 2014, p. 359) described from Kerguelen Islands, and with *H. templiniana* (Lange–Bertalot et Rumrich) Lowe, Kociolek, Johansen, Van de Vijver, Lange–Bertalot et Kopalová (LOWE 2014, p. 359) described from Lauca River, Chile. All these species present similar valve outline, dimensions and overall appearance when observed with LM but none of them possess the internal apical depressions at both sides of the sternum near the apices, and their central area is formed by 4–5 striae, whereas in *H. sebastianii* it is delimited by 6–7 striae. Additionally, *H. komarekiana* differs for having proximal raphe endings expanded and lower stria density. The prominent central nodule observed in our materials is absent in *H. subantarctica* and *H. templiniana*. The latter species also has lower stria density and the mantle foramina are continuous at the apices. Comparison of *H. sebastianii* to most similar taxa is presented in Table 5.



Figs 86–92. *Humidophila subtropica* (Metzeltin et al.) Lowe et al.: (86–89) LM valve views showing population variability; (90–91) SEM external valve views, note the simple distal raphe end terminating at 3 to 5 striae from the apices; (92) SEM internal valve view, note distal raphe end terminating far from the apex. Figs 93–94. *Humidophila* aff. *biscutella* (Moser et al.) Lowe et al.: (93) LM valve view; (94) SEM external valve view. Figs 95–98. *Humidophila* sp. 1: (95–97) LM valve views, showing population variability; (98) SEM external valve view. Figs 99–105. *Humidophila* sp. 2: (99–102) LM valve views showing population variability; (103–104) SEM external valve views; (105) SEM frustule in girdle view. Figs 106–107. *Humidophila* sp. 3: (106) LM valve view; (107) SEM external valve view. Fig. 108. *Humidophila* sp. 4: (108) SEM external valve view. Fig. 109. *Humidophila* sp. 5: (109) SEM external valve view. Fig. 110. *Humidophila* sp. 6: (110) SEM external valve view. Scale bar 5 μ m (86–89, 93–110), 2 μ m (90–92).

***Humidophila subtropica* (Metzeltin, Lange–Bertalot et García–Rodríguez) Lowe, Kociolek, Johansen, Van de Vijver, Lange–Bertalot et Kopalová (Figs 86–92)**

Basionym: *Diademsis subtropica* Metzeltin, Lange–Bertalot et García–Rodríguez in METZELTIN, LANGE–BERTALOT & GARCÍA–RODRÍGUEZ 2005, p. 47, Pl. 56

Type Locality: Río de la Plata estuary near Colonia del Sacramento (Uruguay).

Valves are linear, slightly tumid at the valve center, and with broadly rounded, subcapitate apices. Axial area is narrow, slightly expanded at the apices and in the center, to form a rounded central area. Externally raphe is straight, filiform, terminating at 3 to 5 striae from the apices. Central and terminal raphe endings without troughs. Internally, the terminal raphe endings

terminate as helictoglossae. Cubiculus-type striae are not resolvable in LM, mostly parallel, slightly radiate near the central area and convergent towards the apices. In some specimens striae are located in a longitudinal depression bordered by a narrow, undulate silica rim. Foramina are elongated, except around the central area where they are small and round. A distinctive vallum, interrupted at valve apices, delimits valve face from mantle. Mantle has elongated foramina, becoming smaller and continuous around valve apices.

Morphometric data (n = 23): length 11.0–16.0 μm , width 2.5–3.0 μm , 40–43 striae in 10 μm .

Distribution: Found in this study at Arrechea, Chico, Núñez and Dos Hermanas waterfalls and unnamed stream. Previously recorded in Hawaii (LOWE et al. 2014) and South America: Uruguay–Río de la Plata (METZELTIN et al. 2005) and Brazil (TREMARIN et al. 2009).

Comments: Compared to the type specimens illustrated by METZELTIN et al. (2005), which were described as having 35 striae in 10 μm , the Argentinian specimens have 40–43 striae in 10 μm . However, reviewing the original illustrations we note the stria density to be 40 μm . LOWE et al. (2014) report intermediate stria densities (35–40 in 10 μm) for the population from Hawaii. Striae located in a depression of the valve wall as seen in some of our specimens has also been reported for this species by LOWE et al. (2014); the facultative presence of this feature has been documented in other species of the genus such as *H. biscutella* (Moser, Lange–Bertalot et Metzeltin) Lowe et al. (LOWE 2014, p. 357) (LANGE–BERTALOT & WERUM 2001), where it is attributed to an incomplete or abnormal development process.

***Humidophila* aff. *biscutella* (Moser, Lange–Bertalot et Metzeltin) Lowe, Kociolek, Johansen, Van de Vijver, Lange–Bertalot et Kopalová (Figs 93–94)**

Valves are elliptic with margins slightly concave and apices broadly rounded. Axial area is broad, narrowing to the apices. Raphe branches are filiform and straight, with conspicuous central and terminal pores. Central area is orbicular. Cubiculus-type striae are parallel, composed of rounded foramina at the central area and more transapically elongated towards the apices. Mantle has slightly elongated foramina, interrupted at the apices.

Morphometric data (n=2): length 8.5–11.0 μm , width 2.5 μm , 42–44 striae in 10 μm .

Distribution: Dos Hermanas and Chávez waterfalls and unnamed stream flowing into Iguazú River.

Comments: We found only one specimen in SEM which exhibits a slightly bent distal raphe end. Valve dimensions and morphology fit rather well with *H. biscutella* (as illustrated for the type material in MOSER et al. (1998, pl. 28, figs 1, 10) and in LANGE–BERTALOT & WERUM (2001, figs 65–71), except for the stria density, somewhat lower in the latter (36–40 in 10 μm) and the shape of the foramina and central area. More specimens

should be examined to confirm the taxonomic affiliation of this taxon.

***Humidophila* sp. 1 (Figs 95–98)**

Valves are elliptic with broadly rounded apices. Raphe is straight, filiform. Externally central and terminal endings are straight. Axial area is moderately broad, narrowing to the apices and central area is orbicular. Cubiculus-type striae are parallel, not visible in LM, with transapically elongated foramina at valve surface. Mantle has elongated foramina, continuous at the apices.

Morphometric data (n=6): length 7–9.0 μm , width 2.5–3.0 μm ; 40–42 striae in 10 μm .

Distribution: This species was found at El Lagarto, Arrechea and Dos Hermanas waterfalls.

Comments: Although this unidentified taxon resembles *H. tahitiensis* when observed with LM, the latter has somewhat larger valves, slit-like areolae and T-shaped central and terminal raphe endings (LANGE–BERTALOT & WERUM 2001; LOWE et al. 2014). *H. lagartiensis* is another similar species but with slightly constricted margins and shorter, rather ellipsoidal foramina.

***Humidophila* sp. 2 (Figs 99–105)**

Valves are elliptic with parallel margins and broadly rounded apices. Axial area is moderately narrow, expanded at mid-valve into a quadrangular central area. Raphe is filiform and straight. Externally central and terminal endings are barely T-shaped, sided by troughs somewhat asymmetrically developed. Cubiculus-type striae are not resolvable in LM, formed by transapically elongated foramina, parallel throughout the valve, shorter and somewhat occluded (“ghost”) around the central area. Mantle high, ornamented with small, rounded foramina, continuous and smaller at the valve apices.

Morphometric data (n=19): length 6.0–9.5 μm , width 2.5–3.0 μm , 38–42 striae in 10 μm .

Distribution: This taxon was found at Arrechea waterfall.

Comments: This diatom differs from *H. contenta* by its parallel, not constricted margins and the lack of a true fascia (LOWE 2015; LOWE et al. 2017). The occurrence of a central area expanded to form a fascia in *H. parallela* (FUREY et al. 2020) also distinguishes the latter species from our materials.

***Humidophila* sp. 3 (Figs 106–107)**

Valves are elliptic with margins slightly concave and apices broadly rounded. Axial area is broad, narrowing to the apices, and widened at mid-valve to form a weakly widened central area. Raphe branches are filiform and straight, with barely expanded central and terminal endings. Cubiculus-type striae are parallel, with foramina not interrupted and shorter at the central area and more transapically elongated towards the apices. Mantle with slightly elongated foramina, uninterrupted at the apices.

Morphometric data (n=6): length 6.5–7.5 μm , width

2.5–3.0 μm ; 36–40 striae in 10 μm .

Distribution: This taxon was found at Dos Hermanas waterfall.

Comments: We could not match this taxon to any other known *Humidophila* and more details of its valve morphology are necessary to elucidate if it is a new species. Our specimens show some resemblance to other species with striae uninterrupted at mid-valve, such as small valves of *H. brekkaensis* (Petersen) Lowe et al. (LOWE et al. 2014, p. 357) and *H. biscutella*. The former species differs in its lower stria densities (28–33 in 10 μm), a gibbous valve center and mantle foramina completely visible in valve view, interrupted at the valve apices (WERUM & LANGE–BERTALOT 2004; CHATTOVÁ et al. 2018). The specimens from Iguazú cannot be affiliated with *H. biscutella* since the latter taxon has more concave margins and mantle foramina discontinuous around the apices (LANGE–BERTALOT & WERUM 2001).

Humidophila sp. 4 (Fig. 108)

Valves are linear–elliptic with margins slightly swollen and apices broadly rounded. Axial area is moderately broad, tapering to the apices and widened at mid-valve to form a weakly widened central area. Raphe is filiform and straight with central and terminal endings simple and flanked by small, rounded troughs. Cubiculus–type striae are mostly radiate, becoming parallel at the central area. Foramina are transapically elongated, shortened around the central area and towards the apices. Mantle foramina are relatively large and rounded, interrupted at the apices. Girdle is composed of bands ornamented with slightly elongated pores.

Morphometric data (n=1): length 10.0 μm , width 3.0 μm , 32 striae in 10 μm .

Distribution: This taxon was found at Arrechea waterfall.

Comments: We observed only one specimen with this morphology and even though it shows some resemblance with other *Humidophila* taxa, we could not affiliate it to any known species. *H. brekkaensis* differs in its mantle foramina visible throughout the valve face (WERUM & LANGE–BERTALOT 2004; CHATTOVÁ et al. 2018). *Humidophila templiniana* (Lange–Bertalot et Rumrich) Lowe et al. (LOWE et al. 2014, p. 359) can be distinguished by its more widened and conspicuous central area. *Humidophila comperei* (Le Cohu et Van de Vijver) Lowe et al. (LOWE et al. 2014, p. 357) differs in the striae composed of narrower, slit–like foramina and raphe distal ends flanked by silica thickenings. *H. keiliorum* Kopalová (KOLAPOVÁ et al. 2015, p. 123) closely resembles the specimen from Misiones in its overall valve appearance and the presence of small troughs flanking the raphe ends; however, the former can be distinguished by its striae located in shallow longitudinal depressions and the proximal raphe ends located in spathulate grooves (KOPALOVÁ et al. 2015).

Humidophila sp. 5 (Fig. 109)

Valves are elliptic with margins slightly swollen and apices broadly rounded. Axial area is moderately narrow, expanded to form a slightly asymmetrical, orbicular central area. Raphe branches are straight and filiform. Terminal raphe endings are flanked by small troughs, giving the appearance of a faintly T–shaped end. Central raphe endings are simple, with asymmetrically elongated troughs present. Cubiculus–type striae have rounded foramina. Mantle foramina are large and rounded, discontinuous at the apices. Girdle and internal morphology not observed.

Morphometric data (n=1): length 9.0 μm , width 3.5 μm , 26–28 striae in 10 μm .

Distribution: This taxon was found at Arrechea waterfall.

Comments: We observed only one specimen with the valve morphology as described herein. Features such as valve outline, raphe morphology and mantle areolae of our specimen are similar to those exhibited by *Humidophila* sp. 4 presented here. However, the latter taxon has foramina transapically elongated instead of rounded, and a higher stria density (32 in 10 μm). *H. vidalii* (Van de Vijver, Ledeganck et Beyens) Lowe et al. (LOWE et al. 2014, p. 359), another species with rounded foramina, differs in valve shape, having a much broader axial area and lacking a central area.

Humidophila sp. 6 (Fig. 110)

Valves are elliptic with slightly constricted margins and broadly rounded apices. Axial area is moderately broad, narrowing towards the central area and the apices. Central area is orbicular. Raphe branches are straight, filiform, with inconspicuous central and terminal endings. Cubiculus–type striae are parallel or slightly radiate, forming an undulate series at both sides of the axial area. Foramina shape is variable from transapically elongated to almost round. Mantle foramina are relatively large.

Morphometric data (n=1): length 6.5 μm , width 3.0 μm , 36–38 striae in 10 μm .

Distribution: This taxon was found at Dos Hermanas waterfall.

Comments: The only specimen observed could not be assigned to any described species. It closely resembles *H. deceptionensis* Kopalová, Zidarova et Van de Vijver (KOPALOVÁ et al. 2015, p. 125) in overall valve morphology. The latter differs, however, by its margins being more markedly constricted, being longer (9–12.5 μm) and having lower stria density (30–32 in 10 μm).

DISCUSSION

Here we report on the presence of 17 *Humidophila* taxa from northeastern Argentina, in a relatively small geographic region. This is the largest concentration of taxa reported for any geographic entity studied. This nearly

doubles the number of species previously reported from the country (7, see Table S2) bringing the total number of *Humidophila* species for Argentina to 16, 14 of which have been identified to species and another 2 whose identities do not match previously described taxa. Since there are many places still to be collected and studied for this genus, the total number for Argentina will likely increase beyond the current 16 *Humidophila* taxa. Table S2 shows the distribution in Argentina (differentiating ecoregions) of the species included in this study and previous *Humidophila* records.

With the exception of *H. contenta*, all the species here described are restricted in Argentina to the Paranaense rainforest, the ecoregion of the country with the highest biodiversity in terms of vascular plants and vertebrates (AVIGLIANO et al. 2019), which comprises northeastern Argentina, southern Brazil and eastern Paraguay. Other recorded species in the country belong to the Puna, Patagonia (Andean forest and steppe) and South Atlantic Islands. Places containing large number of *Humidophila* taxa include the Sub–Antarctic/Antarctic region (14 taxa), other parts of Central and South America (13), New Caledonia (6), China (5) and Hawaii (5). In Antarctica, New Caledonia and China, most of the species present are endemics (LE COHU & VAN DE VIJVER 2002; VAN DE VIJVER et al. 2002b; KOPALOVÁ et al. 2015; CHATTOVÁ et al. 2018; MOSER et al. 1998; LOWE et al. 2017), while in Central and South America as well as Hawaii there is a mix of widely distributed and endemic taxa. For example, TREMARIN et al. (2009) list 7 species (under the genus *Diademsis*) for Paraná State, Brazil, with no endemics and including species from New Caledonia, Uruguay and cosmopolitan species. And while the genus has its greatest representation in the southern Hemisphere, there are endemic species in North America, Europe and the Arctic (FUREY et al. 2020; WERUM & LANGE–BERTALOT 2004; LANGE–BERTALOT & WERUM 2001). Thus, although the genus is geographically widely distributed (cosmopolitan), most of the species are endemic to particular regions of the world.

Analyzing the worldwide distribution of the studied species we can see that *H. contenta*, *H. nienta* and *H. parallela* are cosmopolitan. The other reported species belong to the same ecoregion (Paranaense rainforest) or other tropical areas: *H. arcuatoides* can be considered an American species, while *H. platensis* and *H. subtropica* seem to be endemic of the neotropics of South America.

In addition to the broad geographic space occupied by *Humidophila* in toto, the genus is also found in quite different ecological conditions, extending from Sub–Antarctic islands (e.g. LE COHU & VAN DE VIJVER 2002; KOPALOVÁ et al. 2015) to tropical and subtropical regions (e.g. RUMRICH et al. 2000; METZELTIN et al. 2005; RUWER & RODRIGUEZ 2018). The spectrum of light and temperature variation in which the genus can be found is thus impressive. Most members of the genus are found in subaerial habitats, and they share this

ability to survive (thrive?) in conditions of high oxygen and low or intermittent water availability. Other genera such as *Luticola* Mann in Round et al. (e.g. LEVKOV et al. 2013; STRAUBE et al. 2017; SIMONATO et al. 2020), *Muelleria* (Frenguelli) Frenguelli (e.g. SPAULDING et al. 1999), *Ferocia* Van de Vijver et Houk (VAN DE VIJVER et al. 2017), *Angusticopula* Houk et al. (HOUK et al. 2017; VAN DE VIJVER et al. 2019), *Orthoseira* Thwaites (e.g. LOWE et al. 2013; GUERRERO et al. 2018) and some species from other genera are also well–represented in these environments.

Though small (both physically and in the number of taxa) and with little ornamentation (as compared to some diatom genera) *Humidophila* does show some morphological variation amongst its component species. All species in the genus have a distinctive feature we have defined as the cubculus. The cubculus consists of a chamber opening externally through two separated foramina, one located on the valve face and the other one on the mantle, but internally it is occluded by a continuous hymen. The hymenate occlusions covering the openings internally comprise multiple rows of very fine, rounded pores, reminiscent of the external coverings of striae in *Pinnularia* Ehrenberg (ROUND et al. 1990; KRAMMER 2000). The cubculus here described for *Humidophila* may be at first sight reminiscent of the macroareolae present in several genera of monoraphid and biraphid diatoms. BUKHTIYAROVA (2006) established the term macroareola to describe the striae in *Karayevia* Round et Bukhtiyarova and it was defined as a foramen occupying the entire area of a stria, internally occluded by a plain hymen. This type of stria has been reported to occur in representatives of different genera such as *Microfissurata* Lange–Bertalot, Cantonati et Van de Vijver (CANTONATI et al. 2009), *Scalariella* Riaux–Gobin (RIAUX–GOBIN et al. 2012), *Pseudachnanthidium* Riaux–Gobin (RIAUX–GOBIN & WITKOWSKI 2015), *Microcostatus* Johansen et Sray (VAN DE VIJVER & ECTOR 2019), *Majewskaea* Van de Vijver, Robert, Witkowski et Bosak (VAN DE VIJVER et al. 2020b) and *Navithidium* Al–Handal et Romero (AL–HANDAL et al. 2021), among others. The presence of macroareolae has also been mentioned as a shared feature within the genus *Diademsis/Humidophila* (CANTONATI et al. 2009; RIAUX–GOBIN et al. 2012; AL–HANDAL et al. 2021). However, unlike the situation described by BUKHTIYAROVA (2006), the cubculus as described here for *Humidophila* is a different, more complex structure.

Besides, it appears that all *Humidophila* species so far illustrated also have what we have termed a vallum, which is apparently unknown in other taxa, suggesting that both structures may be synapomorphic for *Humidophila*. This structure consists of a groove running longitudinally on either side of the raphe near the margins and delimited (to the side of the axial area) by raised or thickened sections of the virgae. In cross section (see *H. nienta*) it appears subtended by a hollow tube or canal running the length of the valve. This tube communicates to the valve interior through the portions

of the hymenes continuous from valve face to mantle, but it does not have external openings, so externally this area appears smooth. This type of longitudinal canal thus differs from those of *Neidium* Pfitzer and *Neidiomorpha* Lange–Bertalot et Cantonati species in which there are fine holes perforating the tubes internally and connections to the exterior are by areolae opening into them (CANTONATI et al. 2010). Other genera exhibiting longitudinal canals are *Fallacia* Stickle et Mann in ROUND et al. (PROCOPIAK & FERNANDES 2003) and *Muelleria* (Frenguelli) Frenguelli (SPAULDING et al. 1999), in which the canals apparently lack perforations internally and have no external connections.

There is some variation in the vallum among species of the genus but in most cases this feature is delimited by a slight elevation or ridge running across the virgae. Recently, VAN DE VIJVER et al. (2020a, p. 5) have described this as “low ridges separating mantle areolae from the valve face areolae”. This condition is found, for example, in *H. difficilis* (VAN DE VIJVER et al. 2020a), *H. undulata* (LOWE et al. 2014), *H. biggiba* (LOWE et al. 2017) and *H. arcuatooides*, *H. misionera*, *H. nienta* and *H. sebastianii* (presented herein). In the majority of cases it appears this might represent a physical separation between the virgae originating on the axial area and the virgae associated with the mantle, as seen in most of the species described from the Antarctic region (e.g. KOPALOVÁ et al. 2015; CHATTOVÁ et al. 2018) as well as *H. contenta* (LOWE et al. 2017) and *H. nienta* (LOWE et al. 2014; presented herein).

The internal lamina of silica covering most of the valve interior of *H. lagartiensis* which appears to be without perforations, is known in this taxon as well as *H. scepacuerciae* Kopalová (KOPALOVÁ et al. 2015, p. 121) and *H. deceptionensis*, the latter two being described from Livingston and Deception Islands, respectively (KOPALOVÁ et al. 2015). However, the possibility cannot be ruled out that the lack of this structure in other species is related to the oxidation treatment of the samples. Similar internal laminae are known in genera such as *Pinnularia* Ehrenberg (ROUND et al. 1990) and *Gomphoneis* Cleve (KOCIOLEK & STOERMER 1988), where they form internal partitions between the valve associated with the exterior and the valve interior.

In terms of morphological variation in other features of the valve face, we can see differences between taxa in terms of the external proximal raphe ends, external distal raphe ends (and whether there are thin ‘troughs’ extending from the raphe ends at both places, just the proximal ends or just the distal ends), whether the raphe is elevated off the exterior valve face, the degree of separation between the valve face and mantle, and the presence of valve depressions internally at the valve apices. These are summarized in Table S3.

For example, among 58 selected *Humidophila* taxa there are species with both external proximal and distal raphe ends that have bifurcated troughs (17 taxa with that condition), with just proximal (3 taxa), or distal ends (4

taxa) bifurcated troughs, or straight (no troughs; 32 taxa). Of those taxa without troughs, 10 taxa have distal raphe ends that terminate well before the valve apex. These shortened raphe systems are found in only two taxa that possess troughs only in distal ends. Five taxa have the raphe elevated off of the external valve face, and four *Humidophila* taxa are reported to produce valves without a raphe system. Five species have a thickened ridge at the valve margin that separates the valve face from the mantle (MOSER et al. 1998; LOWE et al. 2017), but most species do not. Three species have marginal spines, all of them are also raphe-less. Seven taxa have striae in a longitudinal depression. Three taxa have pseudosepta. *H. sebastianii* and *H. fukushimae* have internal depressions at the valve apices (LANGE–BERTALOT & WERUM 2001; WERUM & LANGE–BERTALOT 2004) and are the only species in the genus in which these structures were observed until now. In addition, nearly all species have filiform raphes although the raphe appears to be lost in most valves of *H. gallica* (COX 2006) and 3 other species. There are a few instances where features may be unique to a single species in the genus, being apparently autoapomorphic for that species.

A further feature that is variable among the species of *Humidophila* is the organization of mantle areolae in the apices. Considering the taxa described herein, in 5 of them the mantle areolae are interrupted at the valve apices whereas in the remaining 12 taxa mantle areolae are continuous around the apices, where they are sometimes smaller and more densely arranged. Moreover, in some of these taxa the apical mantle areolae are clearly visible even in valve view. Mantle areolae entirely located on the same level as the areolae of the valve face occur in species such as *H. brekkaensis* (CHATTOVÁ et al. 2018) and *H. ingeae* (Van de Vijver) Lowe et al. (2014, p. 358) (Van de Vijver et al. 2002b), but this is not the case for any of the taxa here described.

While the shared morphological similarities among *Humidophila* taxa may reflect phylogenetic affinities in the genus, a formal analysis of relationships is lacking. These similarities do suggest that there are some character combinations that are only found together (raphe ends that are without troughs can also be shortened); to the exclusion of other character combinations (raphe ends with troughs are not seen with taxa that have shortened raphe systems). Less clear is whether there are features found only in some regions of the world and not others. Further analysis of taxa will be required to assess the phylogenetic relationships within this interesting genus.

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