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Five new species of the genus Humidophila (Bacillariophyta) from the Maritime Antarctic Region

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Five new species of the genus *Humidophila* (Bacillariophyta) from the Maritime Antarctic Region

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Five unknown taxa belonging to the newly established genus *Humidophila* were found during ongoing taxonomic revision of the freshwater and limno-terrestrial diatom flora of the Maritime Antarctic Region. These taxa were previously identified as *Diadesmis arcuata*, *D. biscutella*, *D. comperei* and *D. ingeae*, but detailed light and scanning electron microscopy observations allowed their clear separation from the already known taxa, and resulted in the description of five new species: *Humidophila sceppacuerciae* Kopalová sp. nov., *H. australoshetlandica* Kopalová, Zidarova & Van de Vijver sp. nov., *H. keiliorum* Kopalová sp. nov., *H. deceptionensis* Kopalová, Zidarova & Van de Vijver sp. nov. and *H. vojtajarosikii* Kopalová sp. nov. All five new taxa are compared with the morphologically most similar taxa, and their ecology and biogeography are discussed. Although the genus *Humidophila* is present worldwide, a large number of *Humidophila* taxa have a restricted distribution within the (sub-)Antarctic Region, showing a clear bioregionalism.

Keywords: Humidophila, *Bacillariophyta, Maritime Antarctic Region, new species, taxonomy*

Introduction

Recently, the genus *Humidophila* R.L.Lowe et al. was established to accommodate most of the taxa that were originally placed in *Diadesmis* Kützing subgenus *Paradiadesmis* Lange-Bertalot & Le Cohu (Lowe et al. 2014). *Humidophila* taxa are characterized by having small valves, rarely protracted apices, striae composed of one, usually transapically elongated, elliptical to ovoid areola that is internally occluded by a porous hymen, and a filiform raphe with straight, simple, drop-like or anchor-shaped (never deflected, bent or hooked) external proximal and distal endings (Lowe et al. 2014).

Humidophila is present worldwide, but a large number of taxa have a restricted distribution confined to the (sub-)Antarctic Region. Typical examples include *Humidophila ingeae* (Van de Vijver) R.L.Lowe et al., *H. inconspicua* (Kopalová & Van de Vijver) R.L.Lowe et al. and *H. crozetikerguelensis* (Le Cohu & Van de Vijver) R.L.Lowe et al. Given the special nature of its microhabitats, including seepage areas, semi-wet moss vegetation and temporary pools, the Antarctic Region is known for the dominance of aerophilic taxa belonging to the genera *Luticola* D.G. Mann (Van de Vijver & Mataloni 2008, Kopalová et al. 2011, Van de Vijver et al. 2011), *Hantzschia* Grunow (Zidarova et al. 2010), *Muelleria* Frenguelli (Spaulding et al. 1999, Van de Vijver et al. 2010, 2014) and *Humidophila* (Van de Vijver et al. 2002, 2010, Kopalová et al. 2009). The majority of the taxa within these genera found in this region are considered endemic, illustrating the highly specific nature of the Antarctic diatom flora. During a survey of the non-marine diatom flora of the Maritime Antarctic Region, one of the three major subdivisions of the Antarctic Region (Chown & Convey 2007) comprising most of the Antarctic Peninsula (up to the so-called Gressitt Line) and the surrounding islands and archipelagos such as the South Shetland Islands, several populations of unknown *Humidophila* taxa were found that could not be identified using the currently available literature.

This paper describes five new *Humidophila* species based on detailed light and scanning electron microscopy. Detailed morphological descriptions are provided for these taxa, and their ecology, biogeography and separation from similar taxa are discussed.

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Based on these data, apart from a few species, such as *H. contenta* (Grunow) Lowe et al. or *H. arcuata* (Heiden) R.L.Lowe, *Humidophila* shows a clear biogeographical pattern in the Antarctic Region. The highest diversity is reached in the southern Indian Ocean, probably because of the higher diversity of aerophilic microhabitats compared to the Antarctic Continent, where diatom diversity is very low.

Material and methods

Samples were collected from various aquatic and terrestrial habitats on Livingston Island, Deception Island and James Ross Island (Fig. 1). Livingston Island and Deception Island belong to the South Shetland Islands (63°00′S, 60°00′W), situated just north of the Antarctic Peninsula. The archipelago consists of 11 larger, and many smaller, islands and islets, with King George Island (1150 km^2) and Livingston Island (972 km^2) being the largest. They have a typically maritime oceanic climate with mean annual temperatures around –5°C, high precipitation rates and strong westerly winds (Chipev & Veltchev 1996). Most of the land areas are covered by permanent ice and snow cover, leaving only small parts ice-free. The terrestrial vegetation is limited to lichens and mosses, with only two flowering plants [*Colobanthus quitensis* (Kunth) Bartling and *Deschampsia antarctica* Desvaux].

Additional sampling was carried out on James Ross Island (64°10′S, 57°45′W), located further south in the Maritime Antarctic Region, in the northwestern part of the Weddell Sea, close to the northern tip of the Antarctic Peninsula. This fairly large island (2450 km^2) is situated in the transition zone between the Maritime Antarctica and Continental Antarctica regions (Øvstedal & Lewis-Smith 2001). Only its northern part, the Ulu Peninsula, where the samples were taken, is ice-free. The

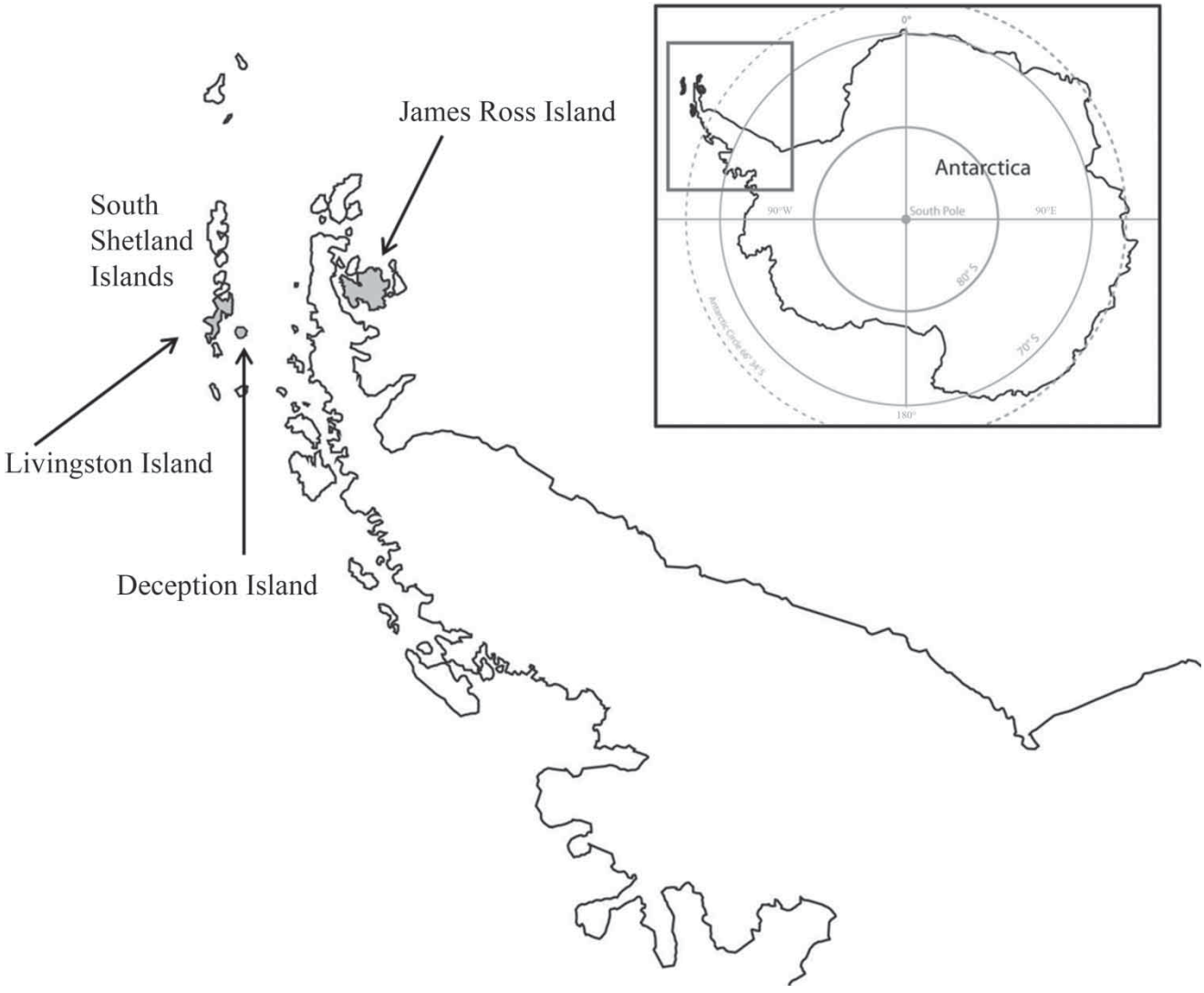

Fig. 1. Map of the Antarctic Peninsula region, showing the position of the South Shetland Island archipelago and indicating the different islands sampled for this study.

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temperature is comparable with the South Shetland Islands but precipitation is limited to only 150 mm y^{-1} in the northern part (Aristarain et al. 1987), with high evaporation rates reducing the formation of large open water bodies. The terrestrial vegetation is limited to non-vascular plants, forming a bryophyte and lichen tundra in places.

Sampling methods follow those described in Kopalová et al. (2012, 2013, 2014) and Kopalová & Van de Vijver (2013). Details on the physicochemical analyses (pH, conductivity, nutrients) can also be found in these references.

Diatom samples were prepared following the method of van der Werff (1955). Small parts of the samples were cleaned by adding 37% H_2O_2 and heating to 80°C for about one hour, followed by addition of $KMnO_4$. After digestion and centrifugation (3 × 10 minutes at 3700 ***g***), the material was diluted with distilled water to avoid excessive concentrations of diatom valves. Cleaned diatom valves were mounted in Naphrax®. Samples and slides are stored at the BR-collection, property of the Belgian Federal Government and given on permanent loan to the Botanic Garden Meise (Belgium). The slides were analysed using an Olympus BX53 microscope, equipped with Differential Interference Contrast (Nomarski®) and the Colorview I Soft Imaging System. For scanning electron microscopy (SEM), part of the suspension was filtered through polycarbonate membrane filters with a pore diameter of 1 µm, pieces of which were fixed on aluminium stubs after air-drying. The stubs were sputter-coated with 20 nm of Au–Pd and studied in a Zeiss Ultra microscope at 3 kV. Terminology is based on Hendey (1964), Ross et al. (1979) and Round et al. (1990). For each new taxon, the number of specimens measured at random on the type slide is

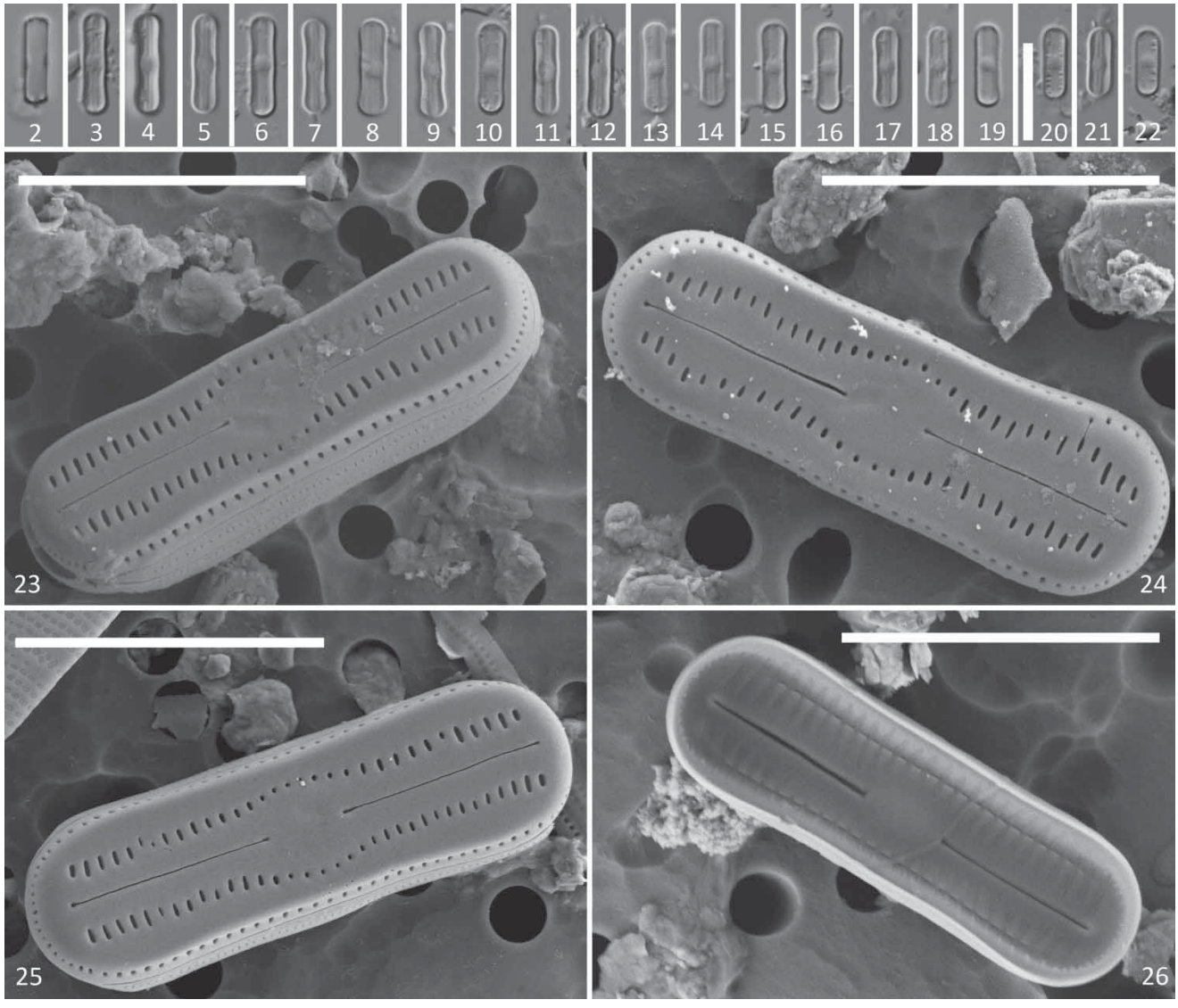
Table 1. List of all *Humidophila* (including *D. gallica*, which has not been transferred yet) species present in the (sub-)Antarctic Region with their geographical distribution.

	Sub-Antarctica		Maritime Antarctic Region			
	Southern Indian Ocean islands	Southern Atlantic Ocean islands	South Shetland Islands	James Ross Island	Antarctic Continent	Cosmopolitan
Taxa observed in this study						
Humidophila sceppacuerciae Kopalová sp. nov.			x	x		
Humidophila australoshetlandica Kopalová, Zidarova & Van de Vijver sp. nov.			x	x		
Humidophila keiliorum Kopalová sp. nov.			x	x		
Humidophila deceptionensis Kopalová, Zidarova & Van de Vijver sp. nov.			x			
Humidophila vojtajarosiki Kopalová, Zidarova & Van de Vijver sp. nov.			x	x		
Taxa observed in other recent studies						
Humidophila crozetikerguelensis	x					
Humidophila brekkaensis	x					
Humidophila comperei	x					
Humidophila costei (Le Cohu & Van de Vijver) R.L.Lowe et al.	x		x?			
Humidophila faurei (Van de Vijver & Beyens) R.L.Lowe et al.	x					
Humidophila latestriata (Van de Vijver, Ledeganck & Beyens) R.L.Lowe et al.	x					
Humidophila subantarctica	x					
Humidophila vidalii (Van de Vijver, Ledeganck & Beyens) R.L.Lowe et al.	x					
Humidophila paracontenta var. magisconcava	x					x
Humidophila arcuata	x				x?	x?
Humidophila ingeae	x					
Humidophila nienta	x	x	x	x		
Humidophila tabellariaeformis			x	x		x
Humidophila inconspicua			x	x	x?	
Humidophila australis			x	x	x	
Diadesmis gallica			x	x	x	x

indicated ($n = X$). The new species were compared with similar taxa from the Antarctic Region (Van de Vijver et al. 2002, Kopalová et al. 2009), Europe (Lange-Bertalot & Genkal 1999, Lange-Bertalot & Werum 2001, Werum & Lange-Bertalot 2004), South America (Rumrich et al. 2000) and New Caledonia (Moser et al. 1998). In addition, new SEM micrographs were taken of the types of *H. arcuata*, *H. comperei* (Le Cohu & Van de Vijver) R.L.Lowe et al., *H. ingeae* (Van de Vijver) R.L.Lowe et al. and *H. subantarctica* (Le Cohu & Van de Vijver) R.L.Lowe et al. supporting the separation of the new species. The type material of each of these taxa (held in the Botanic Garden Meise) was used for these observations. Based on the present study, our personal unpublished observations and literature data (Lowe et al. 2014), a list of all known *Humidophila* taxa in the (sub-)Antarctic Region together with their distributions was compiled and is presented in Table 1.

Results

Five *Humidophila* taxa in the investigated samples could not be identified using the available literature and are described as new species: *Humidophila sceppacuerciae* Kopalová sp. nov. (Figs 2–26), *H. australoshetlandica* Kopalová, Zidarova & Van de Vijver sp. nov. (Figs 27–48), *H. keiliorum* Kopalová sp. nov. (Figs 49–70), *H. deceptionensis* Kopalová, Zidarova & Van de Vijver sp. nov. (Figs 71–91) and *H. vojtajarosikii* Kopalová, Zidarova & Van de Vijver sp. nov. (Figs 92–118).



Figs 2–26. *Humidophila sceppacuerciae* sp. nov. type population from Domo Lake, Byers Peninsula, Livingston Island. Fig. 2–26. LM of a frustule in girdle view. Figs 3–22. LM valve face views. Figs 23–25. SEM of an entire valve (externally). Fig. 26. SEM valve (internally). Scale bars = 10 µm (Figs 2–22); 5 µm (Figs 23–26).

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***Humidophila sceppacuerciae* Kopalová sp. nov. (Figs 2–26)**

Holotype (here designated). BR–4378 (Botanic Garden Meise, Belgium).

Isotype (here designated). Slide PLP–263 (University of Antwerp, Belgium).

Type locality. Domo Lake, Byers Peninsula, Livingston Island, South Shetland Islands (62°38′50.1″S, 60°58′24.6″W), sample BY–037, leg. B. Van de Vijver, coll. date 12/01/2009. The sample was unvegetated sediment in the littoral zone.

Etymology. The new species was named after a special friend from Argentina, Ignacio Sceppacuercia.

Morphological observations

Light microscopy (Figs 2–22). Frustules rectangular in girdle view (Fig. 2). Valves linear. Smaller specimens with parallel margins, larger specimens with gibbous centre. Apices non-protracted, broadly rounded (Figs 3–22). Valve dimensions ($n = 25$): length 7.4–10.7 µm, width 2.3–2.6 µm. Axial area broad, linear. Central area slightly widened, never forming a fascia. Raphe filiform, hardly visible in LM, straight with simple straight proximal and distal endings. Striae almost not discernible in LM, parallel throughout the entire valve.

Scanning electron microscopy (Figs 23–26). Striae composed of one transapically elongated areola, c. 45 in 10 µm (Figs 23–25). At the apices, striae usually terminating near the distal raphe endings (Fig. 25). Mantle areolae positioned in a very shallow depression running from one apex to the other, lacking any interruption at the apices (Figs 23, 25). External raphe branches straight with simple proximal endings (Figs 23–25). Distal raphe endings short, terminating in a small expanded pore on the valve face, near the last striae (Figs 24–25). Internally, well-developed central nodule present. Internal proximal raphe endings straight, weakly T-shaped (Fig. 26). Distal raphe endings terminating on weakly developed helictoglossae (Fig. 26). Areolae covered internally by porous hymenes (Fig. 26). Valve face and mantle areolae separated by a narrow longitudinal groove (Fig. 23). Girdle composed of a few (probably two) open copulae, perforated by a single row of elongated, slit-like poroids (Fig. 23).

Ecology and distribution

Humidophila sceppacuerciae is widely distributed in the Maritime Antarctic Region, present on James Ross Island and the South Shetland Islands: Livingston Island (reported as '*Diadesmis* sp1' in Kopalová et al. 2014), King George Island and Nelson Island (Zidarova, pers. obs.), although rarely in populations exceeding 5% of the total diatom counts. The largest populations were observed in semi-wet to wet terrestrial moss vegetation. On James Ross Island, smaller populations (2–4%) were present in a large number of lakes with a circumneutral to slightly alkaline pH (6.9–7.6) and rather low conductivity (26–238 µS cm^{-1}). Other typical taxa in the samples include *Nitzschia homburgiensis* Lange-Bertalot, *Psammothidium papilio* (Kellogg et al.) Kopalová & Van de Vijver, *Hantzschia amphioxys* Ehrenberg and *Humidophila vojtajarosikii* Kopalová, Zidarova & Van de Vijver sp. nov.

Taxonomic remarks

Based on valve outline, *H. sceppacuerciae* closely resembles *H. ingeae*, described from Îles Crozet in the southern Indian Ocean (Fig. 1). Kopalová et al. (2013, 2014) and Kopalová & Van de Vijver (2013) reported the species under its old name (*Diadesmis ingeae* Van de Vijver). However, both taxa can be easily separated based on the structure of the mantle areolae. In *H. ingeae*, the mantle areolae are not separated from the valve face by an edge, as is the case in *H. brekkaensis* (J.B.Petersen) R.L.Lowe et al., but are clearly visible at the edge of the valve face (Fig. 121), unlike *H. sceppacuerciae* whose mantle areolae are entirely located around the mantle (Figs 23–25). *Humidophila paracontenta* (Lange-Bertalot & Werum) R.L.Lowe et al. also has a similar valve outline but always has a clear fascia, never present in the new taxon (Lange-Bertalot & Werum 2001, fig. 62). *Humidophila biscutella* (Lange-Bertalot) R.L.Lowe et al. usually has centrally constricted valve margins, although sometimes valves with a gibbous centre have been observed (see for instance Lange-Bertalot & Werum 2001, fig. 69). However, constricted valves have never been observed in *H. sceppacuerciae*.

***Humidophila australoshetlandica* Kopalová, Zidarova & Van de Vijver sp. nov. (Figs 27–48)**

Holotype (here designated). BR–4379 (Botanic Garden Meise, Belgium).

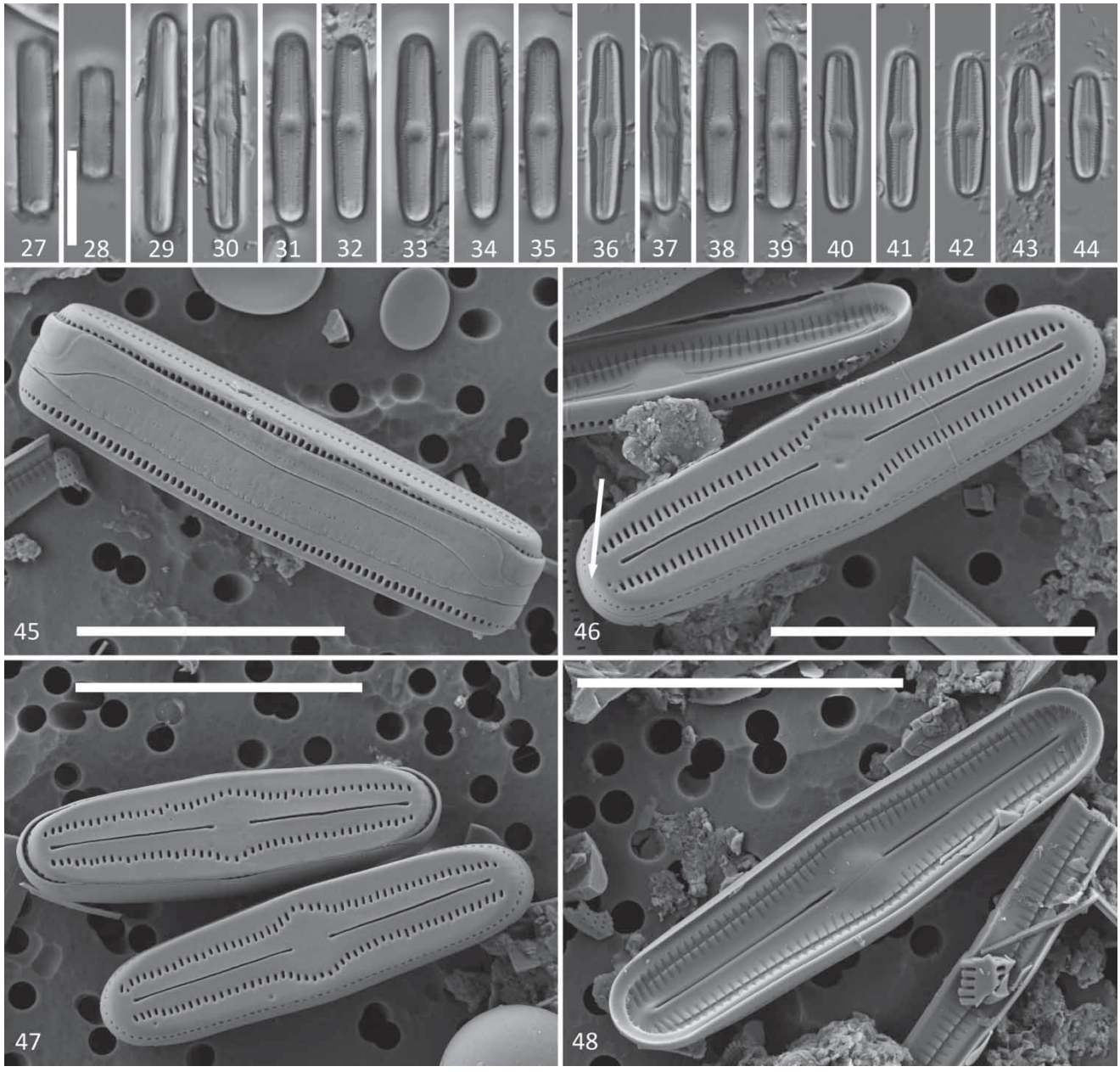
Isotype (here designated). Slide PLP–264 (University of Antwerp, Belgium).

Type locality. Clark's Nunatak, Byers Peninsula, Livingston Island, South Shetland Islands (62°40′15.6″S, 60°55′25.5″W), sample BYM–041, leg. B. Van de Vijver, coll. date 12/01/2009. The sample was dry mosses collected close to the nest of a Wilson's storm petrel [*Oceanites oceanicus* (Kuhl)].

Etymology. The specific epithet refers to the South Shetland Islands from where the new species is described.

Morphological observations

Light microscopy (Figs 27–44). Frustules rectangular in girdle view (Figs 27–28). Valves linear to weakly linear–lanceolate in larger specimens, with slightly gibbous central part and non-protracted, broadly rounded apices (Figs 29–44). Valve dimensions ($n = 30$): length 11.6–24.5 µm, width 3.6–4.3 µm. Axial area moderately broad,



Figs 27–48. *Humidophila australoshetlandica* sp. nov. type population from Clark's Nunatak, Byers Peninsula, Livingston Island. Figs 27–28. LM of girdle views. Figs 29–44. LM of valve views. Fig. 45. SEM girdle view. Figs 46–47. SEM of an entire valve (externally). Arrow (Fig. 46) indicating no mantle areolae interruption at the apices. Fig. 48. SEM of valve (internally). Scale bars = 10 µm.

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linear. Central area rounded, weakly widened, never forming a fascia. Raphe filiform, straight with simple straight proximal and distal endings. Striae parallel throughout the entire valve, 31–32 in 10 µm.

Scanning electron microscopy (Figs 45–48). Striae located in a shallow longitudinal depression, composed of one transapically elongated areola (Fig. 46). Near the apices, striae converge, usually terminating beyond the distal raphe endings (Fig. 47). Mantle areolae enlarged, becoming smaller near the apices, continuing around the apices without any interruption (Fig. 46, arrow). External raphe branches straight with inconspicuous proximal endings (Figs 46–47). Distal raphe endings short, terminating on the valve face, well before the apices (Figs 46–47). Internally, well-developed central nodule present (Fig. 48). Internal proximal raphe endings straight, simple (Fig. 48). Distal raphe endings terminating on weakly developed helictoglossae (Fig. 48). Areolae covered internally by porous hymenes (Fig. 48). Valve face and mantle areolae separated by a narrow longitudinal groove (Fig. 48).

Girdle composed of three open copulae, perforated by a single row of very small, rounded poroids (Fig. 45).

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Ecology and distribution

Humidophila australoshetlandica is confirmed from the South Shetland Islands: Livingston Island (reported as *Diadesmis arcuata* (Heiden) Lange-Bertalot in Kopalová et al. 2014), King George Island and Nelson Island (Zidarova, pers. obs.). The new taxon entirely dominated the sample from which it was described (almost 90% of all counted valves). The type population was taken from rather dry moss vegetation close to a nesting Wilson's storm petrel. Apart from *Psammothidium germainii* (Manguin) Sabbe and *Eunotia pseudopaludosa* Van de Vijver et al., no other diatoms were found in the sample. Other relatively large populations of this species were recorded in soil under moss vegetation close to the nests of giant petrels, as well as among cyanobacterial mats on the bottom of a small shallow pool, with a pH of 8.5 and specific conductance of 317 μS cm^{-1}.

Taxonomic remarks

Humidophila australoshetlandica was reported in previous papers as *D. arcuata* (now *H. arcuata*), but can be separated from the former by its valve outline lacking the clear gibbous centre, the typical narrow ridge that surrounds the raphe in *H. arcuata* (Fig. 119), striae that are never in shallow depressions and that never shorten towards the valve apices. The new taxon can also be separated from *H. subantarctica* (Fig. 122), another sub-Antarctic taxon described from the islands in the southern Indian Ocean, by the ridge that surrounds the raphe in the latter, the more pointed valve apices and striae that are composed of large, elliptical areolae. *Humidophila virginiana* (Lange-Bertalot) R.L.Lowe et al. has similar striae lying in shallow depressions but has a different valve outline, being more lanceolate, and has different mantle areolae near the apices (Werum & Lange-Bertalot 2004, plate 71, fig. 1). Unlike *H. australoshetlandica*, *H. virginiana* has mantle areolae that are almost on the apices and around the mantle. For a comparison with *H. keiliorum*, see below under this taxon.

***Humidophila keiliorum* Kopalová sp. nov. (Figs 49–70)**

Holotype (here designated). BR–4380 (Botanic Garden Meise, Belgium).

Isotype (here designated). Slide PLP–265 (University of Antwerp, Belgium).

Type locality. Byers Peninsula, Livingston Island, South Shetland Islands, sample LIV–BY16A (62°38′10.9″S, 61°6′27.4″W), leg. M. Toro, coll. date 16/12/2006. The sample was a terrestrial microbial mat.

Etymology. The species was named, as a wedding present, after Kateřina and Pavel Keil, family of the first author.

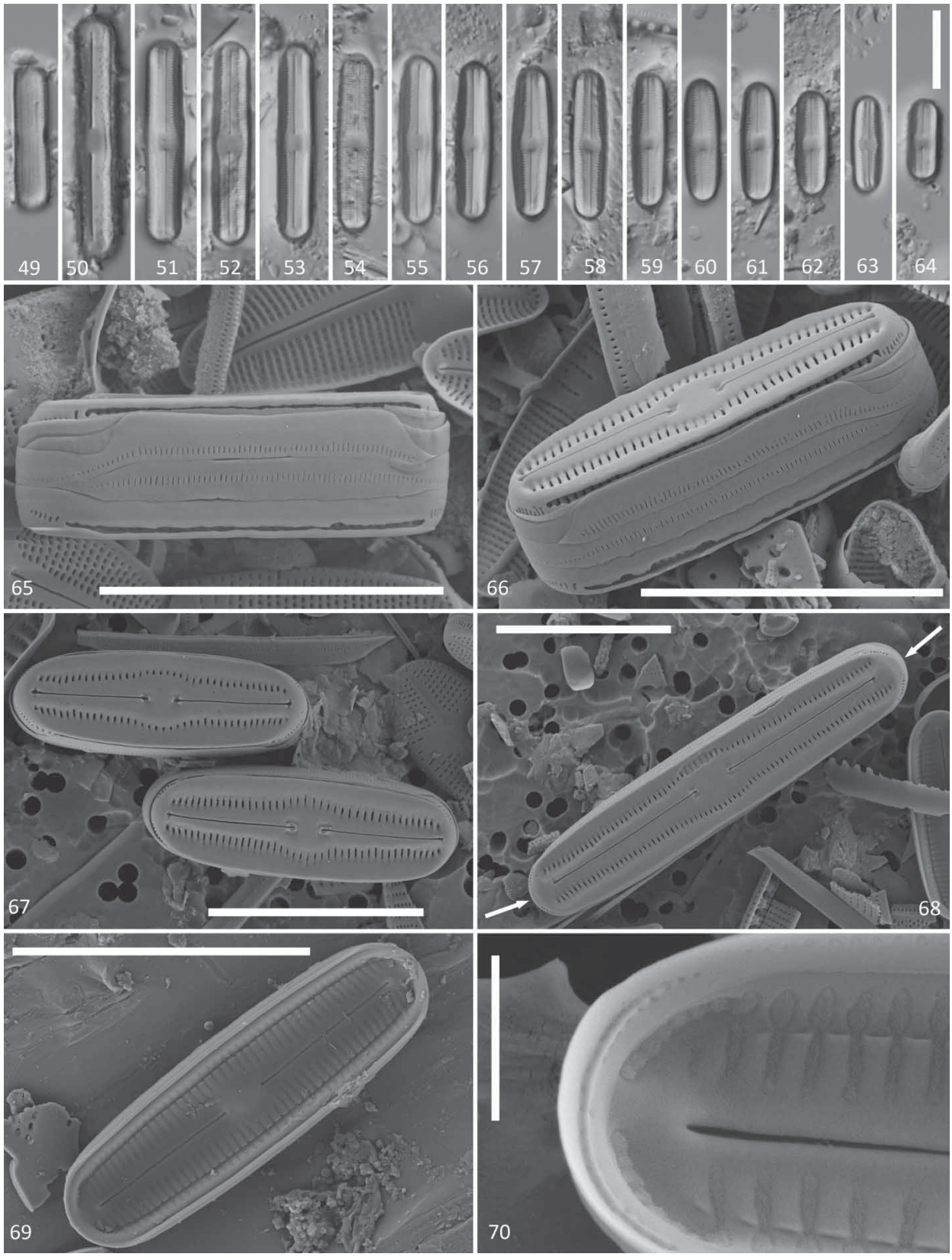
Morphological observations

Light microscopy (Figs 49–64). Frustules rectangular in girdle view (Fig. 49). Valves linear with almost parallel margins and non-protracted, broadly rounded apices (Figs 50–64). Smaller specimens occasionally with more linear–elliptic valve outline (Fig. 60). Valve dimensions ($n = 25$): length 10.4–31.2 μm, width 3.2–5.2 μm. Axial area moderately broad, linear. Central area weakly widened, never forming a fascia. Raphe filiform, straight with weakly expanded, straight, proximal and distal endings. Striae parallel throughout the entire valve, 27–30 in 10 μm.

Scanning electron microscopy (Figs 65–70). Striae located in a shallow depression, each comprising one transapically elongated areola (Figs 66–68). At the apices, striae usually terminating near the distal raphe endings (Figs 66–67), sometimes beyond the distal raphe endings (Fig. 68). Mantle areolae positioned in a longitudinal groove running from one apex to the other. Grooves disappearing near the apices, revealing the areolae on the mantle (Figs 65, 66), which are clearly interrupted at the apices (Fig. 68, arrows). External raphe branches straight with inconspicuous proximal endings, located in a spathulate groove (Fig. 67). Distal raphe endings short, terminating on the valve face, near the last striae (Fig. 67). Small depressions bordering the proximal and distal endings (Fig. 67). Internally, well-developed central nodule present (Fig. 69). Internal proximal raphe endings straight, simple to weakly expanded (Fig. 69). Distal raphe endings terminating on weakly developed helictoglossae (Fig. 70). Areolae covered internally by porous hymenes (Fig. 70). Clear interruption in mantle areolae visible at the apices (Fig. 70). Valve face and mantle areolae separated by a narrow longitudinal groove (Fig. 69). Girdle composed of three open copulae, perforated by a single row of elongated, slit-like pores (Figs 65–66).

Ecology and distribution

Humidophila keiliorum is a rather common diatom in moss vegetation and seepage areas on both James Ross Island and the South Shetland Islands (Livingston Island, King George Island and Deception Island). Its distribution in Antarctica is, however, unclear due to the presence of *D. arcuata* under which name this species was reported in Kopalová et al. (2013, 2014). The new taxon is also present at very low abundance in aquatic (i.e., lakes, streams) conditions ($<$ 2% of all counted valves). On James Ross Island, *H. keiliorum* seems to prefer wet seepage areas, whereas on the South Shetland Islands the species is more common in wet to semi-dry terrestrial mosses, although it is also regularly observed in seepage areas. The type population was sampled from a biofilm in an area flooded by freshwater between stones on Byers Peninsula close to the main plateau. The sample is dominated by various *Luticola*, *Hantzschia*, *Pinnularia* and *Humidophila* species.



Figs 49–70. *Humidophila keiliorum* sp. nov. type population from Byers Peninsula, Livingston Island. Fig. 49. LM girdle view. Figs 50–64. LM of valve views. Figs 65–66. SEM of girdle views. Figs 67–68. SEM of an entire valve (externally). Fig. 68. Arrows indicate interruption of mantle areolae clearly at the apices. Fig. 69. SEM of internal valve view. Fig. 70. SEM of internal view showing a detail of the distal raphe ending and the interruption in the mantle areolae. Scale bars = 10 µm (Figs 49–69); 1 µm (Fig. 70).

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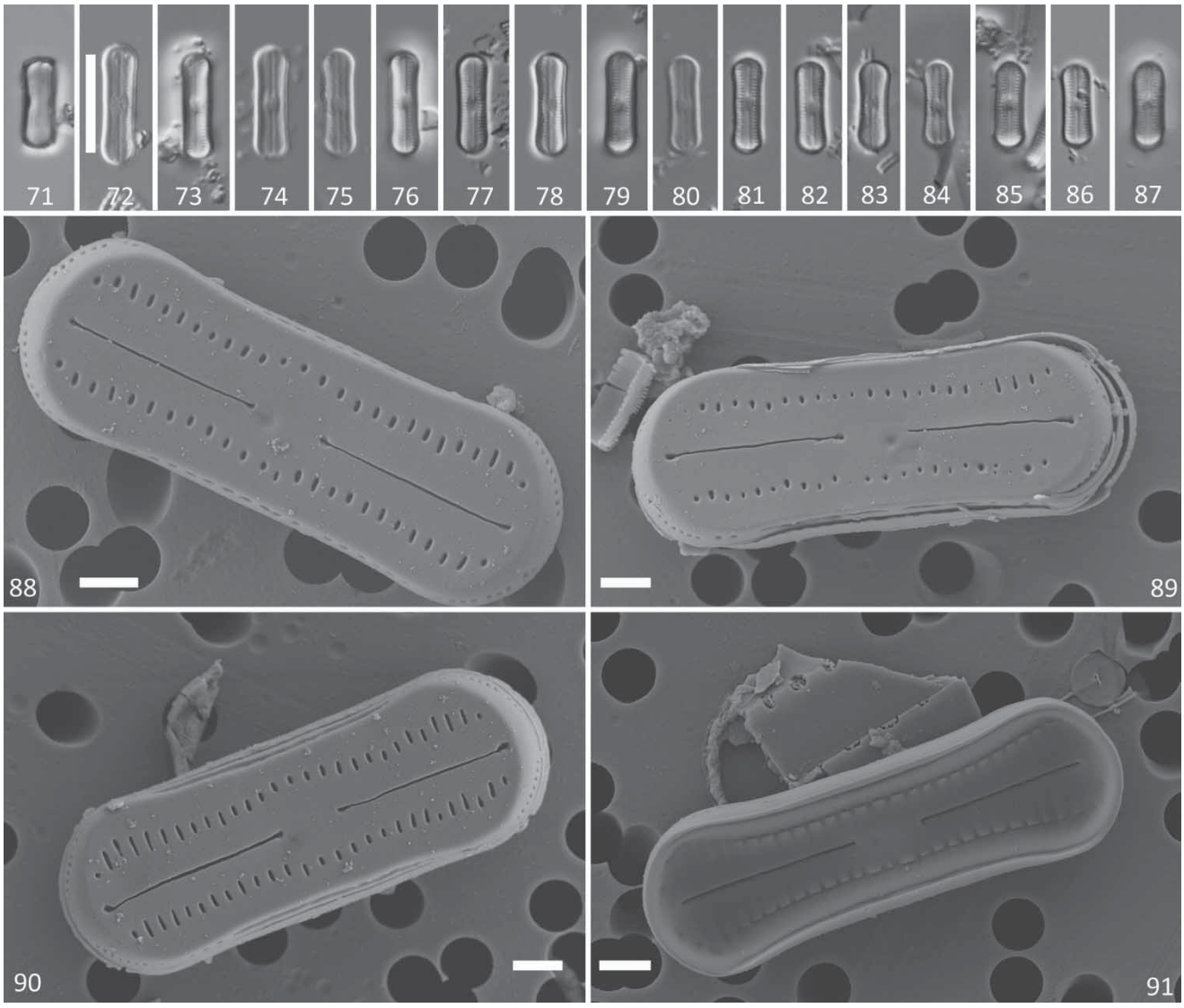

Figs 71–91. *Humidophila deceptionensis* sp. nov. type population from Deception Island. Fig. 71. LM girdle view. Figs 72–87. LM valve views. Figs 88–90. SEM of an entire valve (externally). Fig. 91. SEM of internal valve. Scale bars = 10 µm (Figs 71–87); 1 µm (Figs 88–91).

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Taxonomic remarks

Humidophila keiliorum was previously reported as *D. arcuata* (now *H. arcuata*), but the latter lacks the typical groove in which the mantle areolae are located. Moreover, in *H. arcuata*, the mantle areolae entirely surround the apices, whereas in *H. keiliorum* the mantle areolae are interrupted (Figs 67–68). The most similar taxon is *H. australoshetlandica* (see above), and it is very hard to separate these taxa with LM. A useful feature is the presence of the small depressions next to the external raphe endings in *H. keiliorum*, which are even visible in LM. In SEM, both taxa are easily separated based on the mantle groove and the interruption in the mantle areolae at the apices in *H. keiliorum*. The latter is missing in *H. australoshetlandica*, and there is a slight difference in valve dimensions, with *H. keiliorum* being larger, with fewer striae (27–30 vs. 31–32 in 10 µm) and more parallel valve margins.

***Humidophila deceptionensis* Kopalová, Zidarova & Van de Vijver sp. nov. (Figs 71–91)**

Holotype (here designated). BR–4381 (Botanic Garden Meise, Belgium).

Isotype (here designated). Slide PLP–266 (University of Antwerp, Belgium).

Type locality. Deception Island, South Shetland Islands (62°58′24.5″S, 60°43′03.2″W), sample D13, leg. R. Zidarova, coll. date: 21/01/2013. The sample was moss growing on a rock.

Etymology. The specific epithet refers to the island from where the new species is described: Deception Island.

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Morphological observations

Light microscopy (Figs 71–91). Frustules rectangular in girdle view (Fig. 71). Valves linear with distinctly concave margins (central constriction) and broadly rounded, non-protracted apices (Figs 72–87). Valve dimensions ($n = 25$): length 9–12.5 µm, width (at the constriction) 2.70–3.10 µm. Axial area broad, linear; in larger valves visibly expanded toward the valve apices. Central area elliptical, never forming a fascia. Raphe straight with slightly expanded proximal, and inconspicuous distal, raphe endings. Striae visible in LM, 30–32 in 10 µm.

Scanning electron microscopy (Figs 88–91). Axial area very broad (Figs 88–90), almost two-fifths of the total valve width, linear, widening slightly near the apices (Figs 88, 90). Central area elliptical, weakly expanded due to the shortening of the central striae (Figs 88–90), raphe filiform. External raphe branches straight with weakly expanded, non-deflected proximal, and short distal, endings (Figs 88–90). Distal endings terminating just beyond the last striae (Figs 88–90). Striae parallel, forming an undulating series in the middle between the raphe and the valve margins, each composed of one short, usually transapically elongated areola (Figs 88–90). Mantle areolae large, clearly interrupted near the valve apices (Figs 88–90). Internally, areolae occluded by porous hymenes (Fig. 91). Internal distal raphe endings simple, terminating on very weakly developed helictoglossae (Fig. 91). Central nodule weakly developed (Fig. 91).

Ecology and distribution

Humidophila deceptionensis is found as only small populations on several islands of the South Shetland Archipelago: King George Island, Livingston Island, Deception Island. Its current distribution in Antarctica is unclear because it is possible that in the past the species was reported as *H. contenta* (= *Navicula contenta* Grunow or *Diadesmis contenta* (Grunow) D.G.Mann & Round). The largest populations were recorded on Deception Island. The type population was found among moist moss vegetation, growing on a rock inland. The sample contained other *Humidophila* taxa (*H. keliorum* and *H. inconspicua*), *Stauroneis pseudomuriella* Van de Vijver & Lange-Bertalot, *S. pseudoschimanskii* Van de Vijver & Lange-Bertalot and various *Luticola* species. Another important population was observed in almost dry soil under moss vegetation cover.

Taxonomic remarks

There are several *Humidophila* taxa that show a clear central constriction: *H. biscutella* (Gerd Moser, Lange-Bertalot & Metzeltin) R.L.Lowe et al., *H. contenta*, *H. discordabilis* (Gerd Moser, Lange-Bertalot & Metzeltin) R.L.Lowe et al., *H. paracontenta* var. *magisconcava* (Lange-Bertalot) R.L.Lowe et al., *H. simplex* (E.Reichardt) R.L.Lowe et al. and *H. tahitiensis* (Lange-Bertalot & Werum) R.L.Lowe et al. *Humidophila contenta* can be easily recognized by its rectangular fascia interrupting the striae near the central area, its T–shaped proximal and distal external raphe endings and uninterrupted mantle areolae around the apices (Werum & Lange-Bertalot 2004, plate 56). *Humidophila discordabilis*, described from New Caledonia (Moser et al. 1998, plate 27, figs 10, 13), is much larger (length 16–20 µm, width 5.5–6.5 µm), also shows a fascia and mantle areolae that continue around the apices, unlike our new taxon which has an interruption in the mantle areolae near the apices. Two other taxa, *H. tahitiensis* and *H. simplex*, are only slightly similar, mostly because of their valve outline. The first has large T–shaped external raphe endings, quite transapically elongated areolae, a clear fascia and continuous mantle areolae (Lange-Bertalot & Werum 2001, figs 79–80), whereas the latter does not always have concave margins, has very short areolae and a clear fascia (Reichardt 2004, plate 7, fig. 1). Larger valves of *H. paracontenta* var. *magisconcava* show a typical fascia, whereas this is absent or reduced in smaller specimens, although in *H. deceptionensis* a fascia was never observed. Moreover, *H. paracontenta* var. *magisconcava* shows no interruption in the mantle areolae and has distinctive markings beside the proximal and distal external raphe endings (Lange-Bertalot & Werum 2001, fig. 62).

The most similar taxon is *H. biscutella* with a similar valve outline, striation pattern and mantle areolae, but a different valve width (2.0–2.5 µm vs. 2.7–3.2 µm in *H. deceptionensis*) and a much higher stria density (36–40 in 10 µm vs. 30–32 in 10 µm), making it almost impossible to discern the striae in LM, whereas they are easily discernible in *H. deceptionensis*.

Humidophila vojtajarosikii Kopalová, Zidarova & Van de Vijver sp. nov. (Figs 92–118)

Holotype (here designated). BR–4382 (Botanic Garden Meise, Belgium).

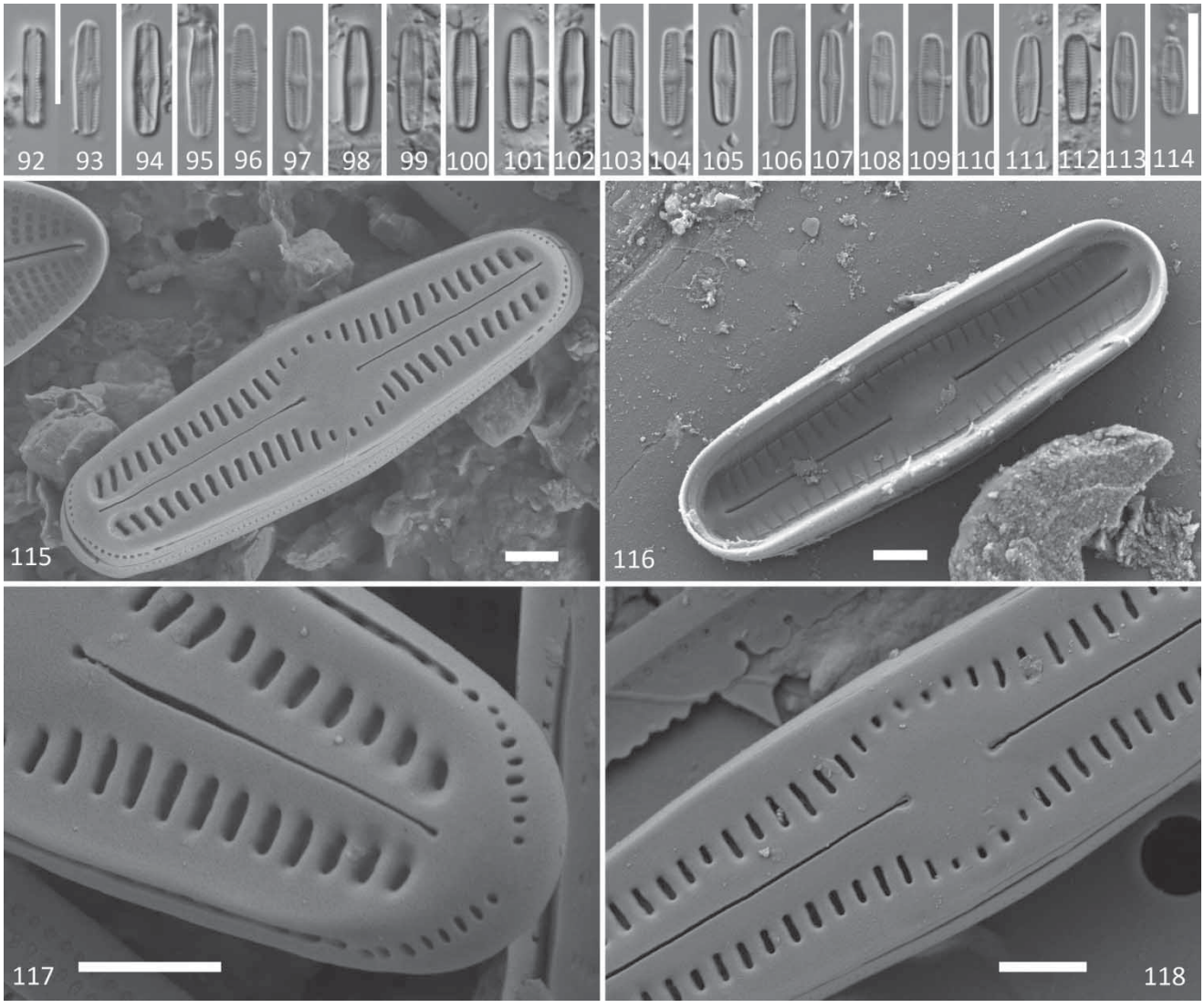
Isotype (here designated). Slide PLP–267 (University of Antwerp, Belgium).

Type locality. Byers Peninsula, Livingston Island, South Shetland Islands (62°39′11.4″S, 61°06′19.4″W), sample BYM–021, leg. B. Van de Vijver, coll. date: 10/01/2009. The sample was taken from submerged mosses at the edge of a small lake.

Etymology. The species is named in memory of a dear friend and colleague, Prof. Vojta Jarošík.

Morphological observations

Light microscopy (Figs 92–114). Frustules rectangular in girdle view (Fig. 92). Valves linear with distinctly convex margins (gibbous central part) and broadly rounded, non-protracted apices (Figs 93–114). Valve dimensions ($n = 25$): length 7.5–12.5 µm, width (at the constriction) 2.5–3.0 µm. Axial area relatively broad (Figs 93–114).



Figs 92–118. *Humidophila vojtajarosiki* sp. nov. type population from Byers Peninsula, Livingston Island. Fig. 92. LM girdle view. Figs 93–114. LM valve views. Fig. 115. SEM of an entire valve (externally). Fig. 116. SEM of valve interior. Fig. 117. SEM detail of interrupted terminal point endings. Fig. 118. SEM detail of central area. Scale bars = 10 µm (Figs 92–114); 1 µm (Figs 115–118).

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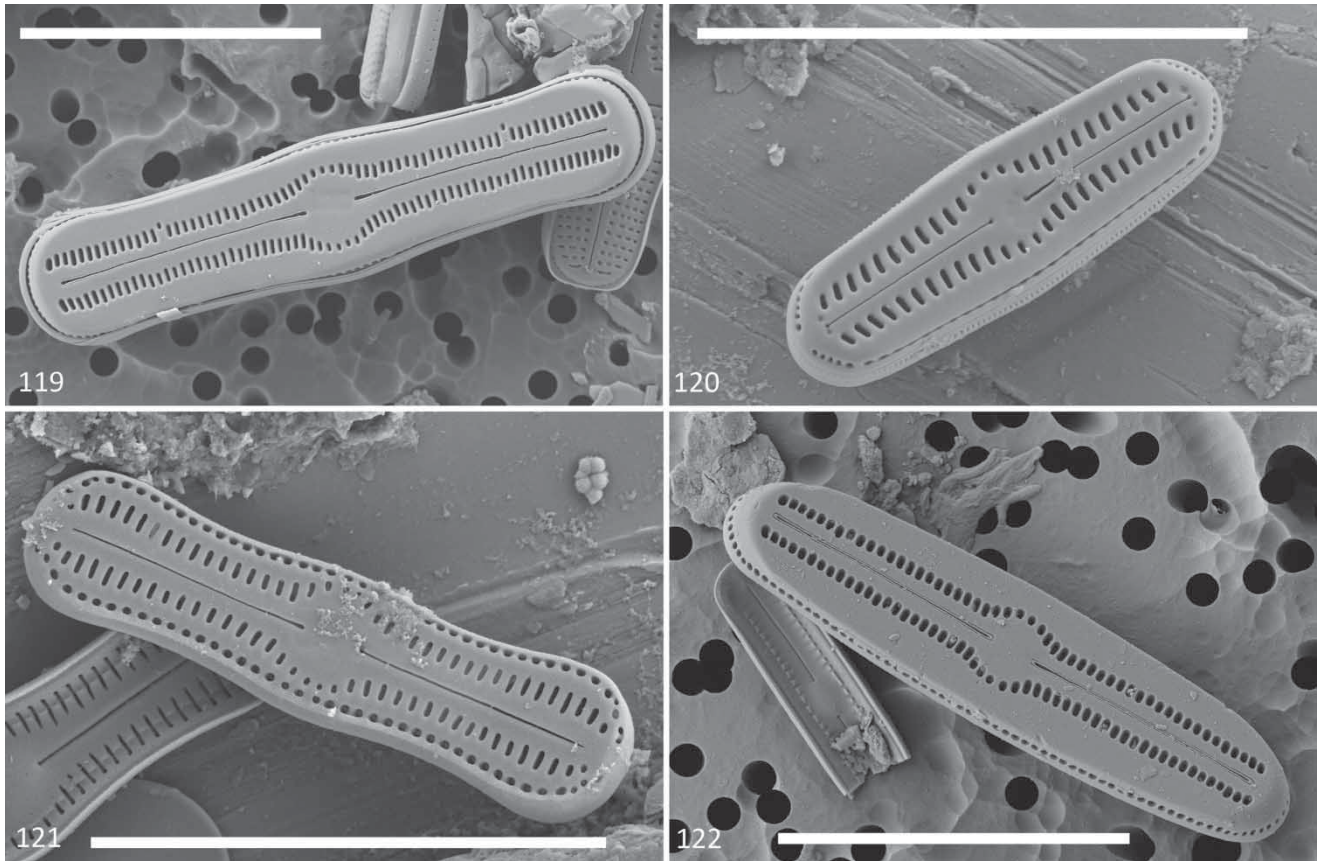
Central area round, slightly widened due to the shortening of the central striae (Figs 93–114), never forming a fascia. Raphe filiform. Striae visible in LM, 30–32 in 10 µm, weakly radiate throughout the entire valve.

Scanning electron microscopy (Figs 115–118). External raphe branches straight with weakly expanded, non-deflected proximal, and short distal, endings (Figs 115, 117–118). Distal endings terminating shortly beyond the last striae (Figs 115, 117). Striae almost parallel to weakly radiate, located in a shallow depression and composed of one elongated areola (Fig. 115). Areolae shortened near the central area (Fig. 118). Mantle areolae opening in a longitudinal groove running from one apex to the other. Grooves disappearing near the apices, showing the areolae on the mantle, clearly interrupted at the apices (Fig. 117). Internally, striae occluded by porous hymenes (Fig. 116). Internal distal raphe endings simple, terminating on very weakly developed helictoglossae (Fig. 116). Central nodule weakly developed (Fig. 116).

Ecology and distribution

Humidophila vojtajarosikii is a common species on both James Ross Island and the South Shetland Islands: Livingston Island (reported as *Diadesmis* sp2 in Kopalová et al. 2014), King George Island, Nelson Island and Deception Island (Zidarova, pers. obs.), although rarely exceeding 10% of the total diatom count in populations. The largest populations were observed in wet terrestrial to submerged aquatic moss vegetation in and around larger lakes.



Figs 119–122. SEM external valve views of four similar species. Fig. 119. *Humidophila arcuata*. Fig. 120. *Humidophila comperei*. Fig. 121. *Humidophila ingeae*. Fig. 122. *Humidophila subantarctica*. Scale bars = 10 µm.

The new taxon seems less abundant in purely aquatic conditions and the rare samples in which it was found all originate from lakes with extensive moss coverage on the shores. Other typical taxa in the samples include other *Humidophila* taxa, such as *H. inconspicua* Kopalová & Van de Vijver and *H. sceppacuerciae* and several *Psammothidium* species [*P. abundans* (Manguin) Bukhtiyarova & Round, *P. germainii*, *P. papilio*]. A relatively large population of *H. vojtajarosikii* was also found on King George Island in a sample of endolithic algae, taken from a costal rock not far from 'Bellingshausen' Russian Station on Fildes Peninsula.

Taxonomic remarks

The taxon most similar to *H. vojtajarosikii* is *H. comperei* and, based on LM observations, it is very hard to tell these taxa apart. The main difference is the presence of shallow, round depressions beside the distal raphe endings in *H. comperei*, giving the impression that *H. comperei* has T–shaped raphe endings (Fig. 120), entirely lacking in *H. vojtajarosikii*. In addition, the striae in *H. vojtajarosikii* are occasionally somewhat sunken, whereas this is not the case in *H. comperei* (Le Cohu & Van de Vijver 2002). *Humidophila templiniana* (Rumrich et al.) R.L.Lowe et al. typically has parallel margins and a strictly linear valve outline compared with the more lanceolate outline in *H. vojtajarosikii* (Rumrich et al. 2000, plate 82, fig. 16).

Discussion

Diatoms (Bacillariophyta) are probably the most species-rich group of algae, with tens of thousands of species (Mann 1999), and one of the most common algal groups in the Antarctic Region (Jones 1996, Van de Vijver & Beyens 1999, Sabbe et al. 2003). For a long time, diatoms were considered to be a protist group whose species were cosmopolitan in distribution, according to the ubiquity hypothesis (Finley 2002). The main objective of this study was to revise the diversity of *Humidophila* species of two islands from the Maritime Antarctic Region, based on a modern morphological concept. This resulted in the description of several new taxa whose identification was based on the morphological features of their silica valves using LM and SEM, taking into account the natural variability within and among populations. The description of five new *Humidophila* taxa from the South Shetland Islands and James Ross Island brings the total species

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richness for the genus in the (sub-)Antarctic region up to 21, making it one of the most diverse genera in this region after *Luticola* (44 taxa: Van de Vijver et al. 2006, 2011, Van de Vijver & Mataloni 2008, Kopalová at al. 2011, Zidarova et al. 2014a) and *Pinnularia* (28 taxa: Van de Vijver & Zidarova 2011, Zidarova et al. 2012). Of the *Humidophila* taxa in the (sub-)Antarctic Region, 17 (or ~ 81%) have not been found outside (sub-)Antarctica. The high percentage of presumably endemic *Humidophila* taxa is not surprising, since similar trends have already been observed for several other genera in Antarctica (e.g., *Muelleria* [Spaulding et al. 1999], *Pinnularia* [Zidarova et al. 2012], *Stauroneis* [Van de Vijver et al. 2005, Zidarova et al. 2014b], *Luticola* [Kopalová et al. 2011]).

Based on our observations, it is clear that, apart from a few species such as *H. tabellariaeformis* (Krasske) Lowe et al. and *H. paracontenta*, *Humidophila* shows a clear biogeographical pattern in the Antarctic Region. The highest diversity is reached in the southern Indian Ocean islands (Van de Vijver et al. 2002, Van de Vijver et al. 2005), which is probably related to the greater diversity in aerophilic microhabitats, followed by the Maritime Antarctic Region (represented by the South Shetland Islands and James Ross Island) (Kopalová et al. 2013). The Antarctic Continent has very low diatom diversity (Jones 1996).

The biogeography of all (sub-)Antarctic *Humidophila* taxa is still insufficiently known, mainly due to taxonomic force-fitting (Tyler 1996) in the past, which has obscured species distributions, together with perhaps the inadequate number of studies in some regions (i.e., southern Atlantic Ocean Islands). The low diversity on South Georgia and the South Orkney Islands is probably the result of undersampling, because almost all published records for these islands date from the period before the current phase of taxonomic revision started, when a different (i.e., broader, more force-fitted) species concept was commonly used (Van de Vijver & Beyens 1996, Håkansson & Jones 1994). However, even based on our current knowledge (Table 1) it is obvious that most taxa show a very restricted distribution: to date, seven *Humidophila* species have been observed with certainty only on the islands of the southern Indian Ocean and never in other (sub-)Antarctic regions (Van de Vijver et al. 2002), whereas all five newly described species are only found in the Maritime Antarctic Region (Table 1). Only one, *Humidophila nienta* (J.R.Carter) R.L.Lowe et al., is common to both the Maritime Antarctic Region and the sub-Antarctic islands in the southern Indian Ocean (Lowe et al. 2014), and only two taxa, *Humidophila australis* (Van de Vijver & Sabbe) R.L.Lowe et al. and *Diadesmis gallica* W.Smith, have confirmed distributions in both Maritime Antarctic and the Antarctic Continent (Van de Vijver et al. 2010). These findings prove once again that there is a highly specific diatom flora not only in the (sub-)Antarctic Region, but also in its different provinces.

This paper is a step forward in our attempt to understand the taxonomic and biogeographical characteristics of the diatom flora of the entire Antarctic Region. Although only two islands were considered, the results are valuable for understanding the refined taxonomy and biodiversity of the Antarctic diatom flora, which can be used further for biogeographical, ecological and paleo-ecological research.

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