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New and interesting aerial diatom assemblages from southwestern Iceland

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Abstract

Examination of algal assemblages from aerial environments around the globe, especially those from pseudoaerial habitats found on moistened rocks underneath waterfalls or around springs and seeps, reveals the presence of unique diatom floras. Yet, diatom assemblages from northern regions like Iceland remain understudied, especially those from the volcanic rock outcrops and boulders that create euaerial habitats where biota receive moisture from the atmosphere or the rock itself. During the summers of 2013 and 2015, we examined the biodiversity of mostly euaerial, but also pseudoaerial, diatom assemblages collected from volcanic rock outcrops or large boulders on the landscape from southwestern Iceland. We used light and scanning electron microscopy to document the biodiversity of common, smaller, new, or interesting specimens, such as *Humidophila* and *Eunotia*. We describe one new *Humidophila* species, *H. eldfjallii sp. nov.*, with triundulate valve margins and include information on another unidentified taxon, *Humidophila* sp. 1, naviculoid in shape with tapering to rounded ends, continuous striae through the length of the valve, and a circular central area. We formally transfer *Diadesmis contenta* var. *biceps* to *Humidophila biceps*. To correct the nomenclature, we recognized *Humidophila parallela* at the species level. Relative abundance estimates of diatom populations provided further characterization of the assemblages on these habitats. *Humidophila* taxa, especially *H. gallica* dominated the diverse diatom flora. We discuss adaptations for survival with access to mostly atmospheric water. The diatom flora described here adds to the flora for this region, highlights the diversity of diatom assemblages that can inhabit euaerial environments, and provides evidence of adaptive success of diatoms in extreme habitats with limited moisture and nutrients.

Keywords: biogeography, *Diadesmis*, *Diatomella*, euaerial, *Eunotia*, Hengill, *Humidophila*, *Hygropetra*, Iceland, *Orthoseira*, pseudoaerial, *Staurosirella*, volcanic rock, wet walls

Introduction

In the last decade or so, despite increased interest in understanding the biogeography and endemism of aquatic microorganisms, including diatoms, northern regions like Iceland and the Arctic remain underexplored (Bouchard *et al.* 2004, 2018, Pointing *et al.* 2015, Hodač *et al.* 2016, Gibbons 2017, Jung *et al*. 2018). Organisms inhabiting areas with relatively low average temperatures experience faster adaptive processes due to the extreme climatic changes compared to other regions (IPCC 2014). The more isolated landscapes of arctic islands promote the presence of unique and often endemic diatoms. For example, over one-third of the diatom taxa collected from lakes and ponds on Spitsbergen of the Svalbard Archipelago, not identifiable to species (Pinseel *et al.* 2017a), will require taxonomic descriptions moving forward (e.g. Pinseel *et al.* 2014, Pinseel *et al.* 2017b). Several species of *Stauroneis* Ehrenberg 1842, including many described as new to science, occurred only in Arctic and not in Sub-Antarctic and Antarctic regions (Van De Viver *et al.* 2004, Kopalová *et al.* 2012). While less is known for the diatom flora from the volcanic landscapes of the high latitude island of Iceland, the stable, unproductive habitats with low anthropogenic disturbance likely support endemic diatom species (Huston 1994, Kilroy *et al.* 2007, Johansen 2010). However, factors like increased tourism, and dispersal by wind and birds (Kristiansen 1996) may promote broader distribution patterns for microbiota. Indeed, as studies increase in Arctic areas, some evidence indicates circumpolar distribution patterns for some diatom taxa (Pla-Rabés *et al.* 2016). Increased taxonomic and biodiversity knowledge of diatoms from Arctic regions, like Iceland, will improve

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understanding of patterns in biogeography and help track changes in the environment associated with climatic shifts or anthropogenic stressors, especially in aerial habits that interface directly with the atmosphere.

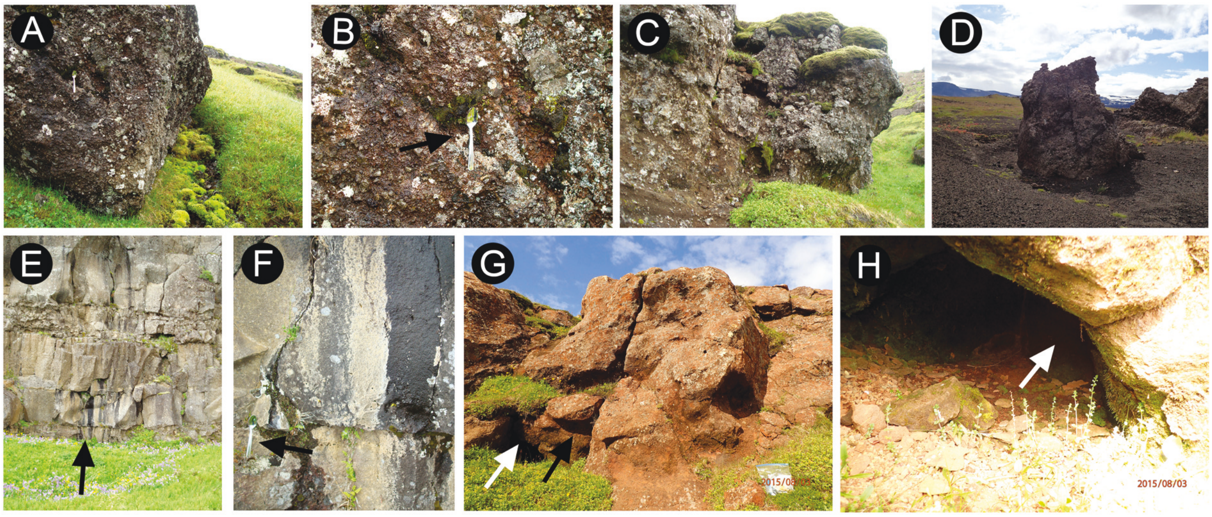

FIGURE 1. Example of wetwall (WW) habitats sampled (arrows; spoon for scale, details in Table 1). Images A–D, G–H. show euaerial sites and E–F. a pseudoaerial site. From the Hengill watershed: A–B. WW 1; C. WW 3; G. WW 52 (black arrow); G–H. WW 53 (white arrow). From along Landmannaleið road: D. near Hekla road turn off (WW 50). From the Þingvellir rift valley: E–F. a pseudoaerial site (WW 42).

The variety of terms applied to diatom assemblages exposed to the atmosphere, such as terrestrial (Fritsch 1922), semiterrestrial (adaptation of marine diatoms to dried up saline pools, Sims *et al.* 2006), aeroterrestrial (Reisser & Houben 2001, Karsten *et al.* 2007), subterranean (Falasco *et al.* 2014), aerial (Johansen 2010), and subaerial (living on stable surfaces above ground, Nienow 1996) differentiate habitats by water source and other environmental conditions. Within these categories of aerial habitats, explorations of pseudoaerial algae, those from mostly moistened rocks underneath waterfalls or around springs and seeps (Johansen 2010) have occurred from of a variety of locations (e.g. Johansen *et al.* 1983, Rushforth *et al.* 1984, Lowe *et al.* 2007, Furey *et al.* 2011). In comparison, euaerial algae, those that inhabit raised, prominent objects that receive moisture exclusively from the atmosphere (Johansen 2010), remain understudied, especially for those on the exposed rocks and boulders in northern regions like Iceland. Aerial environments support diverse diatom assemblages (Rushforth *et al.* 1984) due to the structural and morphological heterogeneity of the exposed rock surfaces (Bergey 2005, Lowe *et al.* 2007), which might aide survival on these exposed habitats.

Euaerial assemblages can experience frequent and rapid changes in temperature, strong winds, stress from direct and radiant heating, intense solar radiation, and shifts in water availability (Karsten *et al*. 2007). Thus, euaerial diatoms must adapt to survive desiccation. While motile diatoms can actively search for refuge in surrounding microhabitats like moist leaf litter or bryophytes (Ledger *et al.* 2008, Souffreau *et al.* 2010, 2013), or retreat deeper into subsurfaces of biofilms, soils, or vegetation where moisture still exists (Evans 1958, 1959), the euaerial, epilithic environment constrains these response options to patches of lichen and bryophytes available on exposed rock. The porous and fractured nature of volcanic rock may provide additional protective habitat complexity and be a source of some moisture. Alternatively, the surrounding atmosphere or the habitat itself may act as a source of moisture for euarial diatoms. Euaerial diatom assemblages of northern ecoregions often experience snow cover, rain, and/or fog most of the year, which may provide a sufficient source of moisture (Souffreau *et al*. 2010). Periods of evaporation during the day, especially during the long summer days, might lead to partial desiccation on exposed lithic surfaces. On an individual level, aerial diatoms could produce heavily silicified valves and occluded punctae and areolae that minimize water loss (Lange-Bertalot *et al.* 2003, Lowe *et al.* 2007), or develop resting stages (Hollibaugh *et al.* 1981, Poulíčková *et al.* 2008, Souffreau *et al.* 2013). Souffreau *et al.* (2013) demonstrated that resting stages of diatoms, especially in terrestrial taxa, could survive desiccation.

In contrast to moisture challenges of euaerial habitats, absorption and retention of heat by the rock could stimulate growth and moderate temperature fluctuations. To support growth, aerial algae, adapted to low nutrient conditions (Johansen 2010), may periodically take advantage of soluble volcanic ash rich in essential nutrients like nitrogen (N) and phosphorus (P) if present in snow melt (Lutz *et al.* 2015). Though more often, these nutrients would remain inaccessible to euaerial species, but available to primary producers close to the ground in contact with melting of ice.

On a broad scale, the diversity of euaerial diatom assemblages depends on abiotic (e.g. light, moisture, pH, etc.) and biotic (competition and grazing) factors. On a localized scale, euaerial diatoms need to respond quickly to shifts in these same conditions and to microhabitat variations.

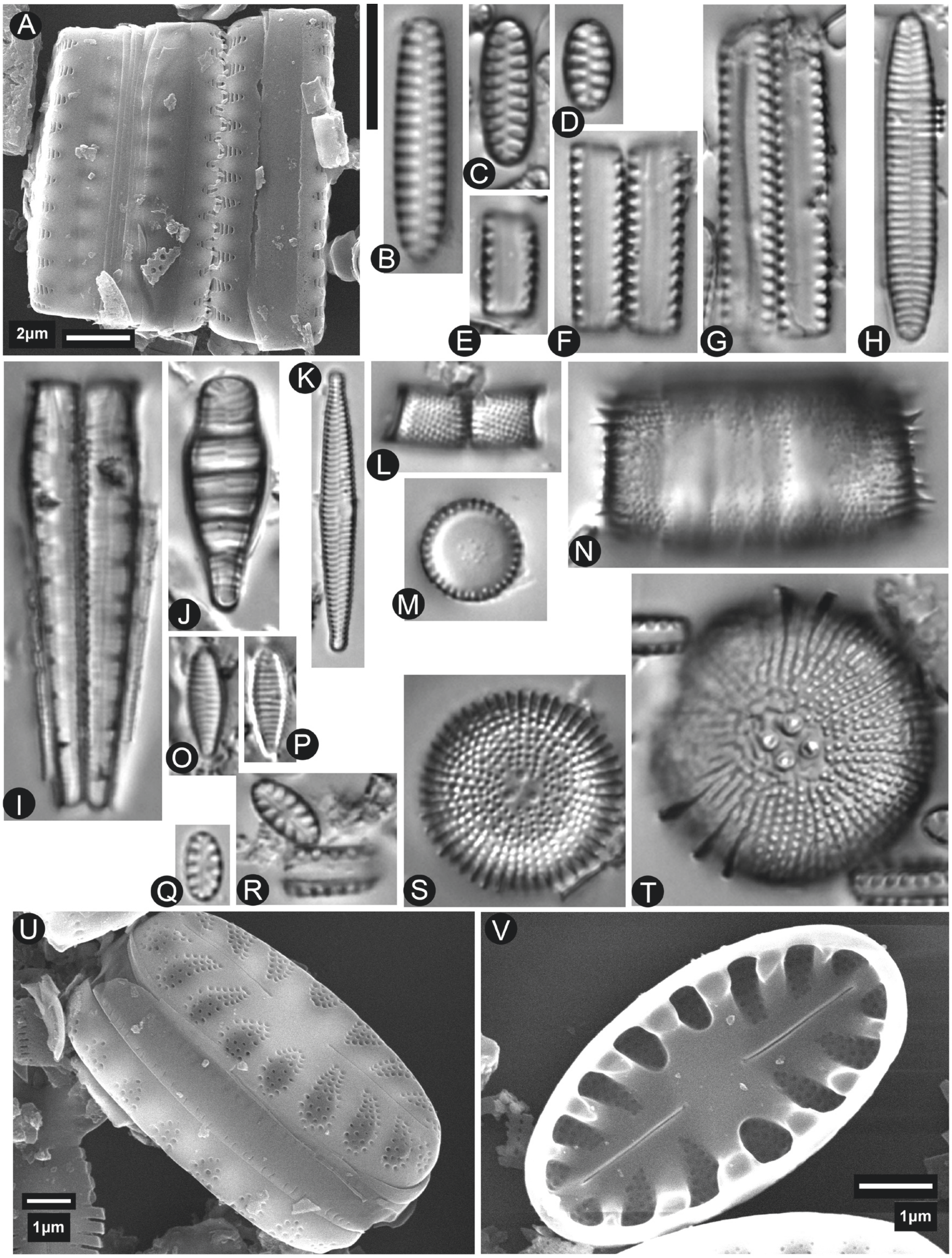

FIGURE 2. Light (B–T) and SEM (A, U–V) microscopy images of diatom assemblages from aerial sites in southwestern Iceland. A–G. *Staurosirella neopinnata*: A. external, girdle view of two linked frustules, left frustule shows the completed synthesis of new valves within the frustule, B–D. size series in valve and E–G. girdle view, F and G. two linked frustules; H. *Fragilaria nitzschioides*: valve view; I–J. *Meridion circulare* var. *constrictum*: I. 2 frustules in girdle view, J. valve view; K. *Fragilaria perminuta*: valve view; L–M. *Aulacoseira alpigena*: L. girdle view and M. valve view; N, S–T. *Orthoseira roeseana*: N. girdle view with irregular linking spines and longitudinal areolae on the valve mantle, S–T. Valve view with 3 to 4 carinoportulae; O–P. *Stauroforma atomus*: valve views; Q, R, U–V. *Hygropetra balfouriana*: Q–R. valve view, U. SEM of a tilted frustule with both valve and girdle views visible, U. shows the nature of the striae, and raphe, V. internal view. LM scale bar = 10 μm, SEM scale bars as shown.

TABLE 1. Location and general description of wet wall (WW) sampling sites, organized by general location * = general coordinates for the Hengill Watershed. ** = streams (S) where numbers follow a previously used system (Woodward *et al.*, 2010); **Moisture** = visual moisture assessment at the time of sampling. **E** = euaerial. **P** = pseudoaerial. All sites were designated euaerial, with the exception of Sites WW 20, 41 and 42 as the presence of some dripping water categorizes them as pseudoaerial.

WW Sample ID #	Sampling Date	Region Location	Coordinates (degrees min sec)		Elev. (m.a.s.l.)	Sample Location**	Sample Descriptions	Moisture	Aerial
1 (**Fig. 1 A–B**)	11-Jul-2013	Hengill watershed	*N 64 3 23.0	W 21 17 1.0		large boulder adjacent to stream 8 (S8); ~ 1m up	scrape; lichen squeeze	damp	E
3 (**Fig. 1 C**)	11-Jul-2013	Hengill watershed	*N 64 3 23.0	W 21 17 1.0		large boulder near S8 & small tributary	scrape; bryophyte squeeze	damp	E
4	11-Jul-2013	Hengill watershed	*N 64 3 23.0	W 21 17 1.0		large boulder near S9	scrape; lichen/ bryophyte squeeze	damp	E
5	11-Jul-2013	Hengill watershed	*N 64 3 23.0	W 21 17 1.0		large boulder near S9	scrape; lichen squeeze	damp	E
16	11-Jul-2013	Hengill watershed	*N 64 3 23.0	W 21 17 1.0		rock outcrop near top of S8	scrape; bryophyte squeeze	near splash zone; damp	E
17	11-Jul-2013	Hengill watershed	*N 64 3 23.0	W 21 17 1.0		large boulder near top of S9	scrape; lichen/ bryophyte squeeze	damp	E
20	14-Jul-2013	Hengill watershed	*N 64 3 23.0	W 21 17 1.0		large boulder near Sll-lower reach; same boulder other side of WW 21	scrape; lichen/ bryophyte squeeze	damp/ dripping	P
21	14-Jul-2013	Hengill watershed	*N 64 3 23.0	W 21 17 1.0		large boulder near Sll-Lower; other side of WW 20 boulder	scrape; lichen squeeze	dry	E
22	14-Jul-2013	Hengill watershed	*N 64 3 23.0	W 21 17 1.0		large boulder downstream sites WW 20 & 21	bryophyte squeeze	wet	E
25	14-Jul-2013	Hengill watershed	*N 64 3 23.0	W 21 17 1.0		rock outcrop near S8 and S9	scrape; lichen/ bryophyte squeeze	damp	E
38	14-Jul-2013	Hengill watershed	*N 64 3 23.0	W 21 17 1.0		rock face river right main channel by parking	scrape; bryophyte squeeze	dry	E
52 (**Fig. 1 G**)	16-Aug-2015	Hengill watershed	N 64 3 24.1	W 21 17 21.6	382	underside of boulder	scrape; bryophyte squeeze	dry/slightly damp	E
53 (**Fig. 1 G, H**)	16-Aug-2015	Hengill watershed	N 64 3 24.1	W 21 17 21.9	381	small “cave” - boulder underside	scrape; lichen/ bryophyte squeeze	damp	E
54	16-Aug-2015	Hengill watershed	N 64 3 23.3	W 21 17 26.2	366	underside of boulder	scrape; lichen/ bryophyte squeeze	slightly damp	E
55	16-Aug-2015	Hengill watershed	N 64 3 23.5	W 21 17 25.6	375	underside of boulder	scrape; bryophyte squeeze	slightly damp	E
39	17-Jul-2013	Sporhellan	Not available	Not available		rock wall face Sporhellan by parking area	scrape; bryophyte squeeze	damp	E
40	17-Jul-2013	Þingvellir rift valley	N 64 16 15.5	W 21 6 37.0	96	rock wall face just after ice-cream shop	scrape; bryophyte squeeze	damp	E
41	17-Jul-2013	Þingvellir rift valley	N 64 16 14.6	W 21 6 37.8	131	large boulder	scrape; bryophyte squeeze	dripping	P
42 (**Fig. 1 E–F**)	17-Jul-2013	Þingvellir rift valley	N 64 16 2.0	W 21 6 56.6	131	rock wall face	scrape	dripping	P
43	17-Jul-2013	Þingvellir rift valley	N 64 15 58.5	W 21 7 2.3	141	rock wall face	scrape	damp	E
50 (**Fig. 1 D**)	2-Aug-2015	Landmannaleið, before Fjallabak	N 64 4 59.9	W 19 37 44.3	446	large boulder along Landmannaleið road; near Hekla road turn off	scrape; lichen/ bryophyte squeeze	dry; soil moist to touch	E
51	2-Aug-2015	Landmannaleið	N 64 4 20.7	W 19 31 43.6	392	rock crevice on large boulder 15 to 20 m from the road	scrape; lichen/ bryophyte squeeze	dry soil but moist to touch	E

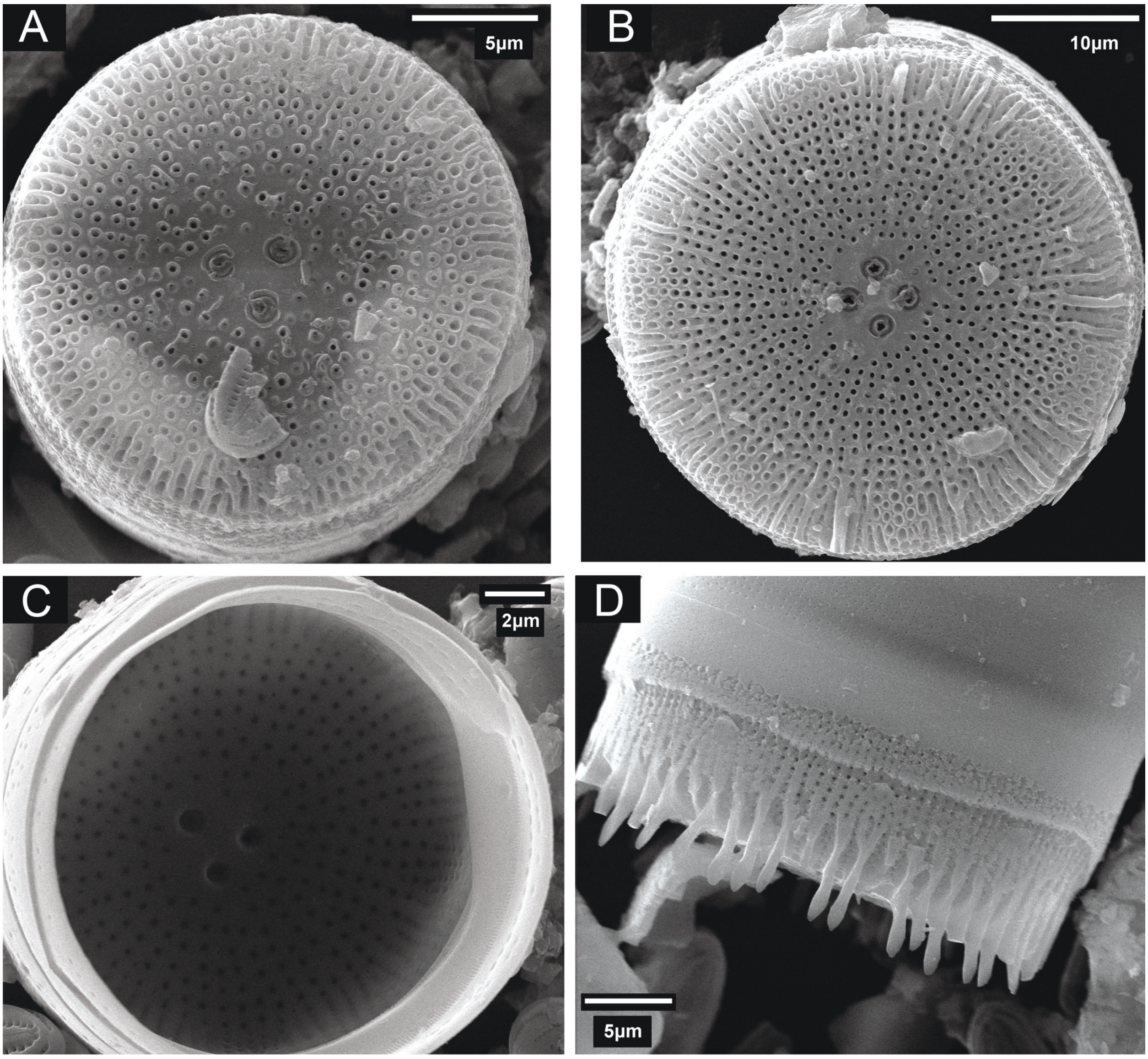

FIGURE 3. SEM microscopy images of aerial diatom assemblages from southwestern Iceland**.** A–D. *Orthoseira roeseana*: A–B. external valve view with 3 and 4 carinoportulae in the center with a rim, and uniseriate striae, C. internal valve view shows the simple opening of the carinoportulae, D. external view of valve mantle and part of the girdle show the spatulate spines and irregular girdle bands. Scale bars as shown.

Early examination of Icelandic algae that included diatoms tended to target terrestrial areas, primarily moist soils and vegetation (e.g. Broady 1978) and less so exposed epilithic habitats. Some sampling expeditions to Iceland, e.g. by Petersen (1928a, b), and Foged (1974), included some algal samples from rock outcrops. Hallgrímsson (2007) compiled a checklist of algal taxa from Iceland that included those from terrestrial and aerial environments from these earlier surveys (i.e. by Petersen & Foged). Despite this, current diatom records from Iceland total 736 (Foged 1974, Ettl & Gärtner 1995, Glushchenko *et al.* 2017). In known databases aerophytic diatoms from arctic areas include 15 records, with only 2 aerophytic diatom records from Iceland. Similarly, reports of terrestrial diatoms total 57, with only 1 report from Iceland (Guiry & Guiry 2018). Public databases contain no records of diatom species classified and defined here as pseudoaerial, subaerial, or euaerial (Guiry & Guiry 2018). Extensive research on euaerial algae from Iceland remains to be completed. Microscope resolution and technological limitations of the earlier surveys hindered the observation and documentation of taxonomically relevant morphological details of aerial diatoms, especially for small taxa.

This research focuses on euaerial diatoms able to survive on exposed volcanic rocks, without constant trickling of water, but with partial cover by lichens and mosses. Here we document the biodiversity of diatom taxa from predominantly euaerial habitats from southwestern Iceland, primarily in the Hengill watershed, but also Sporhella, Þingvellir Rift Valley, and the southern Highlands. We propose one new *Humidophila* Lowe, Kociolek, Johansen, Van de Vijver, Lange-Bertalot et Kopalová (2014: 352) species, include information on an unidentified *Humidophila* taxon, and formally transfer *Diadesmis contenta* var. *biceps* (Grunow in Van Heurck 1880: expl. Pl. XIV, fig. 31B) P.B. Hamilton in Hamilton *et al.* (1992: 30) to *H. biceps* comb. nov. We include scanning electron microscope (SEM) micrographs of common, smaller, new or interesting specimens, such as *Humidophila*, *Orthoseira* Thwaites (1848: 167), and *Eunotia* Ehrenberg (1837: 44) to document taxonomically relevant internal and external morphological characteristics. For dominant taxa documented, we consulted available current and historic taxa lists with previous analyses of aerial environments in Iceland. Relative abundance estimates provide additional ecological information. We discuss the unique ecology of these habitats.

Materials and methods

Diatom collection and analysis. We collected primarily euaerial and a couple of pseudoaerial algal assemblages during the summer of 2013 (x16) and 2015 (x6) from rock outcrops or large boulders on the landscape from southwestern Iceland (wetwall sites (WW); Fig. 1, Table 1). We sampled primarily from euaerial habitats in the Hengill watershed, a volcanic area with hyaloclastite rocks ~30 km east of Reykjavík, but also from Sporhella, Þingvellir rift valley, and along Landmannaleið in the southern part of the Highlands. We categorized two sites with some dripping water (WW 41 and 42) and one (WW 20) with a slight drip as more pseudoaerial, though the water drip may be ephemeral. We scraped epilithic surfaces with a spoon and/or squeezed/shook material from bryophytes or lichen when present (Fig. 1). When detectable, we recorded GPS coordinates and elevation of sampling locations (Table 1). We noted general moisture conditions (dry, damp to touch, dripping water, splash zone, wet), but were not able to assess pH or nutrient levels directly associated with the sampling sites. We examined samples under the microscope within 24 hrs of collection to confirm the presence of live diatoms as indicated by the presence of plastids or movement.

For identification, we cleaned collected material in boiling nitric acid to remove organic material (Patrick & Reimer 1966, Round *et al.* 1990), and air-dried cleaned material onto coverslips. We stored slides and cleaned material in P.C. Furey's personal collection, St. Catherine University, and deposited material at the Georgia College and State University Natural History Museum, diatom collection (GCAC7001). We made diatom slides using Naphrax® mounting medium (RI = 1.7). We examined the slides with differential interference contrast optics under oil immersion at 1000x on a Leica DM LS2 (Iowa Lakeside Lab), a Leica DM2500 photomicroscope with a Leica DFC295 Camera (Georgia College and State University), and a Leica DM6B photomicroscope with a Leica DFC7000 GT Camera (St. Catherine University) (Leica Microsystems, Wetzlar, Germany). We determined relative abundance of diatom taxa from the 2013 samples. We counted 600 valves when possible (i.e. when the cell density on the slide was high enough), otherwise we counted a minimum of 300 valves. For sites with particularly sparse numbers of diatoms, either we counted 2 whole slides or 3 additional transects beyond the count of 45. For assessment of internal and external ultrastructure, we mounted coverslips onto aluminum stubs and sputter coated with 10 nm of AuPd (Postek *et al.* 1980) for examination under a JEOL 6610LV SEM (JEOL USA Inc.). We further documented frustular ultrastructure with a JEOL JSM-IT100 SEM at Georgia College and State University. We deposited holotype slides and materials at the Georgia College and State Natural History University Museum Algae Collection.

Taxonomic keys used in diatom identification included, but were not limited to: Foged (1953, 1955, 1964, 1981), Lange-Bertalot *et al.* (2003, 2011), Patrick & Reimer (1966, 1975) and Krammer & Lange- Bertalot (1986, 1988, 1991a, 2000). Specific sources also used included literature such as Van de Vijver *et al.* (2004) from the Arctic and Antarctic, and Veselá & Johansen (2009) for European regions. For specific genera, we consulted other taxonomic texts like Krammer (2000), Lowe *et al.* (2014), Zidarova *et al.* (2010, 2012) and Levkov *et al.* (2013, 2016).

We compared observations of common diatom taxa with those previously reported from terrestrial or aerial habitats in Iceland, especially by Petersen (1928a), Foged (1974), Broady (1978), Hallgrímsson (2007), and Dagsson-Waldhauserova *et al.* (2015). Terminology used followed Anonymous (1975), Ross *et al.* (1979), and Round *et al.* (1990).

Results and discussion

Samples contained many live diatoms as indicated by the presence of intact, active plastids. We also considered moving cells as alive. We identified a total of 92 diatom taxa from volcanic rock outcrops or large boulders on the landscape from southwestern Iceland. Diatoms were generally abundant in samples at sites in Hengill, but less so in those from the Þingvellir rift valley. The sample from Sporhella contained very few valves and those present primarily belonged to *Eunotia nymanniana* Grunow in Van Heurck (1881, fig. 34: 8, pro parte [left side specimen]). All sampled sites included representatives of several genera such as *Humidophila, Eunotia* and *Pinnularia* Ehrenberg (1843b: 45). All ecological niches sampled, with the exception of the site at Sporhella (WW 39) and a sparse site in Hengill (WW 21), contained the taxon *H. perpusilla* (Grunow 1860: 552) Lowe, Kociolek, Johansen, Van de Vijver, Lange-Bertalot et Kopalová (2014: 358). A total of 84% of the taxa were identified to species, with the remainder of taxa considered unknown mostly due to morphological parameters being outside of published literature. Dominance of aerophilic representatives of the genera *Humidophila* and *Eunotia* was expected, but we also documented representative high-nutrient taxa of *Nitzschia* and *Amphora*.

Below, we first discuss common genera (*Humidophila* and *Eunotia*), along with diatoms present at >5% at a minimum of one site (Table 2). We then discuss rare or less common taxa present at <5% relative abundance (Table 3). We follow this with a discussion on the ecology of these aerial environments, in particular in the context of moisture, heat, and nutrient sources.

Common genera

Humidophila

Humidophila taxa commonly occurred in association with bryophytes and/or lichen on the euaerial habitats in Iceland (absent only from two sites sparse in diatoms; WW 39 and 21). Of the seven species present, 50% or more co-occurred together, altogether often contributing >50% to the relative abundance of taxa present. Within these, *H. gallica* (Smith 1857: 11) Lowe, Kociolek, You, Wang et Stepanek (2017: 281) and *H. perpusilla* contributed the most to relative abundance. The checklist of algae from Iceland (Hallgrímsson 2007) lists several *Diadesmis* Kützing (1844: 109) and *Humidophila* taxa from aerial environments including those recorded here, such as *H. biceps*, *H. contenta* (Grunow in Van Heurck 1885: 109) Lowe, Kociolek, Johansen, Van de Vijver, Lange-Bertalot et Kopalová (2014: 357), *H. gallica*, and *H. perpusilla*. We describe one *Humidophila* species new to science, present information for another unidentified *Humidophila* taxon, and propose the transfer of *Diadesmis contenta* var. *biceps* to *Humidophila biceps*.

***Humidophila* sp. 1** (LM = Fig. 8 N–O; SEM = Fig. 8 P–Q)

Description:—The raphe is filiform and continuous from the central area to the end of the row of areolae. Lateral depressions flank proximal raphe ends. Distal raphe ends appear to lack lateral depressions. Axial area is lanceolate. Valves are naviculoid tapering to rounded ends. There is a subtile construction near the ends of the valves. The striae are continuous through the length of the valve and flair in the center leaving a circular central area. We were not able to view specimens with SEM in girdle view nor valve interior.

Collection Information:—ICELAND. Scrape and a bryophyte and lichen squeeze, collected from a rock outcrop in the Hengill watershed (~N 64 3 23.0, W 21 17 1.0, WW 5 Table 1), *P.C. Furey, 13 July 2013*. (Cleaned material –GCAC4212, and representative specimen circled on slide GCAC4212 deposited in the diatom collection at Georgia College and State University, USA. Here illustrated as Fig. 8 N).

Comments:—This unidentified taxon should be compared to *Humidophila arctica* (Lange-Bertalot et Genkel 1999: 40) Lowe, Kociolek, Johansen, Van de Vijver, Lange-Bertalot et Kopalová (2014: 357) but differs in the valves being more naviculoid. Both taxa have areolae that are interrupted in the central area, but frustules of *H. arctica* have broadly rounded ends (Lange-Bertalot & Genkal 1999, Tafel 21 Figs 8–14) in contrast to the more tapered ends of *Humidophila* sp. 1. More information, especially around interal and girdle views are needed to establish details key to a new taxon description, therefore, we currently designated this taxon as unidentified *Humidophila* sp. 1 until more information can be gathered.

Specimens were generally absent from most samples, but occasionally contributed <5% to the relative abundance at sites in Hengill and Þingvellir rift valley, though at WW5 relative abundance reached 5.5% (Table 2).

Humidophila eldfjallii *sp. nov.* (LM = Fig. 8 E–H; SEM = Fig. 8 A–D)

Description:—Valves strongly triundulate, length 12.2–14.9 µm, width middle 3.0–3.6 µm, width apices 3.0–3.6 µm; 33.0–35.4 striae in 10 µm (for n=5 LM, n=5 SEM). The raphe is filiform with distal ends bending slightly in opposite directions. The axial area is lanceolate leading to a round central area. Both distal and proximal raphe ends lack any lateral depressions.

TABLE 2. Taxa found at >5% relative abundance at a minimum of one site, presented with documented relative abundance. (Note taxa from sites WW 21, 25, and 39 that were exceptionally sparse (<50 valves counted) are not included here). Listed alphabetically.

Taxon	**Euaerial (E) or Pseudoaerial (P)**	**Plate**	**Fig.**	**Relative Abundance (Sample ID WW#)**			
				<5%	**>5 to 10%**	**>10 to 20%**	**>20%**
Diatomella balfouriana Greville	E, P	10	A – E	3,17, 51, 55			42
Eunotia bigibba Kützing	E, P	5	A – F, H – I	1, 4, 5, 20, 54		41	
Eunotia curtagrunowii Nörpel-Schempp et Lange-Bertalot	E, P	6	A – J	20, 38, 40		1	
Eunotia cf. *neofallax* Nörpel-Schempp et Lange-Bertalot	E	4	Q – W			40	55
Humidophila parallela Petersen	E	7	M – P	4, 5, 17, 20, 38, 40	3		
Humidophila biceps (Grunow in Van Heurck) Furey, Manoylov et Lowe	E, P	7	A – E	4, 17, 20	42	38	1, 5, 40, 41
Humidophila sp. 1	E, P	8	N – Q	1, 40, 41		5	
Humidophila eldfjallii Furey, Manoylov et Lowe *sp. nov.*	E	8	A – H	5, 40	38	54	
Humidophila gallica (W. Smith) Lowe, Kociolek, You, Wang et Stepanek	E, P	9	A – J	5, 17, 41	20, 38	1, 42, 54	3, 4, 51, 52, 53
Humidophila perpusilla (Grunow) Lowe, Kociolek, Johansen, Van de Vijver, Lange-Bertalot et Kopalová	E, P	7	F – L		1, 53	3, 38, 40, 53	2, 5, 17, 20, 41, 42, 51, 52, 54
Hygropetra balfouriana (Grunow ex Cleve) Krammer et Lange-Bertalot	E	2	Q – R, U – V	55	4	3	53
Melosira varians Agardh	E	No image shown		51		50	
Orthoseira roeseana (Rabenhorst) Pfitzer	E, P	2, 3	2, N, S – T; 3, A – D	51		20	
Psammothidium marginulatum (Grunow) Bukhtiyarova et Round	E	10	Y – Z	40		55	
Stauroneis cf. *borrichii* (Petersen) Lund	E	11	X – a	41	38, 40		
Staurosirella neopinnata (Morales, Wetzel, Haworth, et Ector	E	2	A – G	4, 25, 54		3	

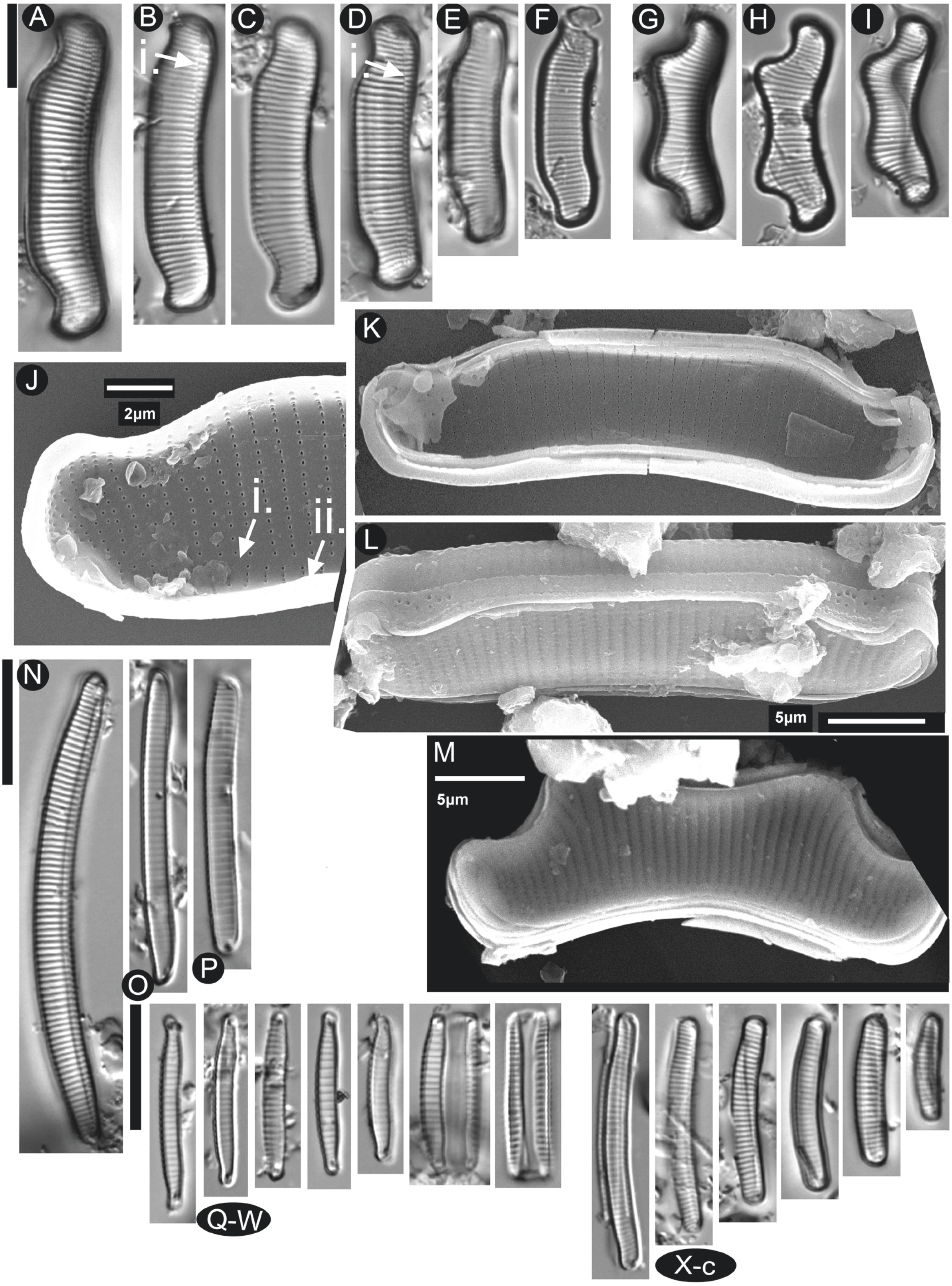

FIGURE 4. Light (A–I, N–c) and SEM (J–M) images of aerial diatom assemblages from southwestern Iceland, *Eunotia* species. A–F, J–L. *Eunotia palatina*: A–F. size diminution series, the striae end short on the valve face to create the appearance of a hyaline strip (i), J. internal views of a valve apex showing the location of the helictoglossa, a hyaline area (i) and swelling where the proximal raphe ends (ii), K. a whole valve, internal view (scale bar as in L), and L. a frustule with both valve and girdle views visible; G–I, M. *Eunotia arctica*: G–I. valve views, M. external view shows striae and hyaline band along the ventral edge; N. *Eunotia* cf. *valida*: valve view; O–P. *Eunotia* cf. *fallax*: valve view; Q–W. *Eunotia neofallax*: valve view, V. half valve / half girdle view, and W. girdle view; X–c. *Eunotia nymanniana*: valve view. LM scale bar = 10 µm, SEM scale bars as shown.

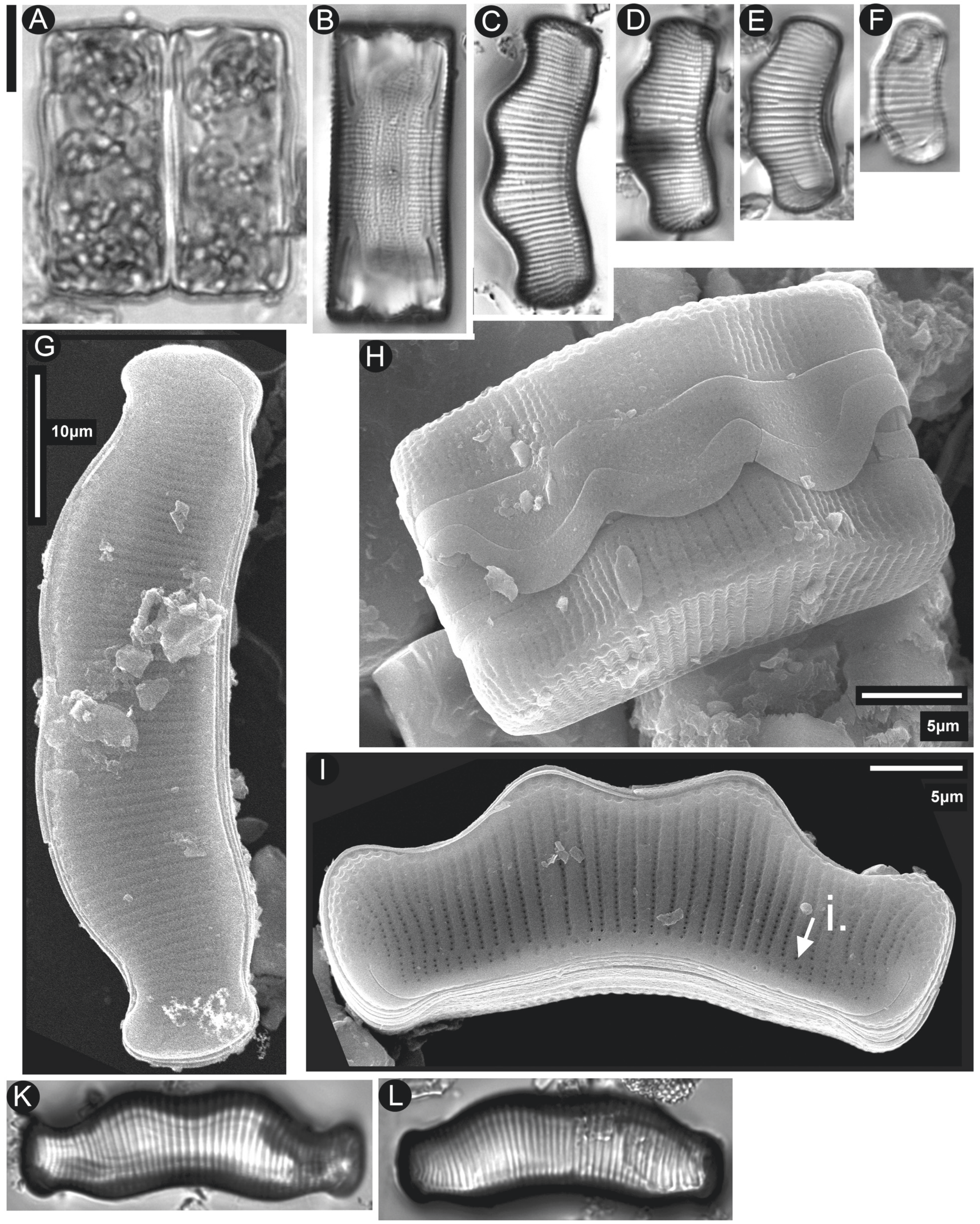

FIGURE 5. Light (A–F, K–L) and SEM (G–I) microscopy images of aerial diatom assemblages from southwestern Iceland, *Eunotia* species. A–F, H–I. *Eunotia bigibba*: A. two live frustules in girdle view, C–F, I. valve view, B–F. size diminution series, and B. girdle view showing raphe position, H. arrangement of the cingulum and areolae on the mantle, and I. valve view showing arrangement of punctate striae and raphe ends on the valve face. Note the appearance of the hyaline area on the ventral edge of the valve where the striae stop short (i); G, K–L. *Eunotia biden*s: all valve views, note the swellings along the ventral margin where the proximal raphe ends. Frustule K slightly tilted. LM scale bar = 10 µm, SEM scale bars as shown.

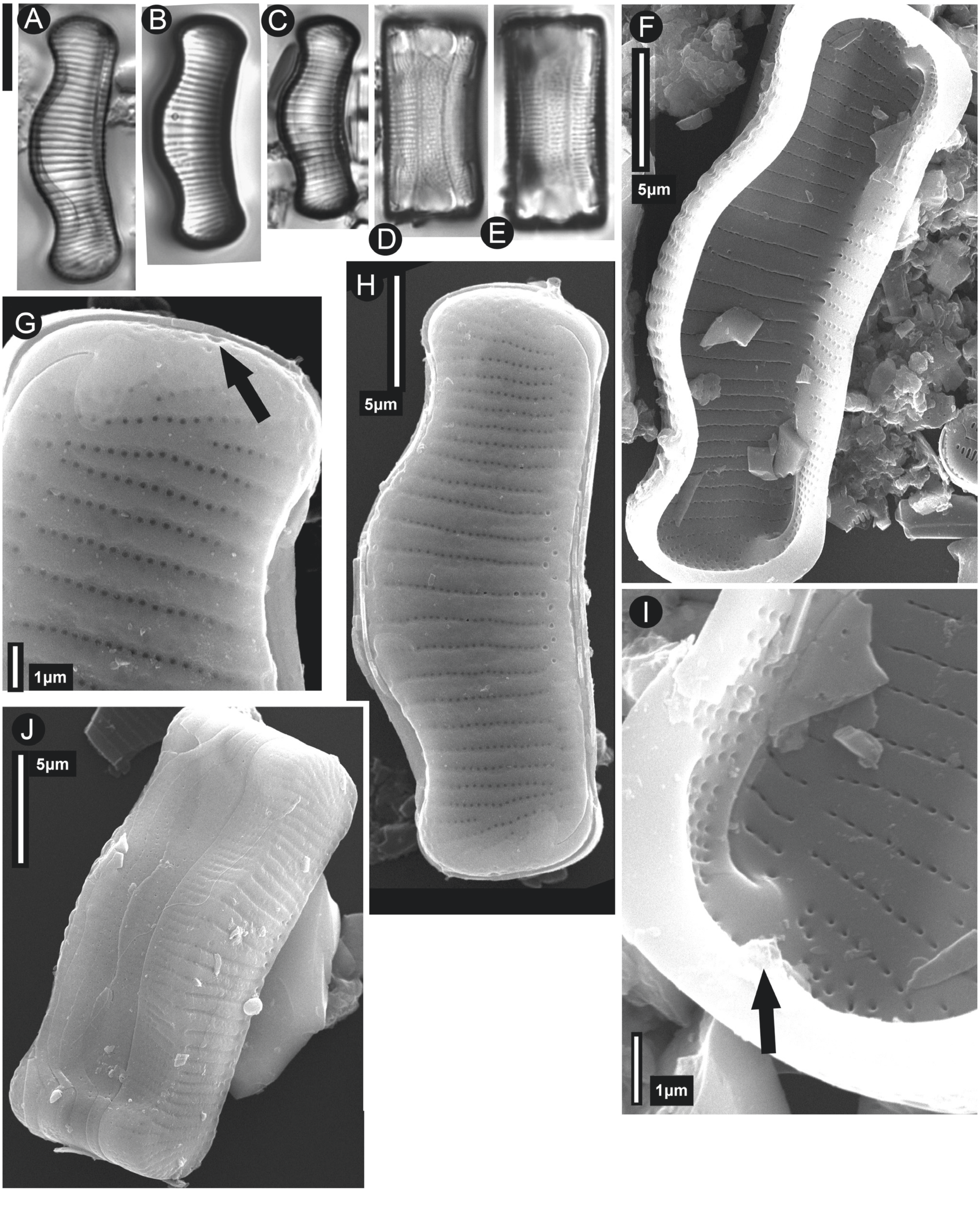

FIGURE 6. Light (A–E) and SEM (F–J) microscopy images of aerial, diatom population of *Eunotia curtagrunowii* from southwestern Iceland. A–C. valve view size diminution series and D–E. girdle view with different focuses, F. internal view showing helictoglossa and internal opening of areolae with a close up of the apex of the same valve in I. to show the internal expression of the rimoportula (arrow), G. close up of valve apex with external opening to the rimoportula (arrow), H. external view, showing arrangement of striae and raphe ends on the valve face, note the markings along the ventral edge of the valve face, J. tilted girdle view showing cingulum. LM scale bar = 10 µm, SEM scale bars as shown.

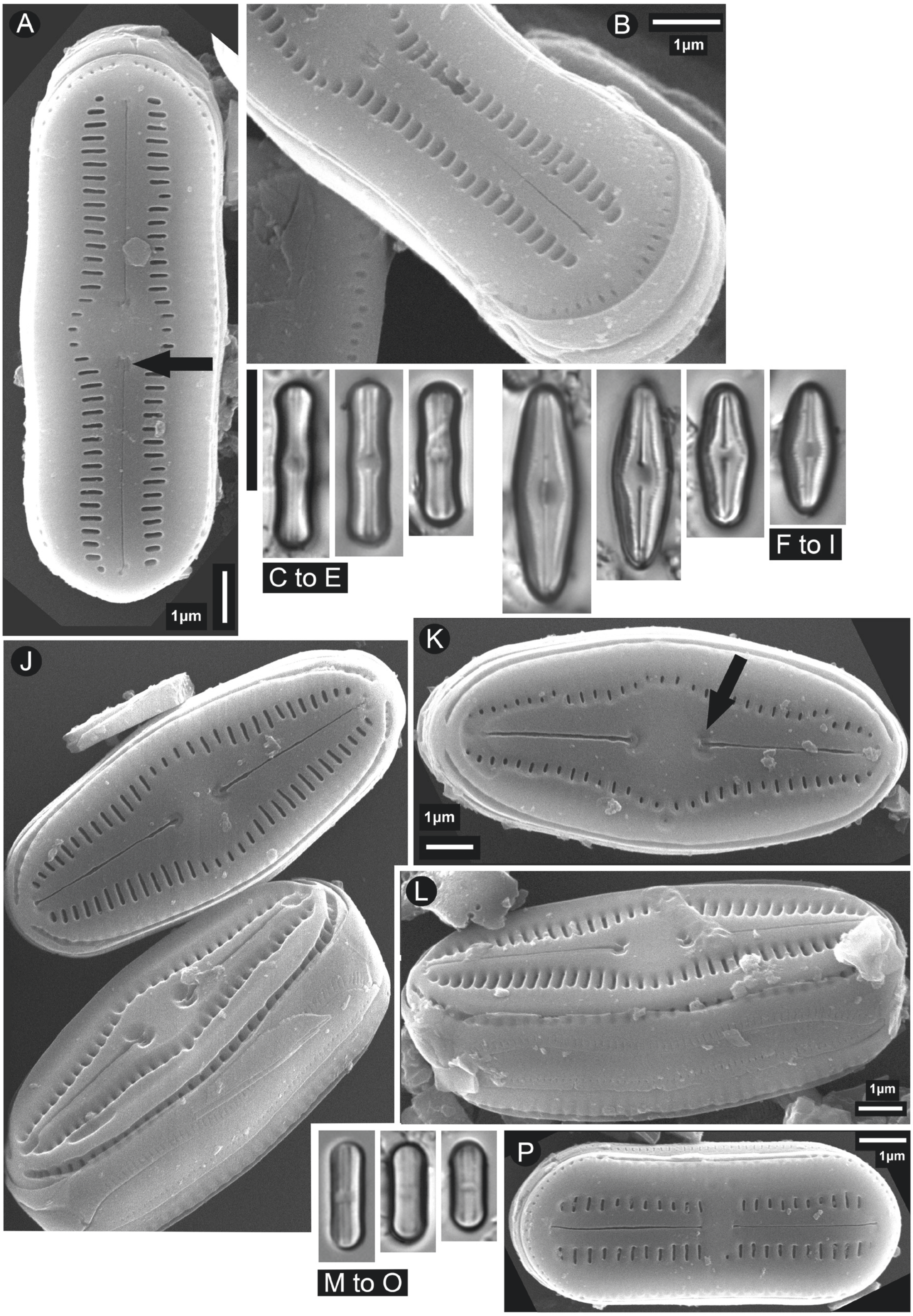

FIGURE 7. Light (C–I) and SEM (A–B, J–L) microscopy images of aerial diatom assemblages from southwestern Iceland. A–E. *Humidophila biceps*: A–B external, valve view showing external expression of areolae, distal raphe endings, and proximal raphe endings with adjacent depressions (arrow). C–E. valve view; F–L. *Humidophila perpusilla*: F–I. size series in valve view, and J–L. external view of valve and tilted frustule showing valve and girdle views. Note depressions flanking proximal raphe ends (arrow). M–P. *Humidophila parallela*: valve view. P. external view showing hints of T-shaped proximal and distal raphe endings. LM scale bar = 10 µm, SEM scale bars as shown.

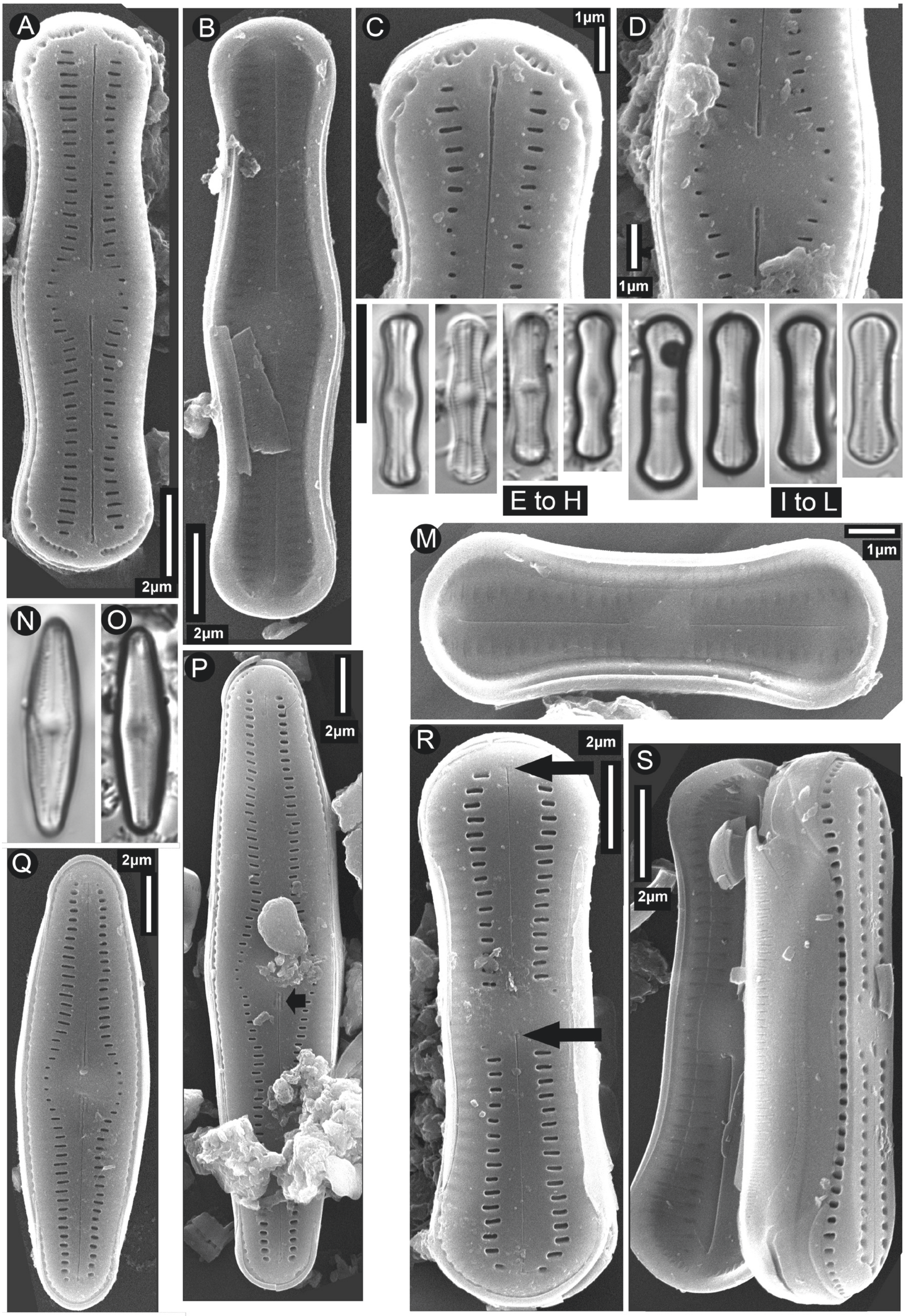

FIGURE 8. Light (E–L, N–O) and SEM (A–D, M, P–S) microscopy images of aerial diatom assemblages from southwestern Iceland. A–H. *Humidophila eldfjallii* Furey, Manoylov et Lowe *sp. nov.*: A. external and B. internal valve views, C. close up valve apex showing distal raphe ends. D. close up of central area showing proximal raphe ends. E–H. valve view, F. holotype; I–M, R–S. *Humidophila paracontenta*: I–L valve view, M. internal valve view, R. external valve, and S. both valve and girdle views. Note depressions flanking distal and proximal raphe ends (arrows); N–Q. *H.* sp. 1, N–O. valve view, N. representative specimen circled on slide GCAC4212, P–Q. external valve view. Note depressions flanking proximal raphe ends (arrow). LM scale bar = 10 µm, SEM scale bars as shown.

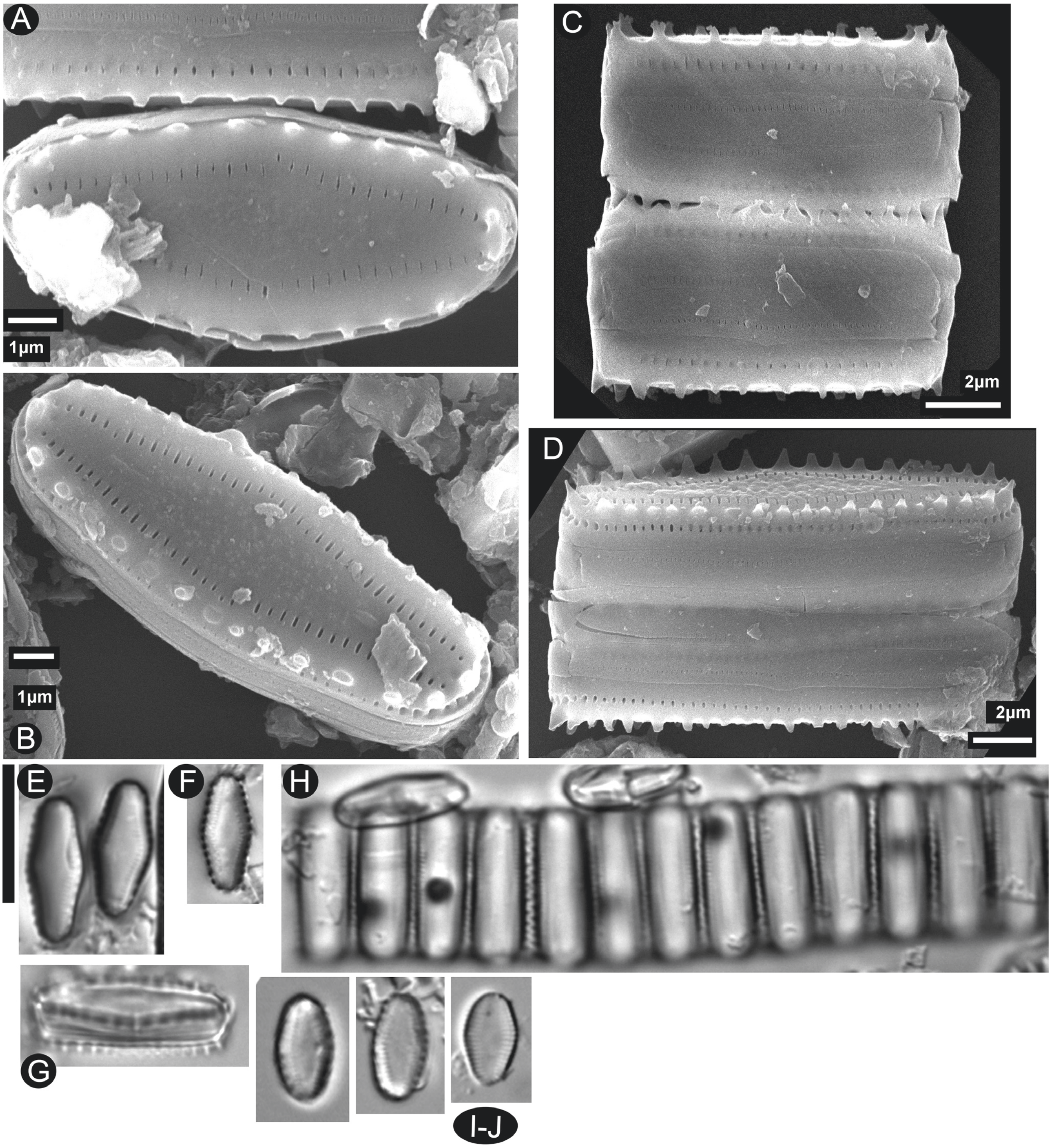

FIGURE 9. Light (E–J) and SEM (A–D) microscopy images of aerial diatom populations of *Humidophila gallica* from southwestern Iceland. A–B. external view showing spine location and external expression of areolae, C–D. girdle view of two linked frustules showing side view of spines and presence of areolae on valve mantle and cingulum, E–F. valve view of longer form, G. tilted girdle view of a single frustule with visible spines, H. girdle view of a chain of cells. I–J. valve view of shorter form. LM scale bar = 10 µm, SEM scale bars as shown.

Holotype:—ICELAND. Surface scrape and a bryophyte and lichen squeeze collected from a rock face located river right of the River Hengladalsá in the Hengill watershed (~N 64 3 23.0, W 21 17 1.0, WW 38 Table 1), *P.C. Furey, 14 July 2013*. Circled specimen on slide GCAC4213, deposited in the diatom collection at Georgia College and State University Natural History Museum, USA. Here illustrated as Fig. 8 F).

Type Material:—Cleaned type material deposited in the Georgia College and State University Natural History Museum, USA diatom collection. GCAC4213.

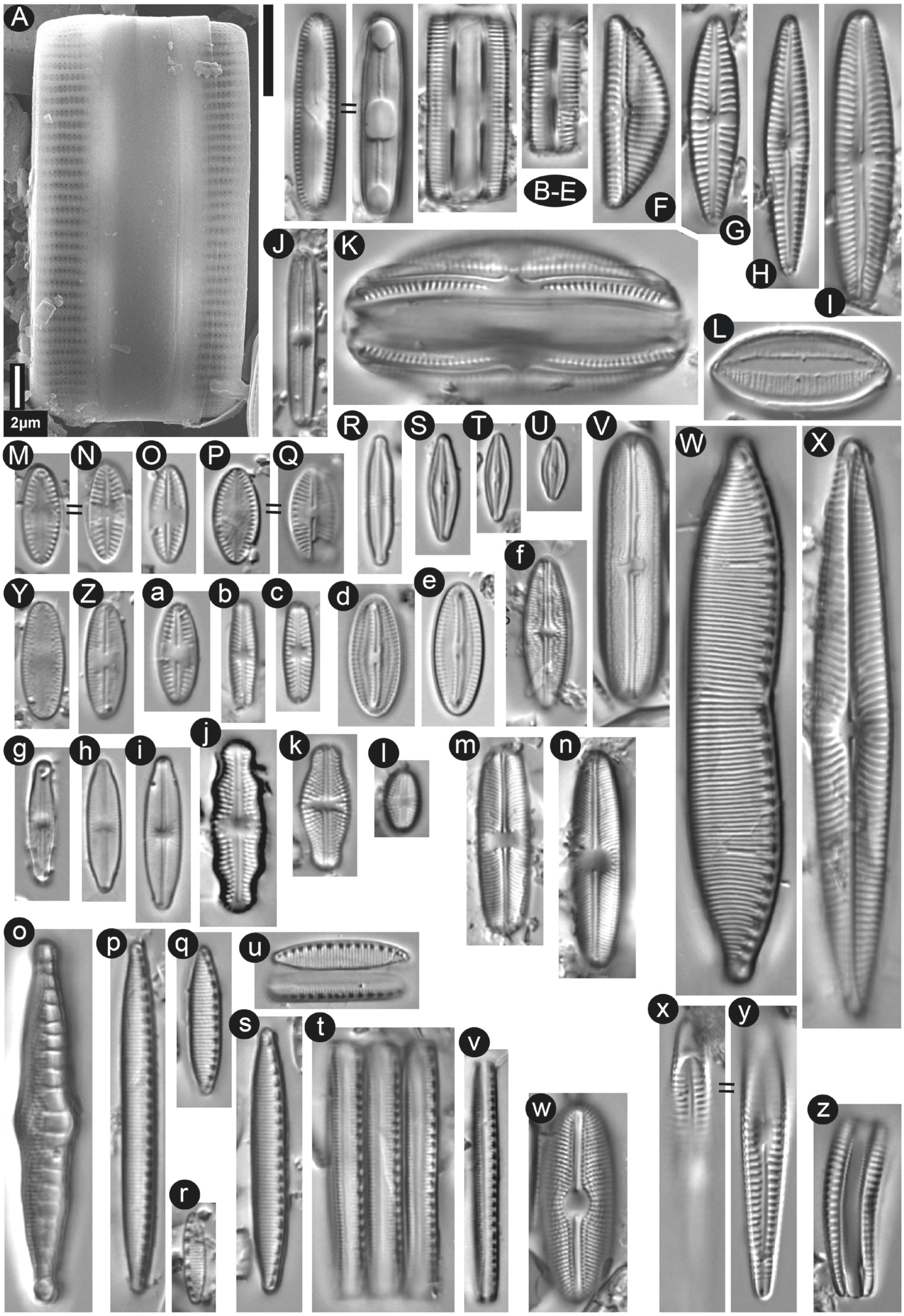

FIGURE 10. Light (B–z) and SEM (A) microscopy images of aerial diatom assemblages from southwestern Iceland, mostly in valve view. A–E. *Diatomella balfouriana*: A, D–E. girdle views, B. valve view with striae in focus, C. septa with openings in focus; F. *Encyonema langebertalotii*; G. *Gomphonema* sp. 1; H. *Gomphonema bipunctatum*; I. *Cymbopleura* cf. *subaequalis*, J. Naviculoid sp. 1; K. *Amphora ovalis*; L. *Tryblionella debilis*; M–O, a. *Platessa rupestris* var. *interrupta*; P–Q. *Platessa rupestris*; R. *Adlafia bryophila*; S–U. *Microcostatus krasskei*; V. *Neidium bisulcatum*; W. *Hantzschia amphioxys*; X. *Navicula* cf. *radiosa*; Y–Z, a. *Psammothidium marginulatum*; b. *Navicula seminulum* var. *radiosa*; c. *Sellaphora seminulum*; d–e. *Fallacia insociabilis*; f. *Brachysira brebissonii*; g. Naviculoid sp. 2; h–i. *Adlafia suchlandtii* j= *Luticola* c.f. *nivaloides,* k. *Luticola* sp. 1; l. *Luticola* cf. *mutica*; m. *Sellaphora rectangularis*; n. *Cavinula variostriata*; o *Nitzschia sinuata;* p–q, s–v. *Nitzschia perminuta;* r. *Nitzschia soratensis*, w. *Diploneis ovalis*; x–y. *Rhoicosphenia* cf. *californica*; z. *Rhoicosphenia abbreviata*. Scale bar =10 µm unless stated otherwise shown, '=' represents focus on each valve of the same frustule.

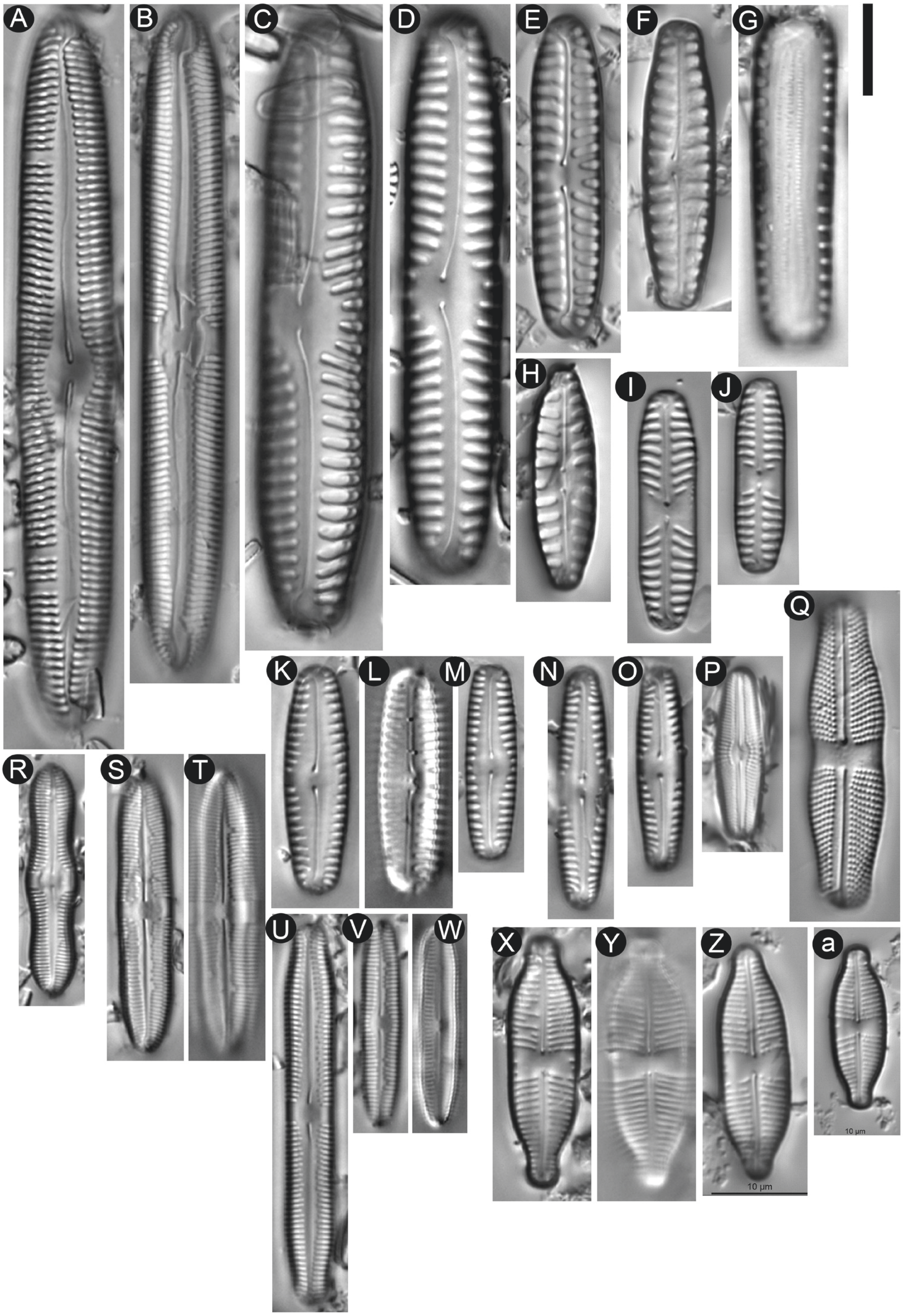

FIGURE 11. Light microscopy images of aerial diatom assemblages from southwestern Iceland. A. *Pinnularia* cf. *subcommutata*; B. *Pinnularia stomatophora*; C. *Pinnularia* sp. 2; D. *Pinnularia* sp. 1; E. *Pinnularia borealis*; F. *Pinnularia borealis* f. *subcapitata*; G. *Pinnularia borealis* var. *islandica* girdle view; H. *Pinnularia borealis* var. *lanceolata*; I–J. *Pinnularia intermedia*; K–M. *Pinnularia parva*; N–O. *Pinnularia minoricapitata*; P. *Muellaria gibulla*; Q. *Achnanthes coarctata*; R. *Caloneis schumanniana*; S–T. *Caloneis silicula*; U–W. *Caloneis tenuis*; X–a. *Stauroneis* cf. *borrichii*. LM scale bar = 10 µm.

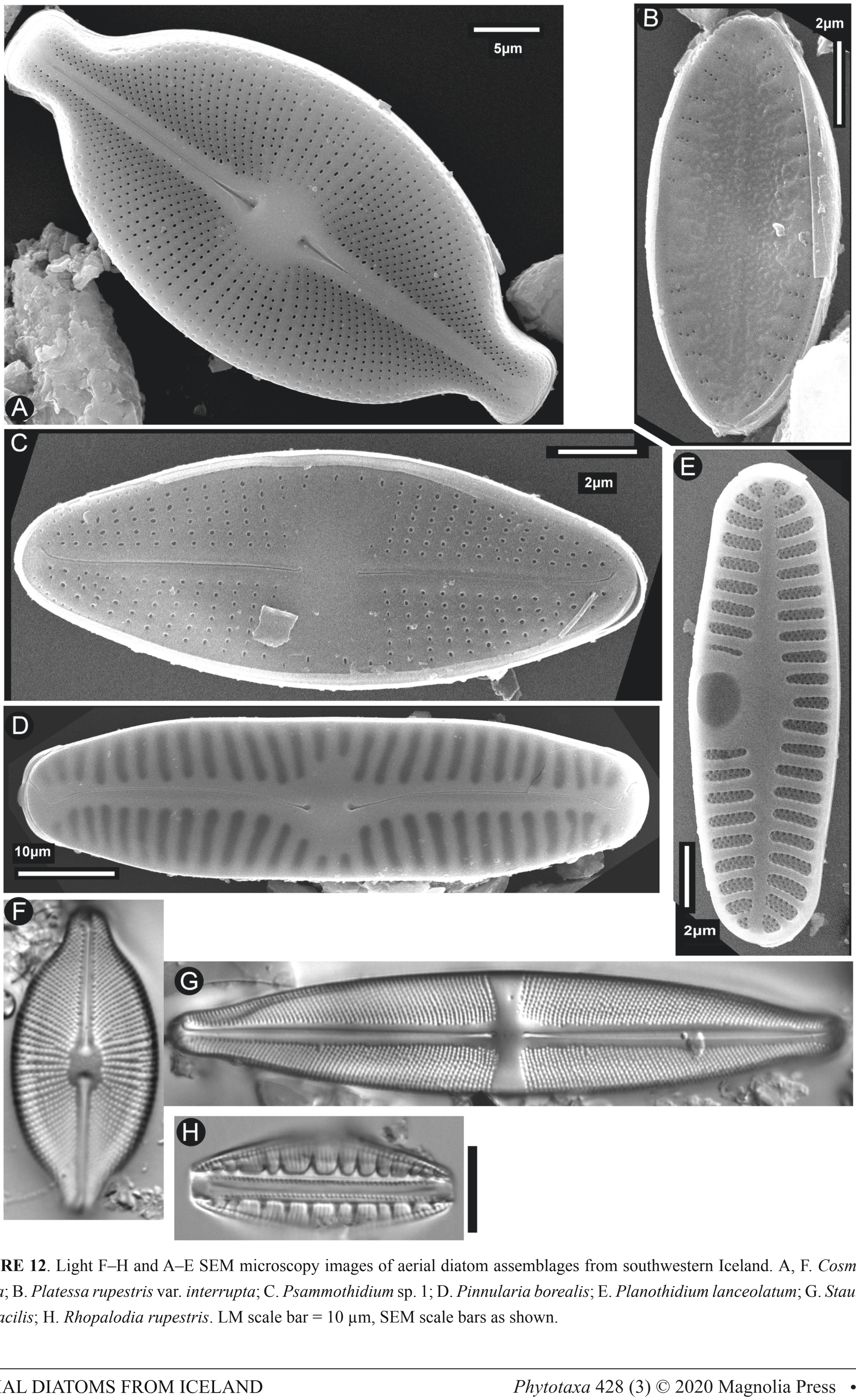

FIGURE 12. Light F–H and A–E SEM microscopy images of aerial diatom assemblages from southwestern Iceland. A, F. *Cosmioneis pusilla*; B. *Platessa rupestris* var. *interrupta*; C. *Psammothidium* sp. 1; D. *Pinnularia borealis*; E. *Planothidium lanceolatum*; G. *Stauroneis subgracilis*; H. *Rhopalodia rupestris*. LM scale bar = 10 µm, SEM scale bars as shown.

Etymology:—This specific epithet refers to the Icelandic word for 'volcano'–'eldfjall' (eldur–"fire", and fjall –"mountain") after the volcanic rock it was collected from in the Hengill watershed; also the location of the Hengill volcano.

Comments:—The strongly triundulate valves of *H. eldfjallii* are different than most species in this genus. *Humidophila eldfjallii* differs from *H. costei* (Le Cohu et Van de Vijver 2002: 122) Lowe, Kociolek, Johansen, Van de Vijver, Lange-Bertalot et Kopalová (2014: 357) and *H. ingeae* (Van de Vijver in Van de Vijver *et al.* 2002: 338) Lowe, Kociolek, Johansen, Van de Vijver, Lange-Bertalot et Kopalová (2014: 358) by valves that are much more strongly triundulate with bulbous valve ends, whereas *H. costei* and *H. ingeae* have more subtly undulated valves. Additionally, *H. ingeae* displays marginal aereola on the valve face while they are on the mantle in *H. eldfjllii*.

Specimens occurred at >5–10% (WW 38) and >10–20% (WW 54) relative abundance in Hengill, but otherwise occurred at low relative abundances in Hengill and the Þingvellir rift valley (Table 2).

Humidophila parallela (Petersen 1928b: 15) *comb. nov*. (LM = Fig. 7 M–O; SEM = Fig. 7 P)

Basionym: *Navicula contenta* var. *parallela* Petersen (1928b: *Dansk Bot. Arkiv*, p. 15, fig 2)

Synonym: *Diadesmis contenta* var. *parallela* (Petersen 1928b: 15) Spaulding in Spaulding *et al.* (1997: 410). Valve dimensions (for n=9 LM, n=3 SEM) length 7.2–9.1 μm, width middle 2.0–3.1, width apices 2.0–3.1; 34.0–34.9 striae in 10 μm. T-shaped depression of the proximal raphe ends absent.

This species was earlier considered to be a variety of *Navicula contenta* Grunow in Van Heurck (1885: 109), and was moved (as a variety) to *Diadesmis contenta* (Grunow 1885: 109) D.G.Mann in Round, R.M.Crawford & D.G.Mann (1990: 666), but SEM views in this study show that it lacks the T-shaped depressions at the proximal raphe ends, a characteristic of *D. contenta*. *Diadesmis arcuata* (Heiden in Heiden et Kolbe 1928: 628) Lange-Bertalot in Moser, Lange-Bertalot et Metzeltin (1998: 136) lacks this depression, and therefore we consider this species to be more closely related to *D. arcuata* than to *D. contenta*. There is currently some question about the validity of *D. arcuata*, as it has a basionym that is illegitimate (*Navicula arcuata* Heiden in Heiden et Kolbe 1928: 628) because it was a later synonym of *Navicula arcuata* Pantocsek (1892: 64 (1905), pl. 6: fig. 97). Lange-Bertalot correctly considered the name *arcuata* available for a species in *Diadesmis,* but he incorrectly made a new combination with Heiden's illegitimate taxon as basionym when he should have simply used *arcuata* as a replacement name (Moser *et al.* 1998). Lowe *et al.* (2014) made the same error in their new combination. Given that the recognition of subspecific taxa in diatoms is a less widespread practice than in prior decades, and the possible incorrectness of the recent combinations with *Navicula arcuata*, we decided to recognize this taxon at the species level.

Valves generally were absent or contributed <2% to the relative abundance of samples from Hengill and Þingvellir rift valley, though relative abundance reached 7% at one site in Hengill (WW 3; Table 2).

Humidophila biceps (Grunow in Van Heurck 1880: expl. Pl. XIV, fig. 31B) *comb. nov.* (LM = Fig. 7 C–E; SEM = Fig. 7 A–B).

Basionym: *Navicula trinodis* var. *biceps* Grunow in Van Heurck 1880: expl. Pl. XIV, fig. 31B
Valve dimensions (for n=14 LM, n=4 SEM): length 10.0–14.5 μm, width middle 2.5–3.5 μm; 39.3–41.6 striae in 10 μm. Valves had a slight convex area in the middle. Short, comma–like depressions flanking the proximal raphe ends were similar to those shown in SEM micrographs in Veselá & Johansen (2009, as *Diadesmis biceps* fig. 199). This taxon is synonymous to *D. biceps* G.A. Arnott ex Cleve (1894: 132) *nom. inval*. and *D. contenta* var. *biceps*.

Frustules occurred at low relative abundance at several sites in the Hengill watershed, but also reached higher relative abundances at sites in both Hengill and the Þingvellir rift valley, four of which were >20% relative abundance (Table 2).

Humidophila gallica (W. Smith 1857: 11) Lowe, Kociolek, You, Wang et Stepanek (2017: 281) (LM = Fig. 9 E–J; SEM = Fig. 9 A–D)

The valve dimensions of *H. gallica* measured at length 9.5–15.0 μm, width middle 3.0–4.2 μm, and 30.8–32.7 striae in 10 μm (for n=11 LM, n=9 SEM). The chain-forming morphology with spines and the absence of a raphe occurred over forms with a raphe but not spines (Cox 2006). Some populations contain valves predominantly on the shorter side (Fig. 9 I–J)

Humidophila gallica, consistently present in the Hengill and the Þingvellir rift valley, consistently occurred at relative abundances >5 %, and at 5 sites >20% (Table 2). *Humidophila gallica* is a typical on mosses and ferns (as *Diadesmis gallica*; Roldán et Hernández–Mariné, 2009).

Humidophila paracontenta (Lange-Bertalot et Werum in Lange-Bertalot & Genkal 1999: 41) Lowe, Kociolek, Johansen, Van de Vijver, Lange-Bertalot et Kopalová (2014: 358) (LM = Fig. 8 I–L; SEM = Fig. 8 M, R–S)

Valve dimensions (for n=8 LM, n=4 SEM): length 9.8–14.4 μm, width middle 2.2–3.8 μm, width apices 2.5–4.3 μm; 28.5–31.2 striae in 10 μm. Short, comma-like depressions flanked the distal and proximal raphe ends (similar to those shown in *H. paracontenta* var. *magisconcava* (Lange-Bertalot) Lowe, Kociolek, Johansen, Van de Vijver, Lange-Bertalot et Kopalová (2014: 358) –Pl 65, 3–7 in vol. 13, Werum & Lange-Bertalot 2004).

Humidophila paracontenta, absent from Þingvellir rift valley, typically comprised <1% of the relative abundance of samples from Hengill, but was the only taxon observed from a sparse sample at WW 21 (Table 3).

Humidophila perpusilla (Grunow 1860: 552) Lowe, Kociolek, Johansen, Van de Vijver, Lange-Bertalot et Kopalová (2014: 358) (LM = Fig. 7 F–I; SEM = Fig. 7 J–L)

The valve dimensions of *H. perpusilla* measured at length 8.0–18.1 µm, width middle 3.4–4.6 µm, and 32.3–36.0 striae in 10 µm (for n=25 LM, n=9 SEM). This taxon, very common at sites from Hengill and the Þingvellir rift valley, occurred at >20 % relative abundance at 9 sites (Table 2).

TABLE 3. Taxa observed at <5 % relative abundance. WW 21, 25, and 39 that were exceptionally sparse (<50 valves counted) are not included here). Listed alphabetically.

Taxon name	Euaerial (E) or Pseudoaerial (P)	Plate	Fig.	**Sample ID WW#**
Achnanthes coarctata (Brébisson ex W. Smith) Grunow	E, P	11	Q	17, 40, 41, 51
Adlafia byrophila (J. B. Petersen) Lange-Bertalot	E	10	R	53
Adlafia suchlandtii (Hustedt) Monnier et Ector	E	10	h – i	17, 53
Aulacoseira alpigena (Grunow) Krammer	E	2	L – M	3, 4, 17, 38, 55
Amphora ovalis (Kützing) Kützing	E	10	K	52
Brachysira brebissonii Ross	E	10	f	54
Caloneis schumanianna (Grunow in Van Heurck) Cleve	E	11	R	55
Caloneis silicula (Ehrenberg) Cleve	E, P	11	S – T	42, 55
Caloneis tenuis (W. Gregory) Krammer	E	11	U – W	3, 5, 55
Cavinula variostriata (Krasske) D.G. Mann et A.J. Stickle	E	10	n	55
Cosmioneis pusilla (W. Smith) D.G. Mann et Stickle	E, P	12	A, F	20, 51
Cymbopleura cf. *subaequalis* (Grunow) Krammer	E	10	I	55
Diploneis ovalis (Hilse) Cleve	E	10	w	53, 55
Encyonema lange-bertalotii Krammer	E	10	F	17
Eunotia arctica Hustedt	E	4	G – I, M	1, 5, 40
Eunotia bidens Ehrenberg	P	5	G, K – L	41
Eunotia cf. *fallax* Cleve	E	4	O – P	55
Eunotia nymanniana Grunow	E	4	X – c	54, 55
Eunotia palatina Lange-Bertalot et Krüger	E	4	A – F, J – L	1, 38, 40 54
Eunotia cf. *valida* Hustedt	E	4	N	55
Fallacia insociabilis (Krasske) Mann	E	10	d – e	53
Fragilaria nitzschioides Grunow	E	2	H	3
Fragilaria perminuta (Grunow) Lange-Bertalot	E	2	K	50
Gomphonema Ehrenberg sp. 1	E	10	G	17, 55
Gomphonema bipunctatum Krasske	E	10	H	55

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TABLE 3 (Continued**)**

Taxon name	Euaerial (E) or Pseudoaerial (P)	Plate	Fig.	**Sample ID WW#**
Hantzschia amphioxys (Ehrenberg) Grunow	E	10	W	17, 38, 50, 51
Humidophila paracontenta (Lange-Bertalot et Werum) Lowe, Kociolek, Johansen, Van de Vijver, Lange-Bertalot, et Kopalová	E, P	8	I – M, R– S	1, 17, 20, 38
Luticola D.G. Mann in Round, Crawford & Mann sp. 1	E	10	k	51
Luticola cf *mutica* (Kützing) Mann	E	10	l	38, 50, 54
Luticola cf. *nivaloides* (W. Bock) Denys et De Smet	E	10	j	51
Meridion circulare var. *constrictum* (Ralfs) Van Heurck	E	2	I – J	3, 17, 25, 50, 55
*Microcostatus krasske*i (Hustedt) Johansen et Sray	E	10	S – U	54, 55
Muelleria gibbula (Cleve) Spaulding et Stoermer	E	11	P	51
Navicula cf. *radiosa* Kützing	E	10	X	55
Navicula seminulum var. *radiosa Hustedt*	E	10	b	3, 38
Naviculoid sp. 1	E	10	g	55
Neidium bisulcatum (Lagerstedt) Cleve	E	10	V	53
Nitzschia perminuta (Grunow) Peragallo	E	10	p – q, s – v	3
Nitzschia sinuata (Thwaites) Grunow	E	10	o	17
Nitzschia soratensis Morales et Vis	E	10	r	55
Pinnularia borealis Ehrenberg	E	11	E	54
Pinnularia borealis var. *islandica* Krammer	E	11	G	50
Pinnularia borealis var. *lanceolata* Hustedt	E	11	H	52
Pinnularia borealis f. *subcapitata* J.B. Petersen	E	11	F	54
Pinnularia intermedia (Lagerstedt) Cleve	E	11	I – J	51
Pinnularia minoricapitata Krammer	E	11	N – O	51
Pinnularia parva W. Gregory	E	11	K – M	51
Pinnularia Ehrenberg sp. 1	E	11	D	51, 55
Pinnularia Ehrenberg sp. 2	E	11	C	53
Pinnularia stomatophora (Grunow) Cleve	E	11	B	55
Pinnularia cf. *subcommutata* Krammer	E	11	A	53
Planothidium lanceolatum (Brébisson ex Kützing) Lange-Bertalot	E	12	E	17, 51
Platessa rupestris var. *interrupta* (Krasske) Lange-Bertalot	E	10; 12	M – O , a; B	38, 40, 54
Platessa rupestris (Krasske) Lange-Bertalot	E	10	P – Q	40, 54
Rhoicosphenia abbreviata (Agardh) Lange-Bertalot	E	10	z	25, 55
Rhoicosphenia cf. *californica* Thomas et Kociolek	E	10	x – y	55

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TABLE 3 (Continued**)**

Taxon name	Euaerial (E) or Pseudoaerial (P)	Plate	Fig.	**Sample ID WW#**
Rhopalodia rupestris (W. Smith) Krammer	E, P	12	H	42, 53, 55
Sellaphora rectangularis (W. Gregory) Lange-Bertalot et Metzeltin	E	10	m	55
Sellaphora seminulum (Grunow) D.G. Mann	E	10	c	3, 55
Stauroforma atomus (Hustedt) D. Talgatti, C. E. Wetzel, E .Morales et L. C. Torgan	E	2	O – P	55
Stauroneis subgracilis Lange-Bertalot et Krammer	E	12	G	55
Tryblionella debilis Arnott ex O'Meara	E	10	L	51
not shown with images				
Achnanthidium minutissimum (Kützing) Czarnecki	E			52
Aulacoseira italica (Ehrenberg) Simonsen	E			50
Caloneis bacillum (Grunow) Cleve	E			54
Cavinula cocconeiformis (Gregory ex Greville) Mann et Stickle in Round, Crawford et Mann	E			53
Epithemia adnata (Kützing) Brébisson	E			55
Hannaea arcus (Ehrenberg) Patrick	E			50
Navicula gregaria Donkin	E			51
*Psammothidium subatomoid*es (Hustedt in Schmidt) Bukhtiyarova et Round	E			52
Staurosira construens var. *venter* (Ehrenberg) Hamilton	E			55
Ulnaria ulna (Nitzsch) Compére	E			25, 52

Eunotia

Eunotia species, considered all together, were common in our samples at relative abundances <5% (Table 3), though at four sites the relative abundance reached 12–33% (Table 2).

Eunotia arctica Hustedt (1937: 169) (LM = Fig. 4 G–I; SEM = Fig. 4 M)

The valve morphology of *E. arctica* from these samples measured at length 23.4–25.7 µm, width inflated area 7.4–8.4, width middle 5.3–6.5 µm, 14.8–16.2 striae (middle) in 10 µm, 18.0–22.1 striae (ends) in 10 µm, and areolae ca 34 in 10 µm (for n=4 LM, n=1 SEM). The raphe curved strongly up the valve apex (Fig. 4 M).

This taxon only occurred at a few sites in Hengill and Þingvellir rift valley, but at <5% relative abundance (Table 3). The checklist of algae from Iceland (Hallgrímsson 2007) includes *E. arctica.* Lange-Bertalot *et al.* (2011) show images of specimens from Iceland (type locality), along with valves from Spitzbergen (Svalbard) with a similar, but slightly different morphology (see outline of inflated areas; plate 73, figs 9–15).

Eunotia bidens Ehrenberg (1843b: 413) (LM = Fig. 5. K–L; SEM = Fig. 5. G)

The valves observed measured at length 37.0–47.3 µm, width inflated area 11.0 – 12.3 µm, width middle 8.2–11.0 µm, 12.2–14.4 striae (middle) in 10 µm, and 12.2–17.0 striae (ends) in 10 µm (n = 3 LM, for n=3 SEM). The checklist of algae from Iceland includes *E. praerupta* var. *bidens* (Ehrenber 1843: 413) Grunow in Cleve & Grunow (1880: 109) (Hallgrímsson 2007; considered a synonym of *E. bidens*), and Petersen (1928a) briefly mentions this taxon. The valves in this study appear similar to a specimen shown in Foged (1974; *E. praerupta* var. *bidens*, Plate V. fig. 8). Our valves are too narrow and short to belong to *E. superbidens* Lange-Bertalot in Lange-Bertalot *et al.* (2011: 229).

Valves of *E. bidens* were only observed at <1% relative abundance in a bryophyte squeeze in the Þingvellir rift valley (WW 41; Table 2).

Eunotia bigibba Kützing (1849: 6) (LM = Fig. 5 A–F; SEM = Fig. 5 H–I)

The valve morphology of *E. bigibba* measured at length 25–36.5 µm, width inflated area 9.8–11.4 µm, width middle 8.3–10.7 µm, 10.6–13.2 striae (middle) in 10 µm, 14.1–16.2 striae (ends) in 10 µm, and areolae 24–30 in 10 µm (for n=10 LM, n=7 SEM). The striae stopped short to give the appearance of the hyaline area (i) on the ventral edge of the valve (Fig. 5 I). In girdle view, the cingulum formed waves following the inflated areas of the dorsal margin (Fig. 5 H). The areolae extended across the valve mantle (Fig. 5 H).

The valves from Iceland align best with valve measurements for *E. bigibba* described from other populations in Lange-Bertalot *et al.* (2011; length 20–43 µm, width inflated area 8–14 µm, striae 10–12 in 10 µm, areolae ca. 30 in 10 µm). The shorter, narrower valves with higher striae density contrast with those of *E. sarek* Berg (1939: 449) (Length 40–57 µm, width inflated area 14–23 µm, striae 7–10 in 10 µm; Lange-Bertalot *et al.* 2011). The narrower depression between the inflated areas sets valves apart from those of *E. suecica* Cleve (1895: 29).

Eunotia bigibba occurred in association with bryophytes and lichens in low densities (<5%) from a number of sites in the Hengill watershed, and at 12% on WW41 in the Þingvellir rift valley (Table 2). *Eunotia bigibba*, included in the checklist of algae from Iceland (as *E. praerupta* var. *bigibba* (Kützing 1849: 6) Grunow in Van Heurck 1881; (Hallgrímsson 2007), was also reported from epiphytic diatom assemblages from terrestrial mosses in in Zackenberg (Northeast Greenland; Van Kerckvoorde *et al.* 2000).

Eunotia curtagrunowii Nörpel-Schempp et Lange-Bertalot in Lange-Bertalot & Metzeltin (1996: 48) (LM = Fig. 6 A–E; SEM = Fig. 6 F–J)

The valve morphology of *E. curtagrunowii* measured at length 21–28 µm, width 7–8.5 µm, 9.4–13.0 striae (middle) in 10 µm, 14.4–18.0 striae (ends) in 10 µm, and areolae 30–35 in 10 µm (for n=10 LM, n=4 SEM). Valve measurements and morphological descriptions conform to those reported in Lange-Bertalot & Metzeltin (1996) and Lange-Bertalot *et al.* (2011). In our specimens, a single rimoportula occurred just below the midpoint of the valve apex with a simple, round opening externally (Fig. 6 G) and a raised opening internally (Fig. 6 I). Note the patterning, and single enlarged areola along the external, ventral margin (Fig. 6 H), also shown in other SEM micrographs (Lange-Bertalot *et al.* 2011; plate 196, fig. 9–12, 13). The narrower valves distinguish specimens from Iceland from those of *E. ewa* Lange-Bertalot et Witkowski in Lange-Bertalot *et al.* (2011: 93) from Greenland (width 9.5–13 µm). The rectangular girdle view of valves from Iceland (Fig. 6 D, E) contrast with the parallelogram-like shape of the girdle view of a similar shaped taxon, *E. parallelogramma* Van de Vijver, M. de Haan et Lange-Bertalot (2014: 274), reported from Antarctica.

Frustules occurred in association with bryophytes and lichen at 11% relative abundance at WW 1, and in low densities other sites in Hengill and the Þingvellir rift valley (Table 2). *Eunotia curtagrunowii* is reported as *E. praerupta* var. *muscicola* Petersen (1928: 377) from terrestrial habitats in Iceland (Petersen 1928a, Broady 1978) and included in the checklist of algae from Iceland (Hallgrímsson 2007).

Eunotia* cf. *neofallax Nörpel-Schempp et Lange-Bertalot in Lange-Bertalot *et al.* (1996: 3) (LM = Fig. 4 Q–W) Valves observed measured at length 9.0–22.0 µm, width 1.7–2.5 µm, and 16–20 striae in 10 µm (for n=9 LM). Valves showed a similar outline to those of *E. neofallax* Nörpel-Schempp et Lange-Bertalot, though stria density in our specimens was slightly denser and the presences of a spine on the apex could not be confirmed.

Relative abundance occurred at >10% at one site in the Þingvellir rift valley and >20% at one site in Hengill (Table 2). Previous reports of *E. neofallax* from intermittently wet subaerial habits included those with melting snow (Bouchard *et al.* 2018).

Eunotia palatina Lange-Bertalot et Krüger in Werum & Lange-Bertalot (2004: 154) (LM = Fig. 4 A–F; SEM = Fig. 4 J–L)

The valve morphology of *E. palatina* from our samples measured at length 24.2–38.5 µm, width middle 5.0–6.8 µm, 15–16 striae (middle) in 10 µm; 16–19 striae (ends) in 10 µm, and areolae 33–35 in 10 µm (for n=8 LM, n=2 SEM). Internal openings of the round areolae were not embedded in a groove (Fig. 4 J). A narrow hyaline area, from the short termination of the striae, extended across the ventral edge of the internal and external valve face, visible in LM (e.g. Fig. 4 B, D) and SEM (Fig. 4 J–i). A slight internal thickening occurred on the internal ventral margin where the proximal raphe ended (Fig. 4 J–ii).

Frustules occurred in association with bryophytes and lichen at low relative abundances (< 5%) in Hengill and the Þingvellir rift valley (Table 3). Lange-Bertalot *et al.* (2011) show specimens from a variety of aerophilous locations including the type population in Germany (see also Werum & Lange-Bertalot 2004, plate 7, figs 10–18) and the synonym from Iceland (as *E. arctica* var. *simplex* Hustedt 1937: 169), as well as Tara Mountains Poland, Southern Alps, Italy, Pyrenees, Andora.

Other *Eunotia*

Other, less common (< 5% relative abundance), *Eunotia* taxa present included *E.* cf. *valida* Hustedt (1930: 178) (Fig. 4 N) and *E. nymanniana* (Fig. 4 X–c), both listed from aerial habitats in the Hallgrímsson (2007) checklist. Observation of more valves of *E.* cf. *fallax* Cleve (1895: 33) (Fig. 4 O, P) would help confirm this taxon (length 22–25 µm, width 2.5–2.8 µm, and 16–18 striae in 10 µm).

Other Common Taxa with Relative Abundance of >5% in at Least One Sample

Diatomella balfouriana Greville (1855: 259) (LM = Fig. 10 A–E)

Valves in our material show biseriate striae on the deep mantles and volvocapulae with evidence of septa, each with an opening at each apex and in the central area. Though previously reported from Iceland (Hallgrímsson 2007, Foged 1974), this taxon, typically not common in our samples, occurred at 28% relative abundance at one site (WW 42) in the Þingvellir rift valley (Table 2).

Hygropetra balfouriana (Grunow ex Cleve 1895: 80) Krammer et Lange-Bertalot in Krammer (2000: 206) (LM = Fig. 2 Q–R; SEM = Fig. 2 U–V)

Valves with ghost filiform raphe (Fig. 2 R), girdle view shows rounded ends (Fig. 2 R). Valve face curved at the margins into a narrow valve mantle. Striae broad, radiate throughout, structured by several rows of areolae, narrowing into a "V" shape towards the axial area and rounded on the mantle (Fig. 2 U). Valve morphology measured at length 5.1–9.6 µm, width middle 2.8–4.1 µm, and striae 9–10 striae in 10 µm (for n=16 LM, n=7 SEM). Some areolae closed by vela. Visible transapical costae in the valve internal view and distant proximal raphe endings (Fig. 2 V). Septa in girdle bands not evident, but irregular linear slits on the volvocopula volvocapula (Fig. 2 U). The algal taxa lists from Iceland, Hallgrímsson (2007) and Foged (1974), include this species as *Pinnularia balfouriana* Grunow ex Cleve (1895: 80). Not common at sites, but in Hengill, *H. balfouriana* specimens occurred at >5 – 10% relative abundance at one site, >10%–20% at another, and at 59.6% at WW 53 (Table 2).

Melosira varians Agardh (1827: 628)

Valves occurred infrequently in general, but were present at 15% relative abundance at a site along the highland road, Landmannaleið, before Fjallabak and at < 1% further along Landmannaleið.

Orthoseira roeseana (Rabenhorst 1848–1860: 383) Pfitzer (1871: 134) (LM = Fig. 2 N, S, T; SEM = Fig. 3)

Valves of *Orthoseira roeseana* from rock scrapings in Iceland had a disc shaped valve face, 13–34.1 µm in diameter, which formed a right angle to the valve mantle, 8–15 µm long. The mantle contained uniseriate striae, 13–15 in 10 µm (Figs 2 N, 3 D). Areolae on the valve face occurred as small, round, uniseriate striae covering 4/5th of the valve face (Figs 2 S, T, 3 A–D). The middle hyaline area contained 3 to 4 carinoportulae with a rim, a feature typical of this genus (Round *et al.* 1990, Crawford 1981, Houk 1993). Short chains were observed. Valves were present with and without spines. When present, marginal spines were straight and spatulate in form, and arranged with distinct pores between them (Fig. 2 T, 3 D). Perforations were present on the girdle bands (Fig. 3 D).

Specimens from Iceland fit into the *Orthoseira roeseana* complex due to the presence of carinoportulae, linking spines, and a fairly deep mantle (Round *et al.* 1990). The radiate striae and number of carinoportulae distinguish *Orthoseira roeseana* from *O. johansenii* Lowe et Kociolek in Lowe *et al.* (2013: 46) (Lowe *et al.* 2013).The absence of rimoportulae (slits) between carinoportulae contrasts with *Orthoseira* species where this feature occurs such as *O. verleyenii* Van de Vijver in Lowe *et al.* (2013: 41) from lava tubes in Île Amsterdam (Lowe *et al.* 2013), *O. gremmenii* Van de Vijver et Kopalová (2008: 108) from the small volcanic Gough Island, southern Atlantic Ocean (Van de Vijver & Kopalová, 2008), *O. limnopolarensis* Van de Vijver et Crawford (2014: 248) from a sediment core Livingston Island (South Shetland Islands, Antarctica) (Van de Vijver & Crawford 2014), and *Orthoseira* taxon 1 and 2 from Madagascar (Spaulding & Kociolek 1998).

Valves occurred infrequently in general, but relative abundance occurred at 12% (WW 20) in Hengill and at 2.6% (WW 51) along Landmannaleið. Both sites contained some moss, a typical association for this genus (Roldán & Hernández-Mariné 2009). This taxon is also commonly reported from moist soils, wet walls, waterfall spray zones, and wet but not submerged habitats (Lowe *et al.* 2013).

Platessa rupestris var. ***interrupta*** (Krasske 1932: 105) Lange-Bertalot in Krammer & Lange-Bertalot (2004: 445) (LM = Figs 10 M–O, a; 12 B**)**

Valves similar in size to *P. rupestris,* but the striae constantly interrupted outlining the central area in both valves in our site, therefore we kept this taxon separate. Observed at >5% relative abundance in one site (WW 54).

Psammothidium marginulatum (Grunow in Cleve & Grunow 1880: 21) Bukhtiyarova et Round (1996: 3) (LM = Fig. 10 Y–Z)

The rapheless valve has marginal striae and adjacent to them a series of ornamentations, on the raphe valve outline irregular axial area, central area wide, rectangular, surrounded by 8 short striae (Fig. 10 Y, Z). Observed at 18.7% relative abundance in one site (WW 55) in Hengill (Table 2) and in low abundance at WW 3, 52, and 54.

Stauroneis* cf. *borrichii (J.B. Petersen 1915: 285) J.W.G. Lund (1946: 63) (LM = Fig. 11 X– a)

Valves, linear/lanceolate with parallel sides and broadly rounded ends, measured at length 23–38 µm, width 5.5–7 µm, and 25–28 striae in 10 µm (for n=10 LM). We used cf. as the length reported in the literature does not go above 30 µm. Axial area linear, narrow. Central area a rectangular fascia with isolated irregularly short striae, widening towards the margins. Raphe filiform, straight with indistinct central pores. Terminal fissures clearly visible, deflected. Transapical striae radiate in the middle, parallel to convergent near the poles. Absent from most wet walls, but present at >5% but <10% relative abundance at one site in Hengill and another in Þingvellir rift valley. Reported as able to survive desiccation (Petersen 1928a).

Staurosirella neopinnata Morales, Wetzel, Haworth et Ector (2019: 82) (LM = Fig. 2 B–G; SEM = Fig. 2 A)

In girdle view, frustules are rectangular and form ribbon-like colonies, joined by linking spines (Fig. 2 A), girdle consists of 5 separate copulae, slightly curved near the poles. Valves linear to elliptical lanceolate, no heteropolarity was observed length 10–25 µm, width 3–4.5 µm, 10 striae in 10µ, (for n=10 LM, n=5 SEM). Axial area fairly narrow, linear to slightly lanceolate. Striae parallel, composed of slit-like areolae, continuing without interruption onto the mantle (Fig. 2 A). Marginal spines almost always detected. No rimoportula, but one or two apical pore fields present. Generally rare or in low abundance at our sites, with the exception of one site (WW 3) where the relative abundance was 20% (Table 2).

Rare Taxa (<5% relative abundance) in Alphabetical Order

Notes on some, but not all, of the rare or less common taxa (relative abundance < 5%) are presented below (See also Table 3). A succinct effort to illustrate euaerial diatoms for Iceland led us to illustrate species enumerated, identified, and observed in at least 3 samples or at least once with relative abundance over 2 %, other taxa like *Muelleria gibbula* (Cleve 1894: 140) Spaulding et Stoermer (1997: 99) and *Rhoicosphenia abbreviata* (Agardh 1831: 34) Lange-Bertalot (1980: 586), documented at least twice in our samples are shown in plates without notes on morphology and distribution.

Adlafia bryophila (J.B. Petersen 1928: 388) Lange-Bertalot in Moser *et al.* (1998: 89) (LM = Fig. 10 R)

Valves linear with parallel margins and (sub-)capitate ends (length 14–20 µm, width 2.5–3.5 µm, 30–38 striae in 10µm). Axial area narrow, linear. Central area small, bordered by irregularly spaced, shortened striae. Striae uniseriate, in the middle strongly radiate changing abruptly to convergent near the poles. Raphe filiform with slightly curved central endings. Terminal fissures sharply hooked into the same direction.

Adlafia suchlandtii (Hustedt 1943: 168) Monnier et Ector in Monnier *et al.* (2012: 139) (LM = Fig. 10 h–i)

Valves lanceolate with protracted ends, length 19–20 µm, width 3.8–4.2 µm, for n=10 LM, hard to discern striae at the end, visible radiate striae surrounding central area. Central area square ⅓ to ½ of the valve width. Our specimens were consistently wider than published literature information (Krammer & Lange-Bertalot 1986, Cantonati *et al.* 2017).

Aulacoseira alpigena (Grunow in Van Heurck 1882: pl. 86) Krammer (1991: 93) (LM = Fig. 2 L–M)

Valves with rows of mantle areolae curved to the right (Fig. 2 L). The valve face is flat with one row of marginal areolae (Fig. 2 M) with visible cluster of 8 tubercules. Spines were not evident.

Caloneis schumanniana (Grunow in van Heurck 1880: 99) Cleve (1894: 53) (LM = Fig 11. R)

Valves linear-lanceolate with tri-undulated margins and cuneately rounded ends (length 25–42 µm, width 7–10 µm, 18–20 striae in 10 µm, for n=5). Axial area narrow, linear. Central area a broad rectangular fascia with crescent-shaped thickenings present on either side of the central area. Raphe straight, linear with weakly deflected central endings. Central pores distinct. Transapical striae parallel to weakly radiate in the middle, parallel towards the ends.

Cosmioneis pusilla (W. Smith, 1853: 52) D.G. Mann et Stickle in Round, Crawford & Mann (1990: 526) (LM= Fig. 12 F, SEM = Fig. 12 A)

Has been reported with central area medium-sized, circular to elliptical (Cantonati *et al.* 2017), but our LM specimen had central area outlining the number ’8’ (Fig. 12 F). Valve morphology measured at length 35.1–59.6 µm, width middle 10.8–24.1 µm, and striae 12–15 striae in 10 µm (for n=5 LM, n=1 SEM). Striae a little coarser than reported in literature, some specimens with shortened striae at the margin (Fig. 12 F). This taxon, known from habitats with variable conditions, can handle increased osmotic-pressure fluctuations on rocks (drying bryophytes) with variable water availability (Cantonati *et al.* 2017).

Cymbopleura* cf. *subaequalis (Grunow in Van Heurck 1880: 61) Krammer (2003: 101) (LM = Fig. 10 I)

Valves slightly dorsiventral (length 36–39 µm, width 8.5–9 µm, 13–15 dorsal center striae in 10µm, for n = 3). Dorsal side convex, ventral side only less convex. Axial area narrow, central area small. Striae both dorsally and ventrally radiate, closer together near the poles, our specimens had dorsal striae spaced in the middle. In LM individual puncta not visible. Raphe slightly ventrally displaced.

Fragilariforma nitzschioides (Grunow in Van Heurck 1881: pl. 44) Lange-Bertalot in Hofmann, Werum & Lange-Bertalot (2011: 268) (LM = Fig. 2 H)

Length 31 µm, valve width 3.9 µm, 16 striae in 10 µm. Population documented from squeezed bryophyte.

Fragilaria perminuta (Grunow in Van Heurck 1881: 150) Lange-Bertalot in Krammer & Lange-Bertalot (2000: 581) (LM = Fig. 2 K)

Rhomboid/lanceolate shape of the valve with slightly rostrate ends strongly unilateral bulging central area, length 21.9 µm, width 2.9 µm, striae 18 striae in 10 µm, the striae are mostly parallel, to slightly radiate toward the valve ends. Striae alternate.

Gomphonema Ehrenberg (1832: 87) **sp. 1** (LM = Fig. 10 G)

Valves weakly clavate, sometimes even lanceolate-elliptical. The largest width is found above the middle. The head poles are usually slightly protracted and flatly rounded while the foot poles are more or less sharply narrowed (length 21.5–28.7µm, width 4.5–6 µm, 9–12 striae in 10 µm, for n=3). Axial area linear, narrow. Central area unilaterally weakly elongated due to 1 or 2 shortened striae (sometimes striae are not shortened, but missing). Raphe lateral to sometimes filiform with almost unmarked terminal and central endings. Transapical striae moderately radiate to parallel, somewhat irregularly arranged. Individual areolae sometimes resolvable in LM but most of the times impossible to see. Stigma, when present, close to longest stria in the middle.

Gomphonema bipunctatum Krasske (1943: 87) (LM = Fig. 10 H)

Valves weakly clavate to linear-lanceolate with shortly protracted, rounded head poles and sharply narrowed foot poles (length 24–33 µm, width 4–5.2 µm, 12–14 striae in 10µm, for n=5). Our specimens a little bit longer and narrower than description in literature (Lange-Bertalot *et al.* 1996). Axial area narrow, linear. Striae radial in the center becoming parallel towards the ends. Central area unilaterally elongated due to one shortened stria in the middle. Stigmata present next to 2 slightly shortened stria in the middle. Raphe filiform with central pores turned towards the 2 stigmata. Transapical striae almost parallel to weakly radiate, more radiate towards the head poles. Areolae not resolvable in LM. Our specimens do not fit the wider *Gomphonema duplipunctatum* Lange-Bertalot et Reichardt in Lange-Bertalot *et al.* (1996: 88) (Levkov *et al.* 2016).

Luticola* cf. *nivaloides (W. Bock 1963: 236) Denys et De Smet (1996: 84) (LM = Fig. 10 j**)**

Valves lanceolate to elliptic-lanceolate. Smaller valves becoming rhombic-lanceolate. Apices slightly rostrate-capitate in longer valves; whereas, in middle-sized specimens, ends usually not protracted but broadly rounded. Valve length 17–35 µm, valve width 6–8 µm. Because the length of the valves in our samples reached up to 35 µm long, over the 24 µm long reported in the description, we list this taxon with the cf. designation. Axial area relatively wide and almost linear. Central area forming a slightly wedge shaped stauros, bordered near the valve face margin by one series of small, rounded areolae. One rounded to weakly transapically elongated stigma present, located rather isolated in the central area. Raphe branches straight to weakly curved. Central raphe endings short, but clearly deflected opposite to the stigma-bearing valve side. Central raphe pores simple. Terminal raphe fissures very short to absent, terminating before the last row of areolae in simple pores. Transapical striae radiate throughout, 16–21 in 10 µm, consisting of two to four small, rounded areolae. Marginal areolae larger and more transapically elongated on the side opposite the stigma but not on the other side. Internally, poroids of the valve face occluded by hymenes. Internal stigma opening consisting of almost rounded, irregularly lipped slit.

Luticola D.G. Mann in Round, Crawford & Mann (1990: 670) **sp. 1** (LM = Fig. 10 k**)**

Valves linear-elliptical with undulated (twice!) margins and capitate ends (valve length 24 µm, valve width 7.5 µm, 16–18 striae in 10µm). Axial area narrow, linear. Central area almost rectangular. Fascia absent due to some shortened striae. Stigma solitary placed. Raphe filiform straight. Central endings curved towards the opposite side of the stigma. Terminal fissures deflected to the same side. Transapical striae radiate in the middle.

Naviculoid sp. 2 (LM = Fig. 10 g)

A single specimen documented related with *Adlafia* (valve length 14 µm, valve width 3 µm), square central area, striae not discernable under LM.

Nitzschia perminuta (Grunow in Van Heurck 1881: pl. 68) Peragallo (1903: 672). (LM = Fig. 10 p–q, s–v) Valves linear-lanceolate with convex margins and with broadly rounded, slightly protracted ends (valve length 21–38 µm, valve width 3–4 µm, 15–21 fibulae in 10 µm, for n=10). Fibulae in the middle equidistantly spaced. Transapical striae not resolvable in LM.

Platessa rupestris (Krasske 1932: 105) Lange-Bertalot in Krammer & Lange-Bertalot (2004: 445) (Fig. 10 P–Q)

Valves lanceolate with subrostrate ends. (length 11.5–23 µm, width 3.5–5 µm, 25 striae in 10 µm). Raphe valve: axial area linear, slightly widened near the central area. Central area with more spaced, (shorter) striae (sometimes at one side, no shorter striae can be observed). Raphe filiform. Rapheless valve: axial area very narrow, linear, wider in the central area. Median striae much shorter. Reported as *Achnanthes rupestris* Krasske (1932: 105) from the Alps (Krasske 1932) and Iceland (Foged 1974). Observed at <5% relative abundance in two sites (WW 40, 54).

Pinnularia borealis Ehrenberg (1843b: 420) (LM = Fig. 11 E; SEM = Fig. 12 D)

Our specimens with measurements of: length 2 –42 µm, valve width 8–10.5 µm, 5–6 striae in 10 µm, for n=10 LM, were larger than those reported in the literature. This taxon, known to be distributed by wind, is reported as pseudaerial and terrestrial (Cantonati *et al.* 2017).

Pinnularia intermedia (Lagerstedt 1873: 2) Cleve (1895: 80) (LM = Fig. 11 I–J)

Valve length 20–29 µm, valve width 5–6.2 µm, and 8–8.5 striae in 10 µm (for n=5 LM). This taxon is previously documented from Iceland (Petersen 1928a, Foged 1974).

Pinnularia minoricapitata Krammer (2002: 175). (LM = Fig. 11 N–O). This taxon was reported by Petersen (1928a: 408) as *P. parva* var. *minuta* as it differs from *P. parva* by the smaller size. In our study length 30–40 µm, valve width 5–7 µm, 8–9 striae in 10 µm (for n=5 LM). Terminal raphe endings hooked to the same direction. Striae interrupted in the center. *Pinnularia minutiformis* Krammer (2000: 29) was used for the same taxon and later changed to the most current synonym.

Pinnularia parva W. Gregory (1854: 98) (LM = Fig. 11 K–M)

Valves linear with parallel margins and obtusely rounded, not protracted ends (length 30–40 µm, width 5–7 µm, 8–9 striae in 10 µm, for n=5 LM). Axial area narrow, straight. Central area a broad, rectangular fascia. Raphe filiform with laterally deflected central endings and teardrop central pores. Distal raphe ends deflected. Transapical striae parallel throughout the entire valve.

Pinnularia Ehrenberg (1843a: 45) **sp. 1** (LM = Fig. 11 D)

Valves linear with parallel margins and broadly rounded, not protracted ends (length 51–65 µm, valve width 9–13 µm, 5–5.5 striae in 10 µm, for n=10). Axial area narrow, linear. Central area rounded more than ½ of the width of the valve, asymmetrical in the middle due to the shortening of some striae on one side and marginal striae on the other. Raphe moderately lateral, slightly arcuate. Proximal raphe ends deflected towards one side, tear-drop shaped central pores. Distal fissures sickle-shaped in prominent terminal areas. Transapical striae broad, radiate in the middle, parallel to convergent near the apices. No longitudinal lines. We considered several taxa, for example *P. rabenhorstii* (Grunow 1860: 515) Krammer (2000: 22) is wider than our specimens and *P. idsbensis* Pavlov et Levkov (2013: 39) has central area always smaller than ½ width of the valve (Pavlov et Levkov 2013), while ours is wider.

***Pinnularia* sp. 2** (LM = Fig. 11 C)

Valves linear with parallel margins and broadly rounded, not protracted ends (length 65–72 µm, valve width 12–13 µm, 5 striae in 10µm, for n=5 LM). Axial area narrow, linear. Central area rounded more than ½ of the width of the valve, asymmetrical in the middle due to the shortening of some striae on one side and on the other no visible striae on valve face and central area reaching margin. Raphe moderately lateral, slightly arcuate. Proximal raphe ends deflected towards one side and curved, no visible central pores.

Pinnularia stomatophora (Grunow in A. Schmidt *et al.* 1876: pl. 44) Cleve (1895: 83) (LM = Fig. 11 B)

Valves broadly elliptic-lanceolate with convex sides and broadly rounded, sometimes protracted, ends (length 83 µm, width 9.5–10 µm, 13–14 striae in 10µm). Axial area narrow, slightly linear-lanceolate, widening towards the middle. Central area has a broad fascia, enlarging towards the valve margins. Raphe filiform, weakly curved with clearly enlarged central pores. Terminal fissures strongly hooked. Transapical striae weakly radiate and even sinuous in the middle, more and more convergent towards the apices. Longitudinal lines absent. This taxon has been reported from cold habitats (Cantonati *et al.* 2017).

Pinnularia* cf. *subcommutata Krammer (1992: 136) (LM = Fig. 11 A)

Valves linear with obtusely rounded ends. Our specimen was a little bit longer than reported in the literature (thus we chose to keep a cf. designation): length 76 µm, width 9 µm, 12 striae in 10µm, length in literature 40–70 µm (Krammer 2000). Axial area moderately broad, widening towards the central area. Central area elliptical. Raphe moderately lateral with bent central endings and distinct central pores. Terminal fissures shaped as hooks. Striae radiate in the middle, parallel towards the poles. A longitudinal band is present. Asymmetrically missing striae.

Sellaphora seminulum (Grunow 1860: 552) D.G. Mann (1989: 2) (LM = Fig. 10 c)

In current literature *Navicula seminulum* var. *radiosa* Hustedt (1954: 473) (Fig. 10 b) is a synonym of *S. seminulum* (Wetzel *et al.* 2015). However, we kept *S. seminulum* separate from the *N. seminulum* var. *radiosa* based on the less convex margins and narrower width for *N. seminulum* var. *radiosa.* The complex is known from intermittently-drying small water bodies.

Stauroforma atomus (Hustedt 1931: 164) D. Talgatti, C.E. Wetzel, E. Morales et L.C. Torgan (2014: 45) (LM = Fig. 2 O–P) known to survive in brackish conditions (Talgatti *et al.* 2014). Our specimens were thinner and longer than given in the literature, length 8–9 µm, width 2.4–2.6 µm, striae 16 striae in 10 µm (for n=10 LM) as compared with the type population length 4.5–7 µm, width 2.5–3.5 µm, striae 16 striae in 10 µm, but it fits Cantonati *et al.* (2017). Has been reported from Iceland as *Fragilaria atomus* Hustedt 1931: 164 (Hallgrímsson 2007) and *Fragilariforma atomus* (Hustedt 1931: 164) Lange-Bertalot in Hofmann, Werum & Lange-Bertalot 2011: 257 (Cantonati *et al.* 2017).

Ecology of Aerial Environments in Iceland

Exposed rock habitats from this study showed remarkable diversity in diatom species, while surprisingly collections from snow and ice habitats within Iceland during the same period as our study contained extremely low numbers of diatom species. Stramenopile representatives in the latter assemblages were predominantly chrysophytes (Lutz *et al.* 2015), which were also present in our samples (personal observation). This suggests that though present in a harsher landscape, the microhabitats available in the rock outcrops of these volcanic rocks provided enough refuge from the environment for diatom assemblages to grow and diversify. Similarly, the diversity of microhabitat conditions present on these aerial habitats likely drive patterns of diatom diversity observed.

The availability of moisture, nutrients, CO_2, and heat, and their interactions can drive the abundance and diversity of diatom taxa in aerial environments. Taxa classified as euaerial in this study applied to those taxa observed with evidence of physiological activity (intact chloroplasts), with relative abundances of > 5%, and with reports in at least 2 other sources as either aerophylic or terrestrial (Table 2). The high diversity of diatoms, along with the higher relative abundance of some taxa like *Humidophila* species observed on the volcanic rock outcrops sampled in this study suggest the availability of microhabitats with adequate and varied sources of moisture, nutrients, and heat. Several of the genera reported, especially those at relative abundances > 5%, such as *Humidophila* and *Orthoseira*, are commonly reported from aerial habitats (Lowe *et al*. 2014, Lowe *et al*. 2007, Furey *et al*. 2007).

Most of the assemblages we observed existed as a thin layer, likely because multi-layer or thicker assemblages observed for pseudoaerial diatom populations struggle to adhere to rock surfaces or proliferate without extensive mucilage production (Lowe *et al.* 2007). Though we observed some colonies of mucilage-producing cyanobacteria like *Nostoc linkia* Bornet ex Bornet et Flahault (1886: 193), the colonies were small and thus not likely to provide a moisture-rich environment for the diatoms. Cyanobacteria require more exposure to light compared to diatoms that can outcompete other taxa within the shading of the surface layer of rock biofilms (Karsten *et al.* 2007). The surrounding atmosphere, supplemented by moisture from the neighboring lichens, bryophytes and other epilithophytes, likely supplied the aerial diatom assemblages with sufficient moisture. Modifications to diatom morphological features can also reduce moisture loss. The frustules of *Humidophila* taxa contain reduced external openings (see for example Figs 7 A, K, P, 8 A, Q, 9 A) that can help reduce moisture loss, as has been shown in other studies (e.g. Furey *et al.* 2007). Some taxa like *Orthoseira roeseana* (Fig. 3 A–C), *Pinnularia borealis* (Figs 11 E, 12 D) and *Hygropetra balfouriana* (Fig. 2 U, V) are relatively more porous, but also frequently reported from aerial and terrestrial environments (Johansen 2010).

As the diatoms in this study existed in aerial settings with minimal or ephemeral moisture, we did not collect measurements of pH, DO, and conductivity. While substrate mineralogy, and chemistry including pH can influence diatom species assemblage structure (Furey *et al.* 2007), it may not be an ultimate driver of species distribution patterns as factors like moisture, coupled with microhabitat variations can act as stronger determinants of biodiversity (Furey *et al.* 2007, Lowe *et al*. 2007). However, the presence of acidophilic taxa, like *Eunotia* and *Pinnularia*, at the sites in this study suggest habitats may be slightly acidic (Krammer & Lange-Bertalot 2000, Denicola 2000, Smith & Manoylov 2007), though the high diversity of other diatoms indicates that sites were not extremely acidic.

Though aerial diatoms are typically adapted to low nutrient environments (Johansen 2010), sources of nutrients are still essential for diatom growth. Variability in habitat conditions on a microscale, i.e. in response to nutrients, can contribute to local-scale diversity. The presence of *Planothidium lanceolatum* (Brébisson ex Kützing 1846: 247)

Lange-Bertalot (1999: 287) (WW 55), *Navicula symmetrica* Patrick (WW 54) and *Melosira varians* (WW 50) suggest intermittent availability of nutrients in those samples. Utilization of nutrients released with microbial digestion could support the localized presence of high nutrient taxa in low abundance. The Icelandic landscape is nitrogen poor, and many juvenile lava fields and streams support an abundant flora of N_2-fixing taxa (Englund 1976). Diatoms like *Epithemia turgida* (Ehrenberg 1832: 80) Kützing (1844: 34), *Rhopalodia gibba* (Ehrenberg 1832 80) Müller 1895: 65) and *Epithemia sorex* Kützing (1844: 33) that contain endosymbiotic cyanobacteria that fix nitrogen (DeYoe *et al.* 1992, Stancheva *et al.* 2013), occurred in low abundances on the wetwalls, though it was not clear if low N-availability, lack of water, or another variable constrained their presence. Samples contained N_2-fixing cyanobacteria, but also in low abundance (personal observation).

Substrata type, including geology, can act as an additional limiting factor, but may also provide a source of minerals for aerial algae. Peterson (1928a), for example, reports that basalt and palagonite-breccia rocks contain insoluble calcium. In contrast, quartz, plagioclase, pyroxene and very high iron levels dominate the mineral composition of the igneous, mostly basalt rocks of Iceland (Lutz *et al.* 2016), and may help support a diverse assemblage of diatoms. In these aerial habitats, other minerals may intermittently come in as dust, especially with snowmelt. Iceland acts as an active dust source in the high-latitude cold region. About 50% of the annual dust events in the southern part of Iceland take place at sub-zero temperatures or in winter, when dust can mix with snow (Dagsson-Waldhauserova *et al.* 2015). During snowmelt, aerial environments may receive pulses of mineral inputs. The deposition of SiO_2 rich volcanic dust on all exposed surfaces in Iceland may also accelerate the thaw of snow and ice, with the potential of positive feedback to increase the anthropogenic Arctic warming. Heated volcanic rocks can create an oasis of habitats with the potential release of essential nutrients like P, Si, Mg, and Fe all needed for photosynthesis and other metabolic processes. Rocks potentially retain heat better than any fluids and therefore might support the well-developed diatom assemblages we observed.

Biogeography

While many diatoms in this study are likely adapted to the euaerial and pseudo-aerial conditions of these habitats, factors affecting dispersal and related biogeography need further study, especially where cryptic diversity of diatom morphospecies are concerned. The diversity of diatoms reported here fill in some knowledge gaps for the diatom flora of arctic regions that may help guide future studies on arctic biogeography. For example, the small fragilaroid taxa in this study exist in cold waters (Douglas & Smol 1999) and may show broader distribution patterns. The monospecific genus *Hygroperta* has been reported from moss habitats (Borchard *et al.* 2018) and as part of the current study as epilithic; both are common in northern landscapes. Representatives of the genus *Stauroneis* reported in this study have been previously reported from the Arctic (Van De Vijver *et al.* 2004). Many of the taxa common in this study (*Diatomella balfouriana*, *Eunotia* species, *Humidophila* species, *Hygropetra balfouriana*) and previously reported in studies from Iceland (Hallgrímsson 2007, Broady 1978, Foged 1974, Petersen 1928a) remain present on the Icelandic landscape. However, closer examination reveals the presence of new and likely new taxa, to suggest that careful taxonomic work remains necessary for underexplored regions like Iceland.

Conclusion

The diatom flora described here adds to the flora for this region, highlights the diversity of diatom assemblages that can inhabit euaerial environments, and provides evidence of adaptive success of diatoms in extreme habitats with limiting moisture and nutrients. Abundant diatoms in this study were well adapted to diel fluctuation in temperature compared to more stable aquatic environments. The presence of enough moisture for photosynthesis and exposure to high light levels might complement the access to atmospheric CO_2 in this environment to promote growth. The descriptions of one new diatom (*Humidophila eldfjallii sp. nov*) and one likely new diatom *Humidophila* sp. 1 further add to the knowledge of the global diversity of aerial diatoms. The SEM images provide additional morphological information for small taxa previously reported from the Icelandic landscape.

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