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The genus *Luticola* D.G.Mann (Bacillariophyta) from the McMurdo Sound Region, Antarctica, with the description of four new species

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Abstract

A revision of the freshwater diatom genus *Luticola* from the McMurdo Sound Region, including the McMurdo Dry Valleys and Cape Royds, Antarctica, was made to contribute to a consistent flora for the entire Antarctic Region. Detailed light and scanning electron microscopic observations, review of pertinent literature, and examination of historical and type material lead to the identification of 12 *Luticola* species. Four new species and one new combination are proposed, including *L. bradyi sp. nov*., *L. spainiae*, *sp. nov*., *L. macknightiae*, *sp. nov*., *L. transantarctica*, *sp. nov*., and *L. elegans*, *comb. nov. stat. nov*. Several of these taxa were previously identified as part of the *L. muticopsis* (Van Heurck) D.G.Mann complex; *Navicula muticopsis* f. *evoluta* W. & G.S. West, *L. muticopsis* f. *reducta* (W. & G.S. West) Spaulding, and *N. muticopsis* f. *capitata* Carlson, or mistaken for the similar *L. mutica* (Kützing) D.G.Mann and *L. cohnii* (Hilse) D.G.Mann. Morphological features of all new species were compared to the closest morphologically similar taxa, and their ecology and biogeography are discussed. All *Luticola* species considered here show restricted Antarctic distributions, and 8 of the 12 reported species are known only from the Antarctic continent.

Key words: biogeography, Cape Royds, diatom taxonomy, Dry Valleys, microbial mats, Ross Island

Introduction

Species of the genus *Luticola* D.G.Mann in Round *et al*. (1990: 670) are typical for terrestrial ecosystems in the Antarctic Region (Kopalová *et al*. 2011, Van de Vijver *et al*. 2011). The genus is characterized by uniseriate striae composed of rounded to transapically elongate areolae covered internally by perforated hymens, an isolated pore in the central area, a longitudinal canal positioned within the valve wall, and a simple filiform raphe with variable raphe endings (Round *et al*. 1990). A book volume for the genus was recently published by Levkov *et al*. (2013), which included 34 Antarctic Region taxa. A large number of new *Luticola* taxa have been described from Antarctica in recent years (Esposito *et al*. 2008, Kopalová *et al*. 2011, Van de Vijver *et al*. 2012, Zidarova *et al*. 2014), making the genus one of the most species-rich in the area. The *Luticola* species of Maritime Antarctica and the sub-Antarctic Islands have been recently revised (Van de Vijver & Mataloni 2008, Kopalová *et al*. 2011, Van de Vijver *et al*. 2011, Zidarova *et al*. 2014), showing that the genus *Luticola* is particularly widespread in the former region with more than 25 taxa compared to the sub-Antarctic islands where only 8 taxa were found. However, focused taxonomic work on the genus from the Antarctic continent is lacking, making a complete biogeographical analysis of the Antarctic Region not possible at present.

The pioneering paper by West & West (1911) gave the world a first look into the phycological diversity of the Antarctic continent and became the taxonomic foundation for the entire region. From collections taken from Shackleton's 1907–9 expedition, two species, one variety, and two forms of *Luticola* alone were described (West & West 1911). These taxa have since become staples in Antarctic species lists (Prescott 1979, Kellogg & Kellogg 2002), making Cape Royds an important type locality for Antarctic diatoms. Numerous investigations into the algal diversity of the McMurdo Sound Region have taken place since West & West (1911), such as Fritch (1912), Fukushima (1964),

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Seaburg *et al*. (1979), Kellogg *et al*. (1980), and Esposito *et al*. (2008). However, the illustrations and descriptions in West & West (1911) were incomplete by modern standards, resulting in a lack of consensus in species identity, and taxonomic species drift can be observed in these subsequent publications (Van de Vijver *et al*. 2012). Of specific concern is the complex of taxa around *L. muticopsis* (Van Heurck 1909: 12) D.G.Mann in Round *et al*. (1990: 671) (*i.e*. Van de Vijver & Mataloni 2008), consisting of (but not limited to) *Navicula muticopsis* f. *evoluta* West & West (1911: 283), *L. muticopsis* f. *reducta* (W. & G.S. West 1911: 284) Spaulding in Spaulding *et al*. (1997: 410), *Navicula muticopsis* f. *capitata* Carlson (1913: 14), and *Navicula muticopsiforme* West & West (1911: 284). Furthermore, the 'force-fitting' of Antarctic diatoms into European taxa (Jones 1996, Tyler 1996), such as *L. mutica* (Kützing 1844: 93) D.G.Mann in Round *et al*. (1990: 670), *L. cohnii* (Hilse in Rabenhorst 1860: 962) D.G.Mann in Round *et al*. (1900: 670), and nomenclatural hybrid formae such as *Navicula mutica* f. *cohnii* (as in Baker 1967: fig. 4o) have likely obscured ecological and biogeographical data.

The McMurdo Dry Valleys (MDVs) are adjacent to Cape Royds, and are home to the McMurdo Long-Term Ecological Research (MCMLTER) program, which has been monitoring Dry Valley streams and associated algal mat transects for over 20 years (mcmlter.org). Within this long-term research, *Luticola* species have been demonstrated to dominate Antarctic stream diatom communities, both in diversity and relative abundances (Stanish *et al*. 2011, 2012). *Luticola* species are also present in cryoconite holes (Stanish *et al*. 2013), within mosses (Kohler, unpublished data), and in ponds (Sakaeva 2014). Diatoms from the MDV region have been used to interpret sediment cores taken from lakes (Spaulding *et al*. 1997, Whittaker *et al*. 2008, Konfirst *et al*. 2011, Warnock & Doran 2013), indicate stream flow conditions (Stanish *et al*. 2011, 2012), and predict community structure as a function of climatic changes (Esposito *et al*. 2006). In order to avoid erroneous conclusions that could be made when comparing biogeographical and ecological work from other regions (*e.g.* Kopalová & Van de Vijver 2013, Kopalová *et al*. 2013, 2014), a standardized Antarctic taxonomy is necessary (Jones 1996), and a reinvestigation into this flora using modern methods and literature is timely.

To promote compatibility among researchers and with other localities in the Antarctic Region, we analyzed samples for the genus *Luticola* taken by the MCMLTER program, which are stored at the Institute of Arctic and Alpine Research (INSTAAR) herbarium at the University of Colorado at Boulder, USA. Additionally, we resampled the lakes of Cape Royds over a century after West & West (1911) in order to evaluate their taxonomic designations, and compare this flora with the original material sampled by Shackelton's expedition stored at the British National History Museum in London, UK. All recovered species from the genus *Luticola* were compared using the most current literature, and are discussed based on detailed light and scanning electron microscopy observations. We here describe four new *Luticola* species, create one new combination, update synonyms to the most current accepted taxonomic unit, and compare all observed McMurdo Sound species with *Luticola* from the other parts of Antarctic Region (the sub- and Maritime Antarctic islands).

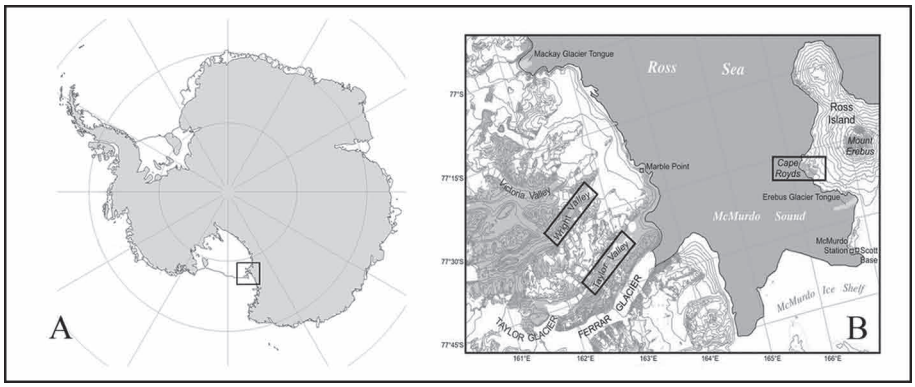

FIGURE 1. Map of Antarctica with detail of the McMurdo Sound region (A) along with the locations Wright Valley, Taylor Valley and Cape Royds (B). Image adapted from the US Geological Survey.

Materials and methods

Site Descriptions:—The McMurdo Dry Valleys (76˚ 30'–78˚ 30' S, 160˚–164˚ E), are the largest ice-free area in Antarctica (~4800 km^2) located along the coast of McMurdo Sound in South Victoria Land (Fig. 1). Here, the terrain consists mostly of unconsolidated alluvium, but streams, ponds, and seepage areas are present in summer, hosting

cyanobacterial mats and mosses (McKnight *et al*. 1999, Ball & Virginia 2014). The ephemeral stream networks drain into perennially ice-covered lakes on the valley floors (McKnight *et al*. 1999). Cape Royds is a coastal area (77˚ 32–33' S, 166˚ 8–11' E) below the Mount Erebus volcano on the west side of Ross Island and across the McMurdo Sound from the MDVs (Fig. 1). It is most famous for being the location of Shackleton's hut, which sits on the opposite side of Pony Lake from an Adélie penguin rookery. Cape Royds consists of volcanic, unconsolidated alluvium, and contains many permanently ice-covered lakes which thaw around the margins, creating "moat" areas and exposing microbial mats below.

Sample collection and analyses:—In the MDVs, algal mat and moss samples are monitored along transects as part of the MCMLTER, and have been sampled annually since 1993–94 using a brass cork borer in early to mid-January. Dry Valley cryoconite holes were opportunistically sampled in January 2014 by scooping organic material with a metal spoon. At Cape Royds, lakes, seeps, and small ponds were sampled in January 2013 and 2014 with forceps to resample historical sites in West & West (1911). All samples were put in 20 mL microcentrifuge vials or Nalgene® bottles, labeled with GPS coordinates, preserved in ~5% formalin (final concentration), and shipped to the University of Colorado. To verify identifications, we obtained the slides from West & West (1911) stored at The Natural History Museum, London (UK), to analyze the original material. All samples used for this study are listed in Table 1, along with sample locations, sample accession numbers, and dates. Samples collected during the 2011–12, 2012–13, and 2013–14 summers with confirmed specimens are listed as accession numbers from the INSTAAR herbarium, and are available online using the Antarctic Freshwater Diatoms Website: http://huey.colorado.edu/diatoms/about/index.php. An exception to this is for *Luticola bradyi*, which due to its extreme rarity, but consistent identification, we included records from the last 20 years.

TABLE 1. INSTAAR diatom collection accession numbers, sample date, name of collector, GPS coordinates, and notes for all samples used in this study.

Sample ASSN number	Sample date	Collector	Coordinates (GPS)	Location description
INSTAAR #566 BCGB03#3	8/1/2003	D. M. McKnight	S77.62331° E163.05767°	*Nostoc* mat sample from the margin of Bowles Creek, Taylor Valley.
INSTAAR #2657-CC9	10/1/2014	A. Mass	S77.58560° E163.30145°	Sediment from a Commonwealth Glacier cryoconite hole, Taylor Valley.
INSTAAR #2467-11	24/1/2013	T. J. Kohler	S77.54224° E166.14967°	Floating marginal mat from Coast Lake, Cape Royds.
INSTAAR #2477-21	24/1/2013	T. J. Kohler	S77.54115° E166.15671°	Floating marginal mat from Clear Lake, Cape Royds.
INSTAAR #2475-19	24/1/2013	T. J. Kohler	S77.54947° E166.15620°	Sampled from a green algae patch at the margin of Green Lake, Cape Royds.
INSTAAR #2350-O2	29/12/2012	T. J. Kohler	S77.72679° E162.27985°	Orange cyanobacterial mat from a tributary to Lyons Creek, Taylor Valley.
INSTAAR #958-WHC11-2	10/1/2012	T. J. Kohler	S77.72520° E162.31097°	Orange cyanobacterial mat from Wormherder Creek, Taylor Valley.
INSTAAR #2257CSYM1	13/1/2013	T. J. Kohler	S77.61363° E163.05227°	Yellow moss from the margin of Canada Stream, Taylor Valley.
INSTAAR #994-OV#1	25/1/2012	T. J. Kohler	S77.52402° E161.69628°	Cyanobacterial mat from the Onyx River at Lake Vanda, Wright Valley.
INSTAAR #2669-LPS#4	7/1/2014	A. Sakaeva	S77.55017° E161.05023°	Orange cyanobacterial mat from a Labyrinth pond, Wright Valley.
INSTAAR #2671-NRP.13.S1	26/12/2013	A. Sakaeva	S77.68438° E162.81473°	Cyanobacterial mat from a pond south of the Nussbuam Riegel, Taylor Valley.
INSTAAR #2665-MHR.13.U	1/2/2014	A. Sakaeva	S77.83347° E166.63353°	Benthic algae from the upper pond on the McMurdo Hut Ridge, Ross Island.
BM 34126	*12/1908 or 1/1909	J. Murray	Unknown?	Moraine, Mt. Erebus.
BM 34124	*12/1908 or 1/1909	J. Murray	Unknown?	Moraine, Mt. Erebus.
BM 34129	Unknown?	J. Murray	Unknown?	Pond, Cape Royds.

*not clear from the original West & West (1911) publication, likely collected about three miles from the camp, altitude from 300 to 400 feet.

Algal-mat samples were digested using heat and hydrogen peroxide (H_2O_2), rinsed several times with distilled water, dried onto cover slips, and permanently mounted on glass microscope slides with Zrax® mounting medium (W.P. Dailey, University of Pennsylvania). Light microscope analyses were performed using an Olympus Vanox microscope (Japan) at 1250× magnification. Scanning electron microscope (SEM) images were made after being air-dried onto aluminum stubs, and sputter-coated with 50 nm of Au (or 20 nm of Au-Pd in London). Some samples for SEM were additionally filtered through cellulose membrane filters with a 0.8 µm pore diameter prior to analysis. Material was observed at Charles University in Prague, Czech Republic (Figs. 11, 29, 55–56, 74, 119–120, and 140–141), using a JEOL JSM-6380LV SEM (20 and 25 kV), the Botanic Garden Meise, Belgium (Fig. 20), with a JEOL-5800LV SEM (25 kV), the National History Museum, London, UK (Figs. 47 and 83), with a ZEISS ULTRA SEM (3 kV), the Nanomaterials Characterization Facility at the University of Colorado at Boulder, United States (Figs. 90–91 and 108–109), with a JEOL JSM 7401 field emission SEM (3 kV), and at the United States Geological Survey Microbeam Laboratory, Denver, United States (Figs. 150–151), with a FEI Quanta 450 FEG field emission microscope (15 kV) at a working distance of 8 mm.

Descriptions of each taxon are given along with LM and SEM micrographs using terminology following Round *et al*. (1990) and Levkov *et al*. (2013). Resulting valve dimensions reflect the maximum and minimum measurements from a population, and stria densities reflect the range based on "n" observations. New species were compared with similar *Luticola* taxa from the Antarctic Region and globally, using Esposito *et al*. (2008), Van de Vijver & Mataloni (2008), Kopalová *et al*. (2009, 2011), Van de Vijver *et al*. (2011, 2012), Levkov *et al*. (2013), and Zidarova *et al*. (2014). Isotypes were sent to British Natural History Museum, London, UK, and the Botanic Garden Meise, Belgium.

Results

A total of 12 different *Luticola* taxa were observed in this study, four of which could not be identified using currently available literature, even though some of these taxa were found to be the dominate species in samples. Furthermore, the geographic distributions of the observed taxa (Table 2) indicate a highly specific *Luticola* flora on the Antarctic continent.

TABLE 2. Distribution of *Luticola* species recorded during this study and those taken from the literature with assigned biogeographic regions defined by Chown & Convey (2007). C = cosmopolitan, CA = Continental Antarctic Region, MA = Maritime Antarctic Region, and SA = sub-Antarctic Region.

Taxon	Distribution
Luticola cohnii (Hilse) D.G.Mann	C
Luticola dolia Spaulding & Esposito	CA
Luticola elegans (West & West) Kohler & Kopalová	CA
Luticola laeta Spaulding & Esposito	CA
Luticola macknightiae Kohler & Kopalová	CA
Luticola murrayi (West & West) D.G.Mann	CA
Luticola pseudomurrayi Van de Vijver & Tavernier	CA
Luticola spainiae Kohler & Kopalová	CA
Luticola bradyi Kohler	CA
Luticola transantarctica Kohler & Kopalová	CA
Luticola adelae Van de Vijver & Zidarova (2011: 148, figs 32–45)	MA
Luticola amoena Van de Vijver, Kopalová, Zidarova & Levkov in Levkov *et al*. (2013: 63, pl. 44, figs. 21–33)	MA
Luticola australomutica Van de Vijver	MA
Luticola bogaertsiana Zidarova, Levkov & Van de Vijver in Zidarova *et al*. (2014: 159, figs. 21–34)	MA
Luticola caubergsii Van de Vijver in Van de Vijver & Mataloni (2008: 455, figs. 8–17)	MA
Luticola contii Zidarova, Levkov & Van de Vijver in Zidarova *et al*. (2014: 162, figs. 35–49)	MA
Luticola delicatula Van de Vijver, Kopalová & Zidarova	MA
Luticola desmetii Kopalová & Van de Vijver in Kopalová *et al*. (2011: 47, figs. 2–13)	MA
Luticola doliiformis Kopalová & Van de Vijver	MA
Luticola evkae Kopalová	MA
Luticola gigamuticopsis Van de Vijver in Van de Vijver & Mataloni (2008: 454, figs. 2–7)	MA
Luticola higleri Van de Vijver, Van Dam & Beyens in Van de Vijver *et al*. (2006: figs 3–42)	MA

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TABLE 2. (Continued)

Taxon	Distribution
Luticola katkae Van de Vijver & Zidarova	MA
Luticola neglecta Zidarova, Levkov & Van de Vijver in Zidarova *et al*. (2014: 157, figs. 2–20)	MA
Luticola nelidae Van de Vijver in Van de Vijver & Mataloni (2008: 458, figs. 29–38)	MA
Luticola olegsakharovii Zidarova, Levkov & Van de Vijver in Zidarova *et al*. (2014: 164, 50–64)	MA
Luticola pusilla Van de Vijver, Kopalová, Zidarova & Levkov	MA
Luticola quadriscrobiculata Van de Vijver in Van de Vijver & Mataloni (2008: 457, figs. 18–28)	MA
Luticola raynae Zidarova & Van de Vijver in Van de Vijver *et al*. (2011: 150, figs. 52–62)	MA
Luticola tomsui Kopalová in Kopalová *et al*. (2011: 56, figs. 73–87)	MA
Luticola truncata Kopalová & Van de Vijver	MA
Luticola vandevijveri Kopalová, Zidarova & Levkov	MA
Luticola vermeulenii Van de Vijver	MA
Luticola austroatlantica Van de Vijver, Kopalová, Spaulding & Esposito	MA/CA
Luticola gaussii (Heiden) D.G.Mann	MA/CA
Luticola permuticopsis Kopalová & Van de Vijver	MA/CA
Luticola muticopsis (Van Heurck) D.G.Mann	MA/CA/SA
Luticola beyensii Van de Vijver, Ledeganck & Lebouvier in Van de Vijver *et al*. (2002: 236, figs. 2–13)	SA
Luticola crozetensis Van de Vijver, Kopalová, Zidarova & Levkov in Levkov *et al*. (2013: 94, pl. 46, fig.s 1–14)	SA
Luticola ledeganckii Van de Vijver in Van de Vijver *et al*. (2002: 56 57, pl. 57, figs. 7–14)	SA
Luticola robusta Van de Vijver, Ledeganck & Beyens in Van de Vijver *et al*. (2002: 59, pl. 58, figs. 1–7)	SA
Luticola subcrozetensis Van de Vijver, Kopalová, Zidarova & Levkov in Levkov *et al*. (2013: 228, pl. 46, figs. 15–31)	SA
Luticola suecorum (Carlson 1913: 15, figs. 1–27) Van de Vijver in Van de Vijver & Mataloni (2008: 467)	SA

Luticola austroatlantica Van de Vijver, Kopalová, Spaulding & Esposito in Esposito *et al*. (2008: 1383, figs. 9–27) (Figs. 2–11).

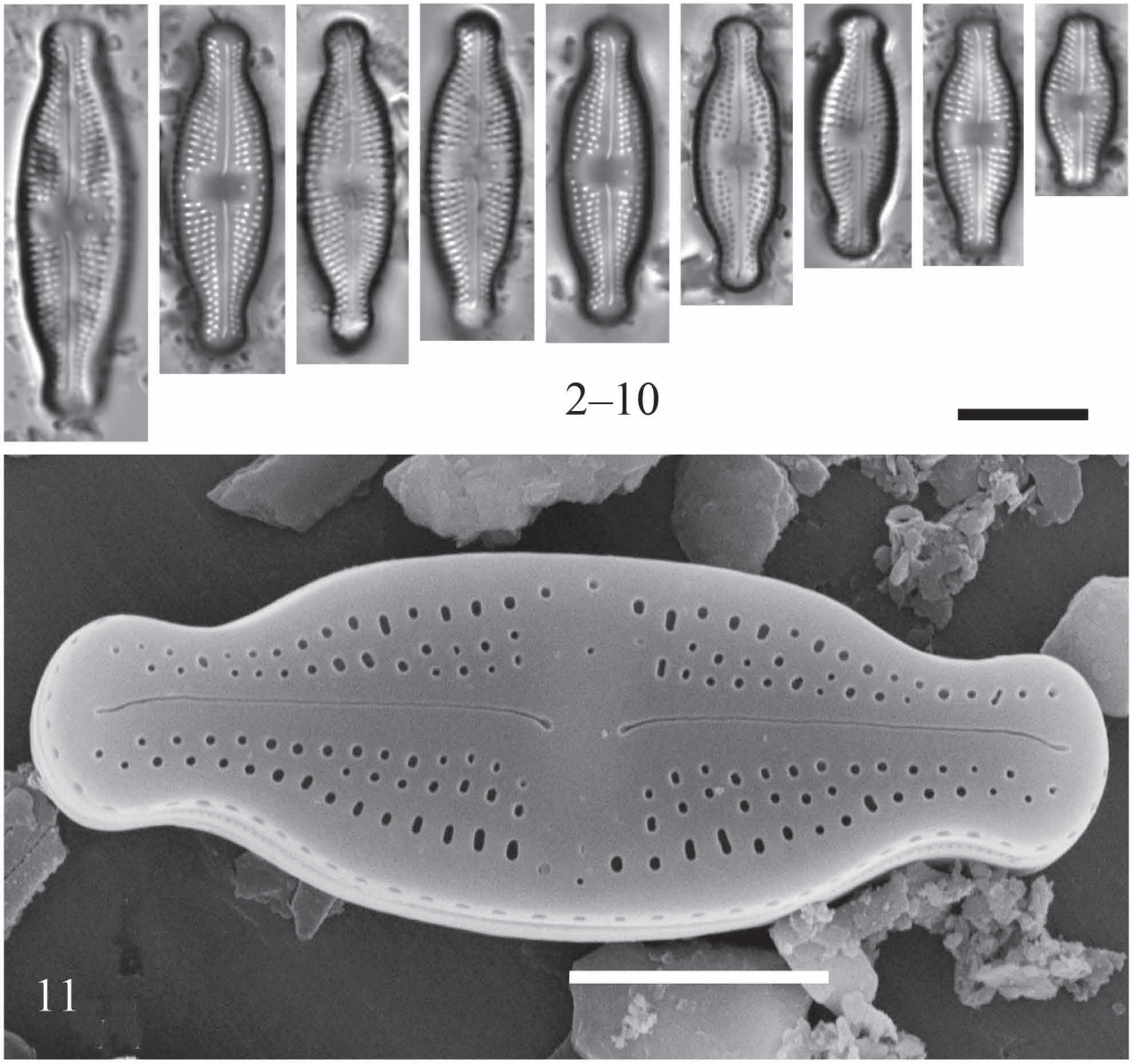
LM observations:—(Figs. 2–10) Valves linear-lanceolate to elliptical-lanceolate with two convex margins. Apices distinctly capitate with constriction most pronounced on isolated pore side, becoming truncate to rostrate in smaller specimens (Figs. 9–10). Valve dimensions (n=37): length 6.4–30.0 µm, width 4.4–8.2 µm. Axial area linear, slightly widening at apices and central area. An isolated pore present in the central area, halfway between the center and valve margin. Central area rectangular to bow-tie shaped, bordered by shortened striae on both sides. Raphe branches straight, deflecting away from isolated pore at both proximal and distal ends. Transapical striae radiate throughout, 16–21 in 10 µm.

SEM observations:—(Fig. 11) Striae composed of 2–3 areolae, 1–2 at apices. Areolae rounded, elongated at valve margins, not extending past distal raphe endings. Isolated pore rounded. Central area bordered by a single row of three rounded areolae on both sides. Proximal raphe endings resolve into open pores, deflect away from isolated pore. Distal raphe endings deflect away from the isolated pore, but slightly curve in the opposite direction at ends, resolving into small pores on valve face. Clear separation between valve face areolae and valve margins. A single row of rounded areolae present along entire valve mantle, not interrupted at apices.

Habitat, ecology and distribution:—*Luticola austroatlantica* is known only from Maritime and continental Antarctica. It is abundant in MDV streams, and was co-described from populations from Bowles Creek, Canada Stream, Delta Stream, and Von Guerard Stream, all in the Fryxell basin of Taylor Valley, along with the type locality on James Ross Island. Because it was historically identified as *L. muticopsis* or a variety therein (see below), its range and distribution may be broader than is currently known. Other records that match our description come from Lake Miers in the McMurdo Dry Valleys as *Navicula murrayi* by Baker (1967: fig. 4p), Deception Island (as *L.* aff. *muticopsis* 1, Van de Vijver & Mataloni 2008: 463, figs. 91–99), and the West Ongul Islands as *Navicula muticopsis* var. *muticopsis* by Ko-Bayashi (1965: pl. 26–27) and *Navicula muticopsis* var. *muticopis* f. *murrayi* (W. & G.S.West) Ko-Bayashi (1963: 9–11) by Fukushima *et al*. (1974: pl. 2, figs. A–C).

INSTAAR herbarium:—Aiken Creek 900–903, 2224–2228; Von Guerard Stream 905–908, 911–913, 916–919, 923–926, 928; Bowles Creek 933–936, 938–940; Commonwealth Stream 945–948, 951–954; Wormherder Creek 955; Priscu Stream 960–961; Bohner Stream 963–966; McKay Creek 976, 977–978; Wharton Creek 979–980, 982; Delta Stream 983–984, 986–987, 990–992; Onyx River 994–996, 998–999, 1001; Canada Stream 1002–1005, 1010–1011, 2257; Green Creek 1018–1019, 1021–022, 1025–1027, 2314–2318; Lawson Creek 1030–1033, 1038, 1041; Miers

Stream 1047–1049; Adams Stream 1051–1057, 1064; Relict Channel 1066–1071, 1077–1081, 1084, 1087; Lyons Stream tributary 2349–2351; Picture Pond 2670; Hughes Glacier Pond 2679; Little Sharpe (unofficial name) 2340; Many Glaciers Pond 2492; Parera Pond 2493; Nussbaum Regal Pond (unofficial name) 2671, Spaulding Pond 2494–2496.



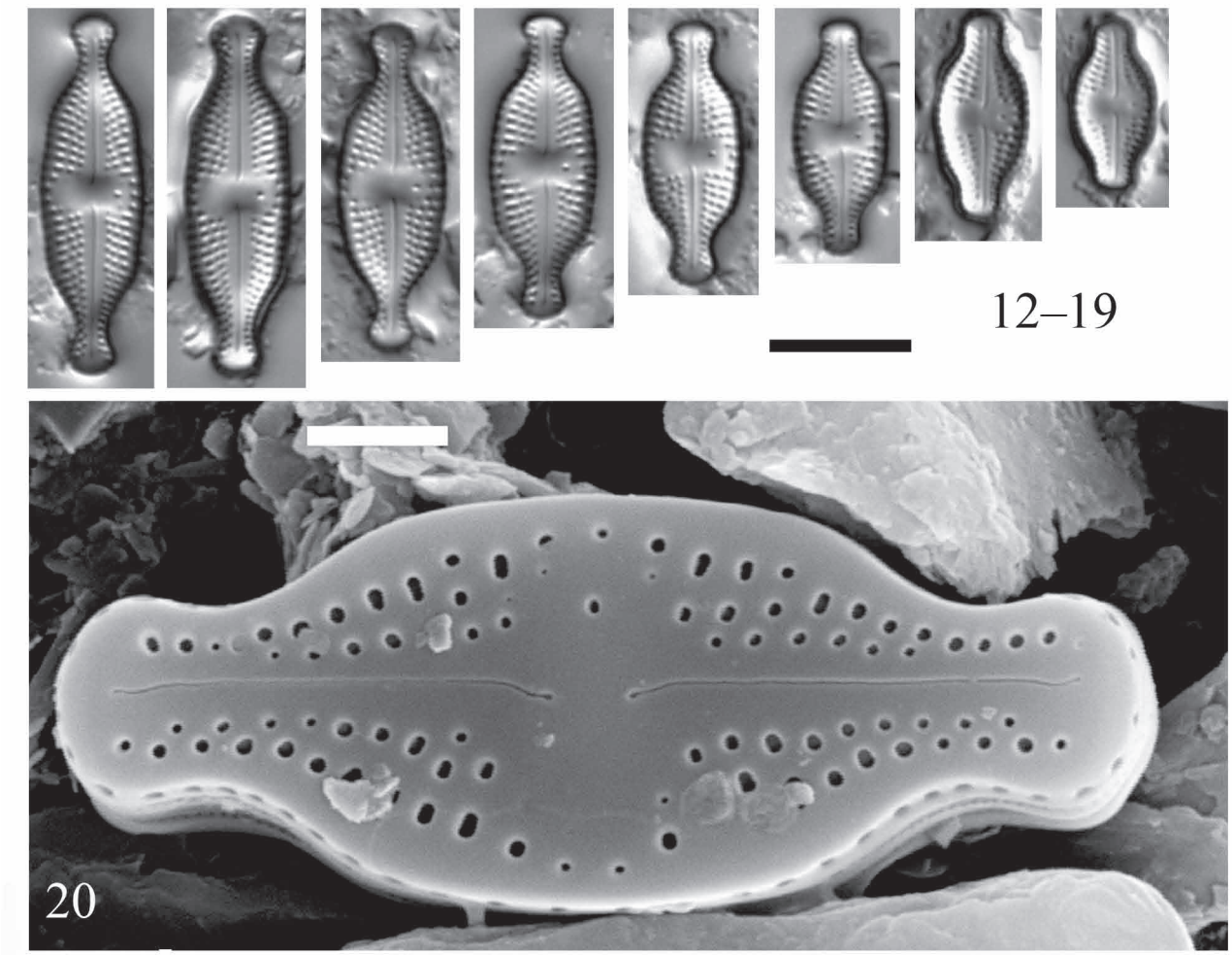
FIGURES 2–11. *Luticola austroatlantica* Van de Vijver, Kopalová, Spaulding & Esposito. Light (LM) and scanning electron micrographs (SEM). 2–10. Specimens from a confirmed locality, Bowles Creek, Taylor Valley, LM. 11. External valve view of specimens from a confirmed locality, Canada Stream, Taylor Valley, SEM. LM scale bar = 10 µm. SEM scale bar = 5 µm.

Observations:—This diatom has been previously identified in Taylor Valley as *N. muticopsis* and *N. muticopsis* f. *evoluta* in Kellogg *et al*. (1980: 176, pl. 1, figs. 10–11), and was described as a new species in Esposito *et al*. (2008). We measured a population from Bowles Creek, INSTAAR #566, which was indicated in Esposito *et al* (2008) as a sample with confirmed *L. austroatlantica*. This population measured 11.8–30.0 µm in length, 5.6–8.2 µm in width, and had 16–21 striae in 10 µm (n=14). We also measured a population taken from the far inland side of Taylor Valley in a tributary to Lyons Stream, INSTAAR #2350-O2 (Table 1). This community was composed almost exclusively of *L. austroatlantica*, and we measured valve lengths from 6.4–26.6 µm and valve widths as 4.4–7.6 µm, with 18–20(24) striae in 10 µm (n=23). Since the size series described and pictured from the Dry Valleys in Esposito *et al*. (2008) does not represent a complete cell cycle (only lengths of 12–17 µm are reported), this species is more variable in the MDVs than the original images and description suggest.

Luticola austroatlantica bears resemblance to *L. truncata* Kopalová & Van de Vijver in Kopalová *et al*. (2009:

118, figs. 34–50), especially at smaller and intermediate size ranges, which is present on James Ross and Livingston Islands. However, *L. truncata* is wider than *L. austroatlantica* (7.0–9.5 µm vs. 4.4–8.7 µm), has margins that are more parallel, and generally has more areolae per stria (3–5). In addition, the apices of *L. truncata* never become rounded and capitate as in *L. austroatlantica*. Among other McMurdo Sound species, *L. austroatlantica* could be confused with *L. macknightiae* Kohler & Kopalová, *sp. nov*., especially at lower size ranges. However, *L. austroatlantica* generally has more areolae within a stria (2–3, rarely 4 vs. 1–2, rarely 3), and has more capitate apices than *L. macknightiae*. Furthermore, *L. austroatlantica* is typically wider than *L. macknightiae* at any given length. *Luticola elegans* (West & West 1911: 285) Kohler & Kopalová *comb. nov*. is similar in valve outline to *L. austroatlantica*, though generally wider in breadth (6.4–9.5 µm *vs*. 4.4–8.2 µm in our population), and more areolae per stria (3–4 *vs*. 2–3, rarely 4). *Luticola elegans* additionally is less constricted between the capitate apices and the valve center compared to *L. austroatlantica*, and apices are generally wider. At the upper size range, *L. elegans* is more rostrate, while *L. austroatlantica* is more capitate.

Luticola dolia Spaulding & Esposito in Esposito *et al*. (2008: 1385, figs. 37–41) (Figs. 12–20).



FIGURES 12–20. *Luticola dolia* Spaulding & Esposito. Light (LM) and scanning electron micrographs (SEM). 12–19. Specimens from the Onyx River, Wright Valley, LM. 20. External valve view of specimens from the Onyx River, SEM. LM scale bar = 10 µm. SEM scale bar = 2 µm (top).

LM observations:—(Figs. 12–19) Valves linear-elliptic with straight to convex margins, becoming slightly undulate in larger specimens (Figs. 12–13). Apices highly capitate, becoming rostrate at small sizes (Figs. 17–19). Valve dimensions (n=12): length 11.3–25.1 µm, width 5.4–7.7 µm. Axial area linear, opening towards central area. An isolated pore is present in the central area, located halfway between the valve center and valve margin. Central area circular to bow-tie shaped, bordered by shortened striae on both sides. Raphe branches straight, deflecting away from isolated pore on distal and proximal ends. Transapical striae radiate throughout, 15–19 in 10 µm.

SEM observations:—(Fig. 20) Striae composed of 2–3 areolae, 1–2 at apices. Areolae rounded to elongated

throughout, not extending past distal raphe endings on the valve face. Isolated pore rounded. Central area bordered by single row of three rounded areolae on side opposite isolated pore, 1–2 rows on isolated pore side. Proximal raphe endings deflected opposite isolated pore, with some specimens having ends that curve back slightly to the opposite direction. Distal and proximal raphe endings terminate into linear slits or small pores on valve face. Clear separation between valve face and margins. A single row of with rounded areolae present along entire valve mantle, not interrupted at apices.

Habitat, ecology and distribution:—At present, this species is known only from the McMurdo Dry Valleys from which it was described. Even here, *Luticola dolia* is sparse throughout Taylor Valley, and rare or absent at Cape Royds (Sakaeva 2014). This species has been shown to be common in the Lake Bonney Basin of Taylor Valley, especially in Wormherder Creek (Stanish *et al*. 2012). In this survey, we found *L. dolia* to be abundant in the mosses of Lake Fryxell Basin streams, as well as the outlet of the Onyx River in Wright Valley.

INSTAAR herbarium:—Aiken Creek 901; Von Guerard Stream 905–908, 911–912, 916–918, 923, 925–926; Harnish Creek 928; Bowles Creek 933, 936, 939, 940; Wormherder Creek 955; Priscu Stream 960–961; Bohner Stream 963–966; Wharton Creek 979–982; Delta Stream 986–987, 990, 992; Onyx River 994–996, 998, 1001; Canada Stream 1010, 2257; Green Creek 1019, 1022, 1027, 2316–2317; Lawson Creek 1038, 1041; Miers Stream 1048; Adams Stream 1051, 1053–1057, 1064; Relict Channel 1066, 1068, 1070, 1077–1081, 1084; Little Sharpe (unofficial name) 2340; Upland Pond 2677–2678; Spaulding Pond 2494–2496; Picture Pond 2668.

Observations:—Identified as *Navicula muticopsis* f. *capitata* in Kellogg *et al*. (1980: 176, pl. 1, fig.12), *L. dolia* was later described as a separate species in Esposito *et al*. (2008). This species is easily recognizable due to the narrow constrictions beneath the highly capitate ends. It is possible that different morphotypes are present within our concept of *L. dolia*, as differences in distal raphe endings, density of striae areolae, valve outline, and central area shape (oval *vs*. bow-tie) have been observed. However, assessing differences between populations of *L. dolia* is difficult both due to the rarity of this taxon, but also because of the images provided in the original description, which are of intermediate lengths. Furthermore, these morphological differences are present within as well as among populations, making it difficult to discern if these represent intraspecific variation, or if two similar morphotypes co-occur. Our measurements in the above description were made from the Onyx River at Lake Vanda, which had abundant *L. dolia*, and is on the other side of the Asgard Range from the type locality Delta Stream (Esposito *et al*. 2008), where we observed *L. dolia* to be more sparse. Additional SEM and LM images from the same population as those presented here are pictured on plate 138 of Levkov *et al*. (2013).

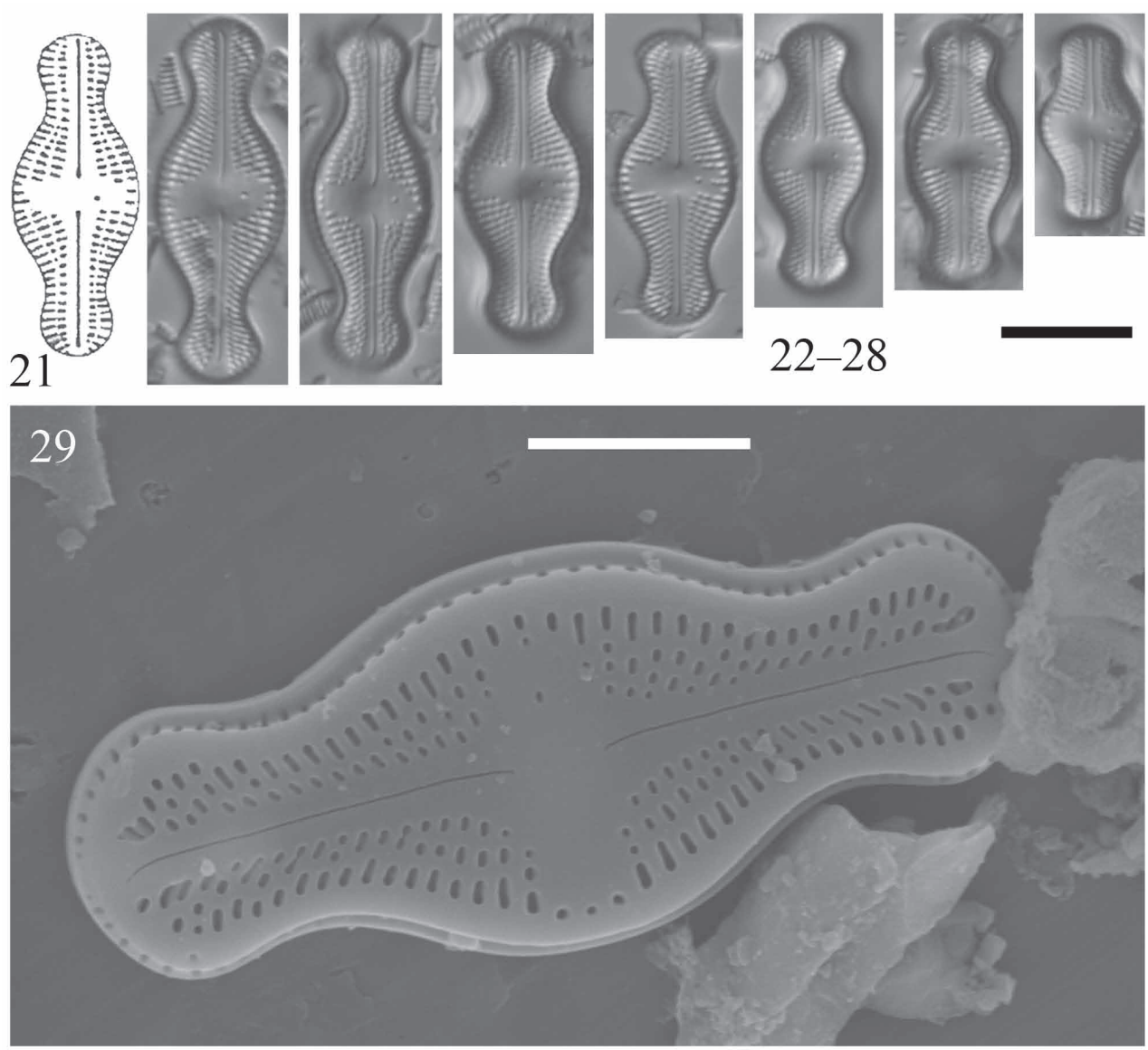
Luticola dolia is virtually unmistakable amongst other MDV *Luticola*, though it shares some similarities with *Luticola* taxa from other Antarctic localities. For example, *Luticola doliiformis* Kopalová & Van de Vijver in Kopalová *et al*. (2011: 49, figs. 14–28) is similar in valve outline, but differs by having broadly rounded, enlarged apices, denser striae (18–20 *vs*. 14–19 in 10 µm), and a wider axial area (Kopalová *et al*. 2011). Furthermore, *L. doliiformis* possesses smaller, more rounded areolae compared to the larger, elongated areolae in *L. dolia*. Lastly, *L. doliiformis* possesses shorter distal raphe fissures, and has an isolated pore closer to the margin than does *L. dolia* (Kopalová *et al*. 2011). *Luticola katkae* Van de Vijver & Zidarova in Van de Vijver *et al*. (2011: 143, figs. 2–15) also looks similar under LM, having similar capitate apices (Van de Vijver *et al*. 2011). However, *L. katkae* may have more areolae per stria (2–4 *vs*. 2–3), and is unmistakable under SEM due its elevated, thickened raphesternum, absent in *L. dolia*. Lastly, *L. dolia* shares several characteristics with *L. evkae* Kopalová in Kopalová *et al*. (2011: 51, figs. 35–50) such as similar central areas and sparse, punctate striae. However, *L. dolia* has a more elongated valve outline and less clearly convex margins than *L. evkae*. Most notably, *L. evkae* has broader, more capitate apices than *L. dolia*, as discussed in Kopalová *et al*. (2011).

Luticola gaussii (Heiden in Heiden & Kolbe 1928: 623, pl. 3, fig. 71) D.G.Mann in Round *et al*. (1990: 670) (Figs. 21–29, Fig. 21 is an original illustration from West & West (1911)).

LM observations:—(Figs. 22–28) Valves elliptical to elliptical-lanceolate with convex margins, rounded in central area. Apices broadly rounded, capitate. Valve dimensions (n=10): length 14.8–27.5 µm, width 7.7–9.7 µm. Axial area linear, expanding towards the central area. An isolated pore present in the central area, halfway between the valve center and valve margin. Central area rectangular, bordered by shortened striae on both sides. Raphe branches straight, deflects away from the isolated pore at both proximal and distal ends. Transapical striae radiate throughout, 19–23 in 10 µm, with longitudinal interruptions present as illustrated by West & West (Fig. 21).

SEM observations:—(Fig. 29) Striae composed of 3–4 areolae, 2–3 at apices. Areolae elongated throughout, becoming broader near valve margins, sometimes extending past distal raphe endings. Isolated pore elongated. Central

area bordered by a single row of three rounded areolae on both sides. Both proximal and distal raphe endings simple, slightly deflecting away from the isolated pore, resolving into slits on valve face. Clear separation between areolae and valve margins. A single row of elongated areolae present along entire valve mantle in shallow depression, interrupted at apices.



FIGURES 21–29. *Luticola gaussii* (Heiden) D.G. Mann. 21. Original illustration from West & West (1911: pl. 26, fig. 135). Light (LM) and scanning electron micrographs (SEM). 22–28. Specimens from Coast Lake, Cape Royds, LM. 29. External valve view of specimens from Clear Lake, Cape Royds, a confirmed West & West (1911) locality, SEM. LM scale bar = 10 µm. SEM scale bar = 5 µm.

Habitat, ecology and distribution:—*Luticola gaussii* was thought to be endemic to the Antarctic continent until it was recently observed from the lakes of James Ross Island, Maritime Antarctica (Kopalová *et al*. 2011). The earliest records from the McMurdo Sound region date from Cape Royds by West & West (1911) as *Navicula* (*Pinnularia*) *globiceps* W.Greg. (1856: 10), and noted from Green and Clear Lakes (Fig. 21). Fritch (1912) may have also found this diatom, and pictured a similar species as *Navicula globiceps* f. *amphicephala* Fritsch (1912: 54). *Luticola gaussii* is a commonly reported diatom from Dry Valley streams (Stanish *et al*. 2011, 2012), lakes (Baker 1967, Spaulding *et al*. 1997), and ponds (Sakaeva 2014), where it is generally rare in relative abundances (especially rare in *Nostoc* mats), but broad in distribution. Lastly, *L. gaussii* is a common *Luticola* species in cryoconite holes (Stanish *et al*. 2013).

INSTAAR herbarium:—Aiken Creek 900–902, 2224–2228; Bowles Creek 936, 938–939; Commonwealth Stream 945–948, 951–954; Priscu Stream 961; McKay Creek 975–978; Wharton Creek 979, 981–982; Delta Stream 983, 990–991; Onyx River 995–996, 999; Canada Stream 1002–1005, 1010–1011; Green Creek 1018–1019, 1021–1022, 1025–1026, 2314–2317; Miers Stream 1046, 1048–1049; Adams Stream 1052–1054, 1064; Picture Pond 2666–

2668, 2670; Blue Lake 2472, 2487, 2497; Many Glaciers Pond 2492; Clear Lake 2501; Coast Lake 2502; Upland Pond 2677–2678; Spaulding Pond 2494–2496; Blue Lake 2498–2500.

Observations:—*Luticola gaussii* was elevated to species by Hustedt (*Navicula gaussii*), and is a likely synonym with *Navicula globiceps* West & West (1911: fig. 135). *Navicula muticopsis* f. *reducta* described by West & West (1911) may also be a synonym of *L. gaussii*, due to the image in Kellogg *et al*. (1980: 176, pl. 1, fig.19) [but not Seaburg *et al*. (1979: 166, pl. 22, fig. 92)] which is likely a small valve of *L. gaussii*. In the illustration provided by West & West (1911) (as *Navicula globiceps*), it is clear that *L. gaussii* has slit-like areolae, which is confirmed by SEM (Fig. 29). Also referenced by West & West (1911) in both the text and illustration are the longitudinal interruptions in striae; two in the middle of the valve, and one at the ends, which is an important distinguishing characteristic. Our measurements agree well with Levkov *et al*. (2013), who report the size of this species to be 14–34 µm length, 7.5–13.5 µm width, and having a stria density of 18–22 in 10 µm composed of 3–4 areolae.

Similar species include *L. pseudomurrayi* Van de Vijver & Tavernier in Van de Vijver *et al*. (2012: 164, figs. 93–110), which is often documented from East Antarctica, though not in the McMurdo Sound Region. *Luticola pseudomurrayi* has less capitate apices than *L. gaussii*, a more elongated central area, does not bear longitudinal interruptions in striae, and may have 4–5 areolae compared to 3–4 in *L. gaussii* (Van de Vijver *et al*. 2012). Within the McMurdo Sound Region, *L. gaussii* is most similar to *L. transantarctica* Kohler & Kopalová *sp. nov*., which also has highly capitate apices and convex margins. However, *L. transantarctica* also does not possess the longitudinal interruptions in striae, has more elongated valve margins, and is generally narrower than *L. gaussii*. Lastly, *L. permuticopsis* Kopalová & Van de Vijver in Kopalová *et al*. (2011: 53, figs. 51–72), possesses a less rounded and more elongated central part of the valve, has more areolae per striae (3–6), and more angular, capitate apices.

Luticola laeta Spaulding & Esposito in Esposito *et al*. (2008: 1383, figs. 28–36) (Figs. 30–47)

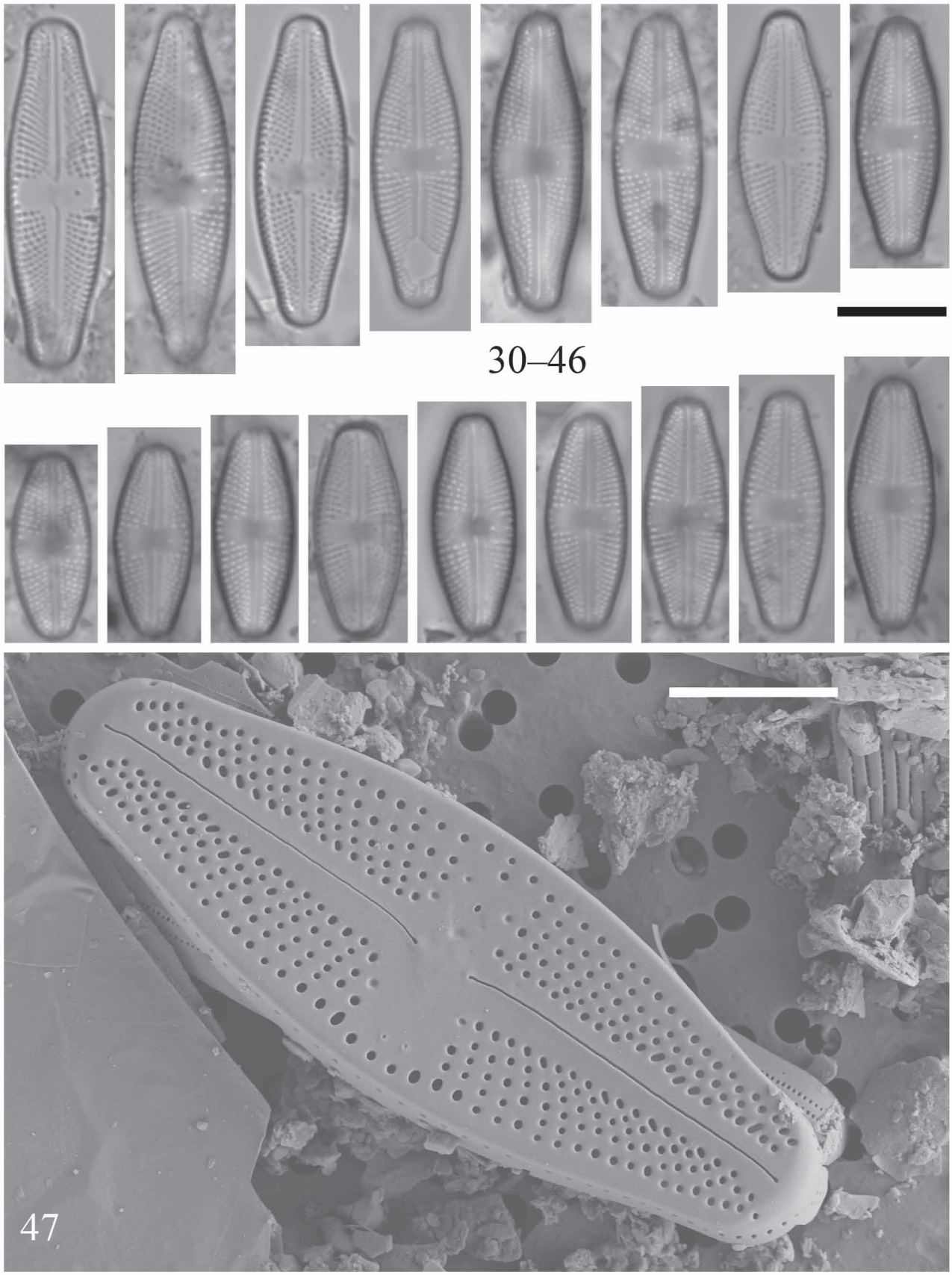
LM observations:—(Figs. 30–46) Valves elliptical-lanceolate to linear-lanceolate with convex margins. Apices rounded at smaller size ranges (Figs. 38–40), rostrate at upper sizes (Figs. 30–36). Valve dimensions (n=13): length 17.4–35.6 µm, width 7.1–8.8 µm. Axial area linear, expanded near central area and apices. Central area rectangular to almost bow-tie shaped, bordered by shortened striae on both sides. An isolated pore present in the central area, half-way between valve center and valve margin. Raphe straight, with external distal and proximal endings deflected into the opposite direction of the isolated pore. Transapical striae radiate throughout, more broadly spaced in valve center, 18–21 in 10 µm.

SEM observation:—(Fig. 47) Striae composed of 4–6 areolae, 3–4 at the apices. Areolae rounded, elongated at axial area, sometimes extending past distal raphe endings. Isolated pore rounded. Central area bordered by 1–2 rows of four rounded areolae on the isolated pore side, a single row on the opposite side. Proximal and distal raphe endings deflect away from isolated pore, terminating into small pores on valve face. Clear separation between valve face areolae and valve margins. A single row of rounded areolae present along entire valve mantle, interrupted at apices.

Habitat, ecology and distribution:—At present, this species is known only from the Antarctic continent, in the MDVs from which it was described. While it is ubiquitous throughout the Dry Valleys, albeit at low relative abundances, the greatest populations have been observed in moss samples from Canada Stream (INSTAAR #2257) and Bowles Creek (INSTAAR #566), the latter of which is the type locality (though not type-habitat) of this species. *Luticola laeta* is also a common *Luticola* species in cryoconite holes, especially on Canada Glacier (Stanish *et al*. 2013), though it appears to be rare in ponds and absent from Ross Island (Sakaeva 2014).

INSTAAR herbarium:—Aiken Creek 901–902, 2224–2228; Von Guerard Stream 905–908, 911–913, 916–919, 923–926; Harnish Creek 928; Bowles Creek 933, 935, 938–940; Commonwealth Stream 946, 948, 952–954; Wormherder Creek 955; Wharton Creek 982; Delta Stream 984, 986–987, 990–992; Onyx River 995; Canada Stream 1010, 2257; Green Creek 1018–1019, 1021, 1025–1026, 2315–2318; Lawson Creek 1031–1033, 1038, 1041; Miers Stream 1046–1047, 1049; Adams Stream 1051–1055, 1064; Relict Channel 1066–1071, 1077–1081, 1084, 1087.

Observations:—The smaller size range of this species has probably been identified as *L. mutica* or *L. cohnii*, which are species complexes similar to that of *L. muticopsis* (Kopalová *et al*. 2011), where small rounded cells have been assigned taxonomically. Described from the Northern Hemisphere, *L. mutica* is more oval-shaped and has eccentric proximal raphe endings terminating in recurved hooks (Levkov *et al*. 2013), a characteristic not present in any MDV *Luticola* species. *Luticola cohnii* is also a species described from Europe (as *Stauroneis cohnii* Hilse in Rabenhorst 1860). Similar to *L. laeta*, it is 19–40 µm in length, and 8.5–11.0 µm in width, but is always ovular in outline (Levkov *et al*. 2013). Most importantly, the external distal raphe endings in *L. cohnii* do not terminate until shortly before valve edge (Van de Vijver *et al*. 2011: figs. 30–31), unlike in *L. laeta*, where the external distal raphe ends terminate on the valve face.



FIGURES 30–47. *Luticola laeta* Spaulding & Esposito. Light (LM) and scanning electron micrographs (SEM). 30–46. Specimens from a confirmed locality, Canada Stream, Taylor Valley, LM. 47. External valve view from Canada Stream, SEM. LM scale bar = 10 µm. SEM scale bar = 5 µm.

Among other *Luticola* from the Antarctic Region, *L. vermeulenii* Van de Vijver in Van de Vijver *et al*. (2011: 145, figs. 16–29) has a similar length range (24–50 µm), but is generally wider than *L. laeta* (9.5–14.0 µm vs. 7.5–10.0 µm) with denser striae (14–17 in 10 µm) and more elongated areolae per stria (5–7; Van de Vijver *et al*. 2011). *Luticola australomutica* Van de Vijver in Van de Vijver & Mataloni (2008: 458) is another similar species both in valve outline and dimensions, with length 17–35 µm, width 6–8 µm, and stria density 16–21 in 10 µm. However, *L. austalomutica* has only 2–4 areolae per stria (compared to 4–6 in *L. laeta*), and the raphe terminates at the apices before the last row of areolae (Van de Vijver & Mataloni 2008), whereas it continues to or past the last row in *L. laeta* (Esposito *et al*. 2008: fig. 35). Valve sides are also generally more convex for *L. laeta*, while one side of *L. austalomutica* is flattened (Van de Vijver & Mataloni 2008).

Among MDV taxa, *L. laeta* shares similarities with *L. spainiae* Kohler & Kopalová, *sp. nov*. and *L. murrayi* (W. & G.S.West 1911: 285) D.G. Mann in Round *et al*. (1990: 671), especially in length and width ratios. *Luticola laeta* differs from these taxa primarily in terms of valve outline. *Luticola spainiae* has more broadly rostrate apices, and generally has fewer areolae per stria than *L. laeta* (4–5, 2–4 at apices). *Luticola murrayi* is widest in the very center of the valve, gradually tapering toward the apices, while *L. laeta* have more convex margins. Furthermore, the areolae and isolated pore in *L. laeta* are rounded, while in *L. murrayi* the outside row of areolae and isolated pore are elongated. Finally, *L. laeta* shares similarities in valve outline to *L. bradyi*, *sp. nov*., but *L. bradyi* is both wider (10.5–12.5 µm) and longer (28.3–44.8 µm) than *L. laeta*, and has broadly rostrate to sub-capitate apices with more areolae per stria (5–7).

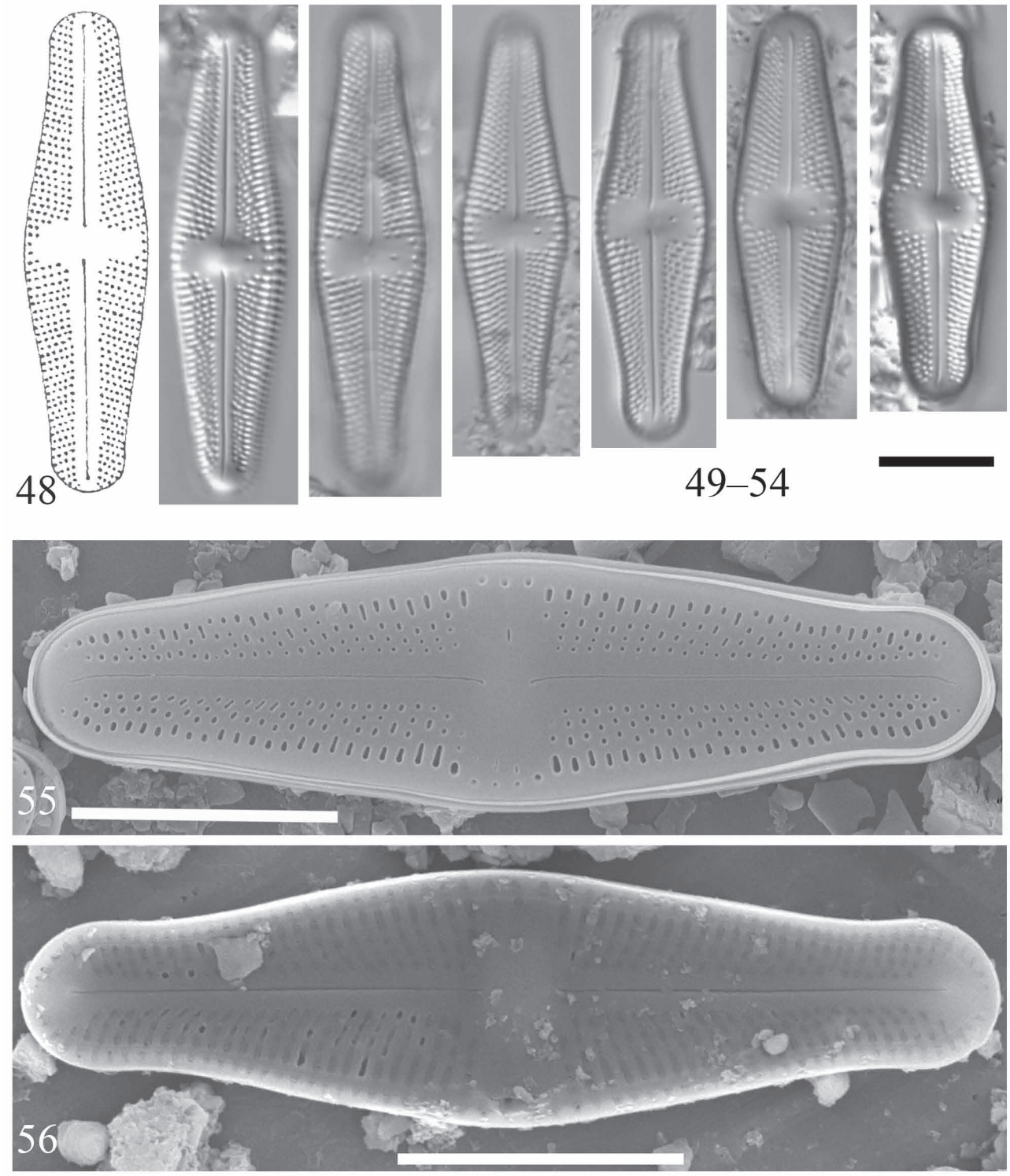
Luticola murrayi (W. & G.S.West 1911: 285, pl. 26, fig. 129) D.G. Mann in Round *et al*. (1990: 671) (Figs. 48–56, Fig. 48 is the original illustration by West & West (1911))

LM observations:—(Figs. 49–54) Valves rhombic-elliptic to elliptical-lanceolate with convex margins, rapidly attenuating to broadly rounded non-protracted apices. Valve dimensions (n=52): length 28.1–40.4 µm, width 6.8–10.2 µm at valve center, 4.5–5.8 µm at apices. Axial area linear, only slightly expanded near central area and apices. An isolated pore present in central area, located halfway between the valve center and valve margin. Central area rectangular to bow-tie shaped, bordered by shortened striae on both sides. Raphe branches straight, deflecting away from isolated pore at both distal and proximal ends. Transapical striae irregular, radiate throughout, 12–16 in 10 µm, 14–18 in 10 µm towards apices.

SEM observations:—(Figs. 55–56) Externally (Fig. 55), striae composed of 3–5 areolae, 2–3 at apices. Areolae elongated and slit-like throughout, becoming more rounded towards central area, extend past distal raphe endings. Isolated pore slit-shaped. Central area bordered on both sides by a single row of 3–4 rounded areolae positioned closer to valve margin than other striae. Distal raphe endings terminate on valve face on before margins, deflected away from isolated pore. Proximal raphe endings defect away from isolated pore, terminate as small pores. Clear separation between valve face and margin, with clear open area at apices around distal raphe endings. A single row of rounded areolae visible along valve mantle. Internally (Fig. 56), central nodule slightly thickened. Both proximal and terminal raphe endings slightly deflected towards isolated pore. Marginal canal slightly visible. Areolae covered by hymenes. Isolated pore covered by solid silica flap.

Habitat, ecology and distribution:—*Luticola murrayi* was described from Cape Royds, Ross Island, as *Navicula murrayi* by West & West (1911). Although commonly referred to in the literature and widely reported from a large number of Antarctic localities (Prescott 1979), this species is often confused with other *Luticola* species and reported distributions should be interpreted with caution. Illustrated specimens from the literature that match our concept of *L. murrayi* include reports from Mirny and Molodezhnaya Stations (as *Navicula muticopsis* f. *murrayi*, Fukushima 1966: fig. 1d) and the greater Ongul Islands at Lützow Holm Bay (as *Navicula globiceps* var. *elongata*, Ko-Bayashi 1963, pl. 4, fig. 2, and as *Navicula muticopsis* var. *muticopsis* f. *murrayi*, Fukushima *et al*. 1974: pl. 2 fig. D). This species has been commonly reported from Southern Victoria Land (as *Navicula muticopsis* f. *murrayi*, Seaburg *et al*. 1979: pl. 22, fig. 91) and the MDVs, though it has probably been confused with *L. laeta* (Van de Vijver *et al*. 2012). While more rare in the MDVs as compared to Cape Royds where it was described (Sakaeva 2014), it has been observed in Taylor Valley streams. In all populations, it is present alongside abundant *Achnanthes taylorensis* Kellogg *et al*. (1980: 174, pl. 1, figs. 3–4, pl. 2 figs. 1–2) and *Navicula shackletoni* W. & G.S.West (1911: 286, pl. 26, figs. 136–138).

INSTAAR herbarium:—Pony Lake 2354, 2355; Coast Lake 2467–2468; Green Lake 2473–2475, 2503; Blue Lake 2487, 2497; Picture Pond 2666–2667, 2670.



FIGURES 48–56. *Luticola murrayi* (W. & G.S.West) D.G.Mann. 48. Original illustration from West & West (1911: pl. 26, fig. 129). Light (LM) and scanning electron micrographs (SEM). 49–54. LM of specimens from Green Lake, Cape Royds. 55. SEM of external valve view from population at Green Lake. 56. SEM of internal valve view from a population from a pond on the McMurdo Hut Ridge. LM scale bar = 10 µm. SEM scale bars = 10 µm.

Observations:—There is a lack of consensus on the concept of *L. murrayi*, probably because the original species description, as well as for its variety, *Navicula (Pinnularia) murrayi* var. *elegans* (West & West 1911: 285, pl. 26, fig. 130), was made from the measurement of one valve. Dimensions are given as single values; length 45 µm, width 11.5 µm and 14 striae in 10 µm. No type specimen or type slide has been recovered, and only one illustration is given in the manuscript (reproduced here as Fig. 48). The illustration furthermore lacks an isolated pore, and the absence of this

feature diagnostic for the genus has been a source of speculation (Ko-Bayashi 1963, Van de Vijver *et al*. 2012, Levkov *et al*. 2013). One year after its description, Fritsch (1912) reported *Navicula murrayi* from Gap Pond, Winter Harbor, and gives a similarly vague description; length 43 µm, 10 µm width (no stria density given), and comments that it is rare. A half century later, Ko-Bayashi (1963: 13, pl. 4) reported several species from the Ongul Islands as different forms of *N. murrayi*, with the result being several new concepts that differ from the original illustration. In a classic case of species drift, one concept of *N. murrayi* by Ko-Bayashi (1963, pl. 5–7) was later reported by Hustedt (1966), Sabbe *et al*. (2003), and Ohtsuka *et al*. (2006) before finally being described as a new species, *L. pseudomurrayi*, by Van de Vijver *et al*. (2012) from material gathered from Lützow Holm Bay, across the continent from Ross Island.

In a recent investigation of the Cape Royds type material, Van de Vijver *et al*. (2012) reported that they were unable to find a single valve that matched the description of *L. murrayi* in West & West (1911). They proceeded to create a new "lectotype" (BM 34129) for *L. murrayi*, even though *L. murrayi* was not observed on the slide. Further, Van de Vijver *et al*. (2012) suggested that the true *L. murrayi* is likely a synonym with *L. laeta*, which is commonly found in the MDVs and roughly matches the illustration. However, neither Van de Vijver *et al*. (2012) nor the authors of this paper have observed any valves of *L. laeta* on Cape Royds or Ross Island. As a result, there is no clear evidence to support the hypothesis that the two species are conspecific.

Another concept of *L. murrayi* comes from Levkov *et al*. (2013), who, unlike Van de Vijver *et al*. (2012), report finding the true *L. murrayi* on the original West & West (1911) slides from the moraines on Mt. Erebus (BM 34124 and BM 34126), with an original note beneath two slides indicating that the species was present as evidence (Levkov *et al*. 2013: 539, pl. 129, figs. 29–30). On this slide were numerous capitate diatoms, along with what the authors explain to be a number of initial cells. It is these initial cells, according to Levkov *et al*. (2013), that most closely fit the original description and illustration, and the capitate diatoms were likely confused with *L. muticopsis*, which are also noted to be present on the slides. Therefore, in the concept of *L. murrayi* advocated by Levkov *et al*. (2013), the original illustration depicts only an initial cell, and they argue that this would make sense given the lack of an isolated pore, which may be possible in initial valves. They then designated a new "lectotype" for *L. murrayi*, slide BM 34126.

However, the *L. muticopsis* specimens illustrated on the same plate in West & West (1911: figs. 123–124) also do not have an isolated pore (see below, Figs. 64–65) and are obviously not initial cells. The presence of an isolated pore is also discussed in the original description of *L. murrayi*, and along with the illustrated straight proximal raphe endings as noted in Van de Vijver *et al*. (2012), the omission of an isolated pore was most likely an oversight and not intentional. Furthermore, the initial cell presented in Levkov *et al*. (2013) is capitate, like the smaller-sized cells, and this is inconsistent with both the illustration and the description of *L. murrayi*. It is our opinion that the species pictured as *L. murrayi* in Levkov *et al*. (2013) better fit the variety "*elegans*," which is illustrated directly beside the nominate species in the original publication (West & West 1911: 285, pl. 26, fig. 130) .

We examined the slides with the original notes (BM 34124 and BM 34126) from the London Natural History Museum, and like Levkov *et al*. (2013) found a capitate *Luticola* to be the dominate species on both slides, along with a few initial valves that have a similar morphology to the illustration in West & West (Fig. 57). Based on this information alone, it is reasonable to speculate that *L. murrayi* is a drawing of an initial valve and the capitate diatom is instead the real species. However, as part of our sampling of recent material on Cape Royds, we found a large population of *Luticola* that we identify as *L. murrayi* from the margin of Green Lake (INSTAAR #2475–19). These specimens are not initial valves as suggested by their integrity in valve outline, uniform striae, and diminution in size. At the lowest size range, this specimen overlaps with the capitate diatoms in Levkov *et al*. (2013), although never presenting capitate apices as part of its morphology. As a result of these observations, we suggest our concept of *L. murrayi* better fits the original description than do previous interpretations.

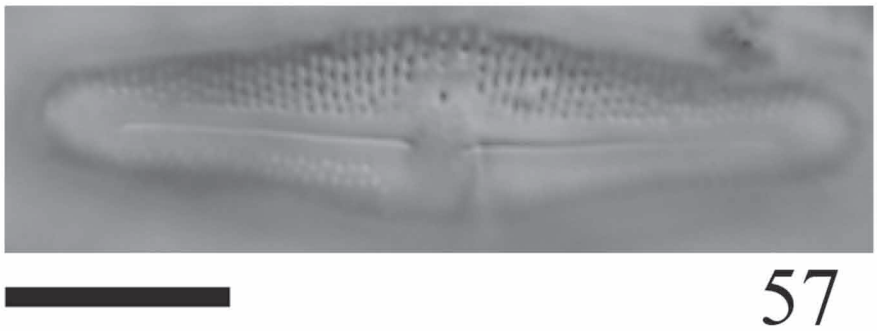
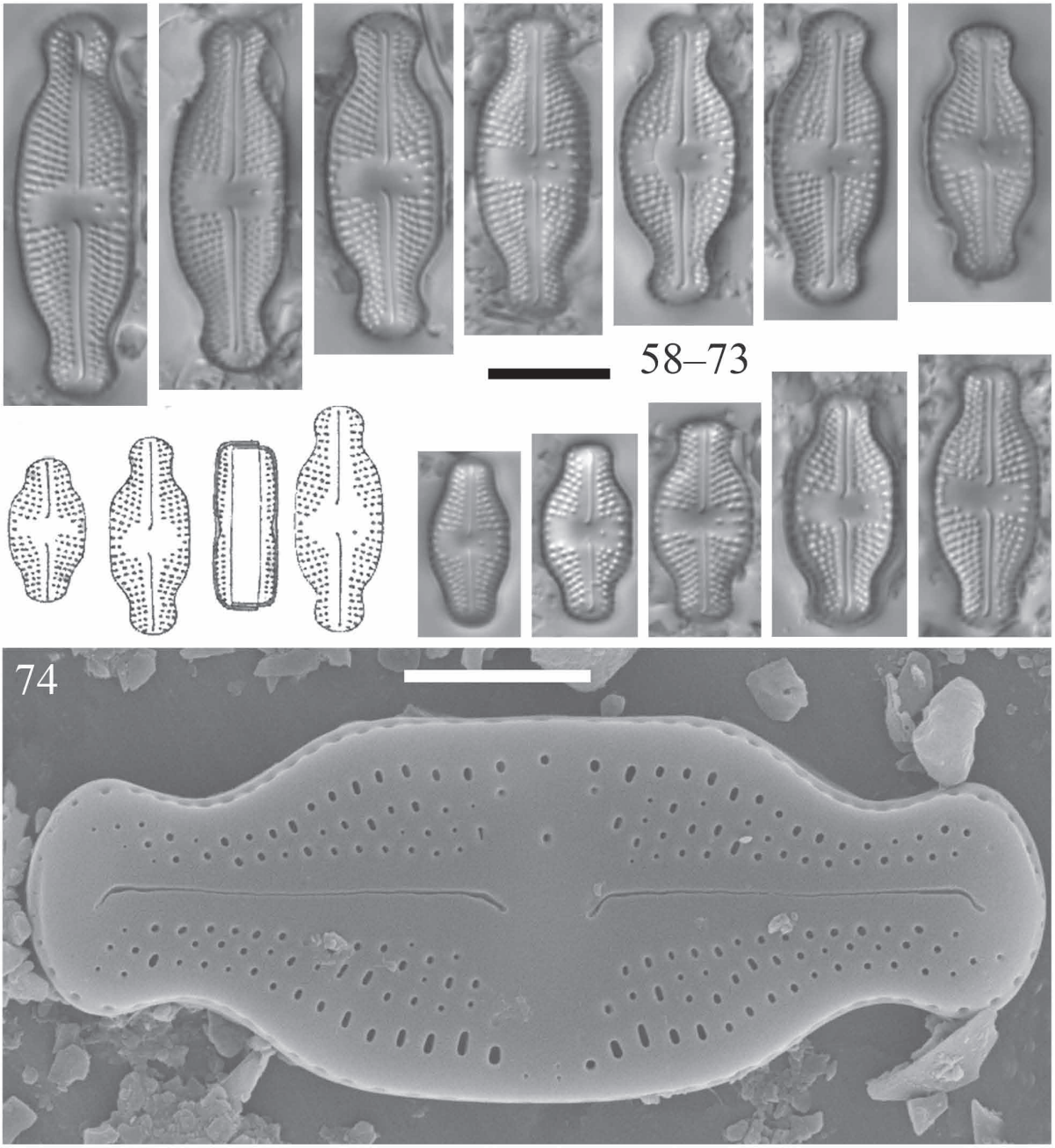


FIGURE 57. Initial cell from BM 34124, an original West & West (1911) slide, LM. Scale bar = 10 µm.

Luticola murrayi differs from other Antarctic species such as *L. australomutica* and *L. laeta* primarily in its valve outline, which is widest in the center and tapers to its apices into broadly rounded to sub-rostrate ends. Both the former taxa resolve into more rostrate endings, with margins of *L. laeta* being both convex, and one convex and one flattened in *L. australomutica*. *L. murrayi* furthermore has slitted outer rows of areolae, whereas areolae are generally rounded in *L. laeta*. Lastly, the distal raphe endings terminate at the last row of areolae in *L. murrayi*, unlike *L. australomutica* where the raphe terminates long before. *Luticola murrayi* further differs from the diatom it was long confused with, *L. pseudomurrayi*, by not having the broad, capitate apices present in the latter (Van de Vijver *et al*. 2012). *Luticola pseudomurrayi* is additionally wider than *L. murrayi* (7.5–12.0 µm), and has more areolae per striae at apices (3–5 *vs*. 2–3).

Luticola muticopsis (Van Heurck 1909: 12, pl. 2, fig. 181) D.G.Mann in Round *et al*. (1990: 671) (Figs. 58–74, Figs. 65–68—first four pictures of the second row, left to right—are original illustrations by West & West (1911))



FIGURES 58–74. *Luticola muticopsis* (Van Heurck) D.G. Mann. 65–68. Original illustration from West & West (1911: pl. 26, figs. 121–124). Light (LM) and scanning electron micrographs (SEM). 58–64 and 69–73. Specimens from Green Lake, Cape Royds, LM. 74. External valve view of specimens from Green Lake, Cape Royds, a confirmed locality in West & West (1911), SEM. LM scale bar = 10 µm. SEM scale bar = 5 µm.

LM observations:—Figs. 58–64, 69–73. Valves linear-elliptical, with the pore-bearing valve margin straight, the opposite convex. Apices broadly capitate, becoming truncate in smaller specimens (Figs. 69–70). Valve dimensions (n=10): length 13.9–31.4 µm, width 6.7–10.2 µm. Axial area present, linear, expanding toward the central area. An isolated pore present in the central area, located halfway between the valve center and valve margin. Central area rectangular to bow-tie shaped, bordered by shortened striae on both sides. Raphe straight, both proximal and distal raphe endings strongly deflecting away from the isolated pore. Transapical striae radiate throughout, 15–19 in 10 µm.

SEM observations:—(Fig. 74) Striae composed of 3–5 areolae, 1–3 at apices. Areolae rounded, becoming elongated at valve margins, sometimes extending beyond distal raphe endings. Isolated pore rounded. Central area bordered by 1–2 rows of three rounded areolae on isolated pore side, one row on the opposite side. Both distal and proximal external raphe endings terminate into slits, deflecting away from isolated pore at strong, 45-degree angles on valve face. Clear separation between areolae and valve margin visible. A single row of areolae present along entire valve mantle, not interrupted at apices.

Habitat, ecology and distribution:—Commonly reported from the entire Antarctic Region, such as Cape Royds on Ross Island (West & West 1911: pl. 26, figs. 121–124), the Ongul Islands (Fukushima 1973: figs. A–E), Southern Victoria Land (Seaburg *et al*. 1979: pl. 22, fig. 90), James Ross (Kopalová *et al*. 2012: fig. 4.5x) and Deception Islands (Van de Vijver & Mataloni 2008: figs. 71–90) from the Maritime Antarctic, and the Kerguelen Islands (Levkov *et al*. 2013: 534, pl. 127, figs. 20–37) and Île de la Possession (Van de Vijver *et al*. 2002: 244, pl. 57, figs. 1–6) from the sub-Antarctic. Although widely reported, this species is probably rare in the MDVs (Sakaeva 2014).

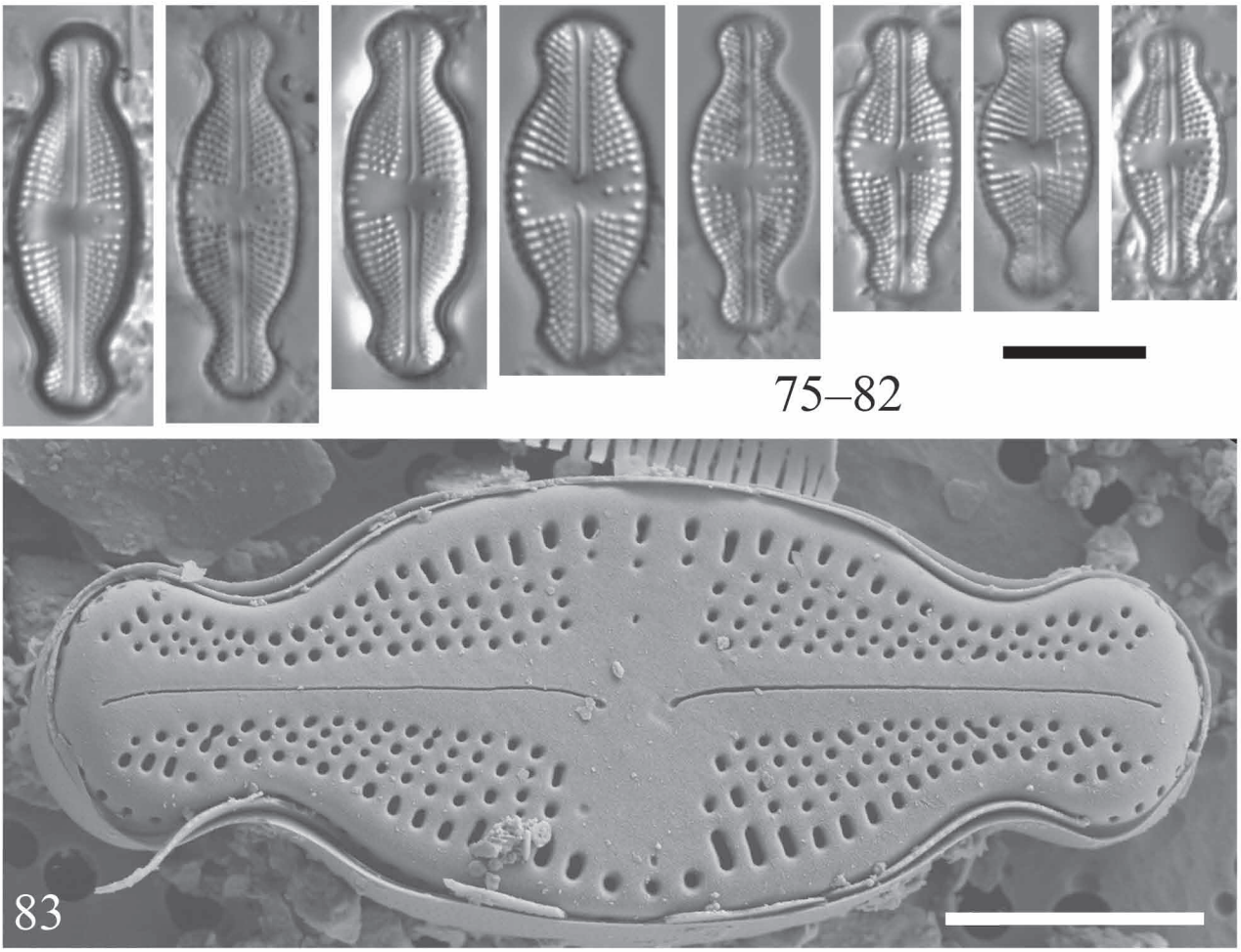
INSTAAR herbarium:—Pony Lake 2352, 2354–2355, 2662; Coast Lake 2466–2467, 2502; Green Lake 2473, 2475.

Observations:—*Luticola muticopsis* is a catch-all species complex for capitate *Luticola* species (Kopalová *et al*. 2011). The identity of this diatom is ambiguous due to only a single specimen present on the type slide (Van de Vijver & Mataloni 2008), and therefore has historically been a place to put all *Luticola* valves with capitate apices (Van de Vijver & Mataloni 2008) or a starting point for creating forms and varieties (*i.e.* West & West 1911, Ko-Bayashi 1963, 1965). After examining the Van Heurck type slide, Van de Vijver & Mataloni (2008) provided a more narrow species concept for *L. muticopsis*, and we base our concept of this diatom on their description of this valve and the Deception Island specimens included in the paper. Despite being widely reported in the MDVs (*i.e.* Stanish *et al*. 2011, 2012), *L. muticopsis* is actually observed rather infrequently in Dry Valley streams (Sakaeva 2014). This is probably due to its confusion with *L. austroatlantica*, which may have begun with the publication by Kellogg *et al*. 1980, where an image of what appears to be *L. austroatlantica* is labeled as *L. muticopsis*. Therefore, reports of this species prior to the description of *L. austroatlantica* in Esposito *et al*. (2008) should be interpreted with caution.

Luticola cognata Levkov *et al*.in Levkov *et al*. (2013: 90, pl. 130, figs. 21–38) is morphologically very similar to *L. muticopsis*. Levkov *et al*. (2013) indicate that *L. muticopsis* has more capitate valve apices, and that *L. cognata* is consistently wider. However, the dimensions given are 7.0–9.5 µm wide for *L. cognata* vs. 7.0–9.0 µm for *L. muticopsis*, and the differences in morphology are not easily observed in the type material as illustrated by Van de Vijver & Mataloni (2008), as well as in the Levkov *et al*. (2013) images of *L. muticopsis*. Therefore, it is possible that *L. cognata* is conspecific with *L. muticopsis*. *Luticola muticopsis* is also similar to *L. truncata* Kopalová & Van de Vijver in Kopalová *et al*. (2009: 118, figs. 34–50), especially at the lower end of the size range. However, *L. truncata* always maintains its rostrate, truncated apices, whereas *L. muticopsis* remains distinctly capitate throughout its entire size range. *Luticola muticopsis* differs from other MDV species such as *L. austroatlantica* and *L. permuticopsis* primarily by having one distinctly straight valve margin, whereas both margins in *L. permuticopsis* and *L. austroatlantica* are convex. *Luticola austroatlantica* furthermore has more elongated valve outline than *L. muticopsis*. Finally, valve apices in *L. austroatlantica* are more rounded and constricted at the neck, while *L. muticopsis* has more flattened apices that are less constricted.

Luticola permuticopsis Kopalová & Van de Vijver in Kopalová *et al*. (2011: 53, figs. 51–72) (Figs. 75–83)

LM observations:—(Figs. 75–82) Valves linear-elliptical with two convex margins. Apices broadly rounded, capitate throughout the size series. Valve dimensions (n=11): length 19.7–28.9 µm, width 7.6–9.4 µm. Axial area linear, widening toward central area. An isolated pore present in the central area, halfway between the valve center and valve margin. Central area bow-tie shaped and asymmetric, sometimes wider opposite isolated pore, with shortened striae present on both sides. Raphe branches straight, both proximal and distal ending deflecting away from isolated pore. Transapical striae radiate throughout, 16–22 in 10 µm.



FIGURES 75–83. *Luticola permuticopsis* Kopalová & Van de Vijver. Light (LM) and scanning electron micrographs (SEM). 75–82. Specimens from Canada Stream, Taylor Valley, LM. 83. External valve view of specimens from Canada Stream, SEM. LM scale bar = 10 µm. SEM scale bar = 5 µm.

SEM observations:—(Fig. 83) Striae composed of 3–5 areolae, 2–4 at apices. Areolae rounded, elongated toward valve margin, extending to distal raphe endings. Isolated pore small, rounded. Central area bordered by 1–2 rows of three rounded to elongated areolae on isolated pore side, and a single row of four rounded areolae on opposite side. Proximal raphe endings resolve into drop-like pores, deflect away from isolated pore. Distal raphe endings resolve into smaller, slit-like pores on valve face. Clear separation between valve face areolae and valve margins. A single row of rounded areolae is present along valve margin.

Habitat, ecology and distribution:—*Luticola permuticopsis* was described recently from the lakes of James Ross Island, Maritime Antarctica (Kopalová *et al*. 2011), and until now has not been documented from elsewhere. This diatom occurs throughout the MDVs, but has been identified as *Navicula muticopsis* f. *capitata*. Therefore, we can confirm its distribution as widespread throughout the Wright, Taylor, and Miers Valleys from the McMurdo Sound Region, though rare or absent on Cape Royds (Sakaeva 2014).

INSTAAR herbarium:—Aiken Creek 900–902, 2224–2228; Von Guerard Stream 905–908, 911–913, 916–919, 923–926; Harnish Creek 928; Bowles Creek 933–935, 938–940; Commonwealth Stream 945–948, 951, 954; Priscu Stream 960–961; Bohner Stream 963–966; Wharton Creek 980, 982; Delta Stream 983–984, 986–987, 990–992; Onyx River 995–996; Canada Stream 1002, 1004, 2257; Green Creek 1018, 1021–1022, 1025–1027; Lawson Creek 1030–1031, 1038, 1041; Adams Stream 1051, 1053–1057, 1064; Relict Channel 1066–1068, 1070–1071, 1077–1081, 1084, 1087; Wales Stream 1580; Lyons Stream tributary 2349; Many Glaciers Pond 2492; Parera Pond 2493; Spaulding Pond 2494–2496; Clear Lake 2501; McMurdo Hut Ridge 2664–2665; Picture Pond 2667; Nussbaum Regal Pond (unofficial name) 2671; Upland Pond 2678.

Observations:—The MCMLTER has historically identified this diatom as *N. muticopsis* f. *capitata* (Esposito *et al*. 2008, Stanish *et al*. 2011, 2012). Peragallo (1921: 17, pl. 1, fig. 40) described what is perhaps a similar species,

Navicula muticopsis var. *capitata*, though the type material of both taxa is wanting (as discussed in Kopalová *et al*. 2011), and as a result the identities of these species are not verifiable. Levkov *et al*. (2013) only briefly mention *N. muticopsis* f. *capitata* and *N. muticopsis var*. *capitata* at the end of their book volume as probably also belonging to the genus *Luticola*, without descriptions or images. Since the existing description of *L. permuticopsis* fits our McMurdo populations well, we suggest that this taxon name be used rather than the former two, and further suggest that the range of *L. permuticopsis* from the Maritime Antarctic extends to the Antarctic continent. In the case that one of the former names should be demonstrated to be conspecific with *L. permuticopsis*, then the name should be replaced by the first published, accepted one.

Luticola permuticopsis is most similar to *L. muticopsis* in valve outline, but *L. muticopsis* has one straight and one convex margin. This is in contrast to *L. permuticopsis*, which always has two convex margins and is generally narrower than *L. muticopsis*. The apices in *L. muticopsis* are always flattened and more rostrate, contrary to *L. permuticopsis*, which are more rounded (Kopalová *et al*. 2011). Furthermore, striae in *L. permuticopsis* can be composed of 3–6 areolae, whereas only 3–5 have been observed for *L. muticopsis*. Finally, the proximal and distal raphe endings in *L. permuticopsis* are weakly deflected and terminate into small pores, whereas raphe endings are deflected at strong 45-degree angles in *L. muticopsis* and resolve into slits. *Luticola permuticopsis* is also similar in morphology to *L. austroatlantica*, although *L. austroatlantica* is more narrow (4.4–8.7 *vs*. 7.3–9.2) and has fewer areolae per stria (2–3 *vs*. 3–6) (Esposito *et al*. 2008). Apices in *L. permuticopsis* are typically broader than in *L. austroatlantica*, and margins in *L. austroatlantica* are generally more elongated. *Luticola gaussii* also resembles *L. permuticopsis*, with both having broadly rounded apices with convex margins. However, the body of *L. gaussii* is typically more rounded than in *L. permuticopsis*, which has a more elongated mid-section. Futhermore, *L. gaussii* has striae that are only comprised of up to 3–4 areolae, whereas *L. permuticopsis* has 3–6. Lastly, a deep depression is visible around the margin of *L. gaussii* that is not present in *L. permuticopsis*.

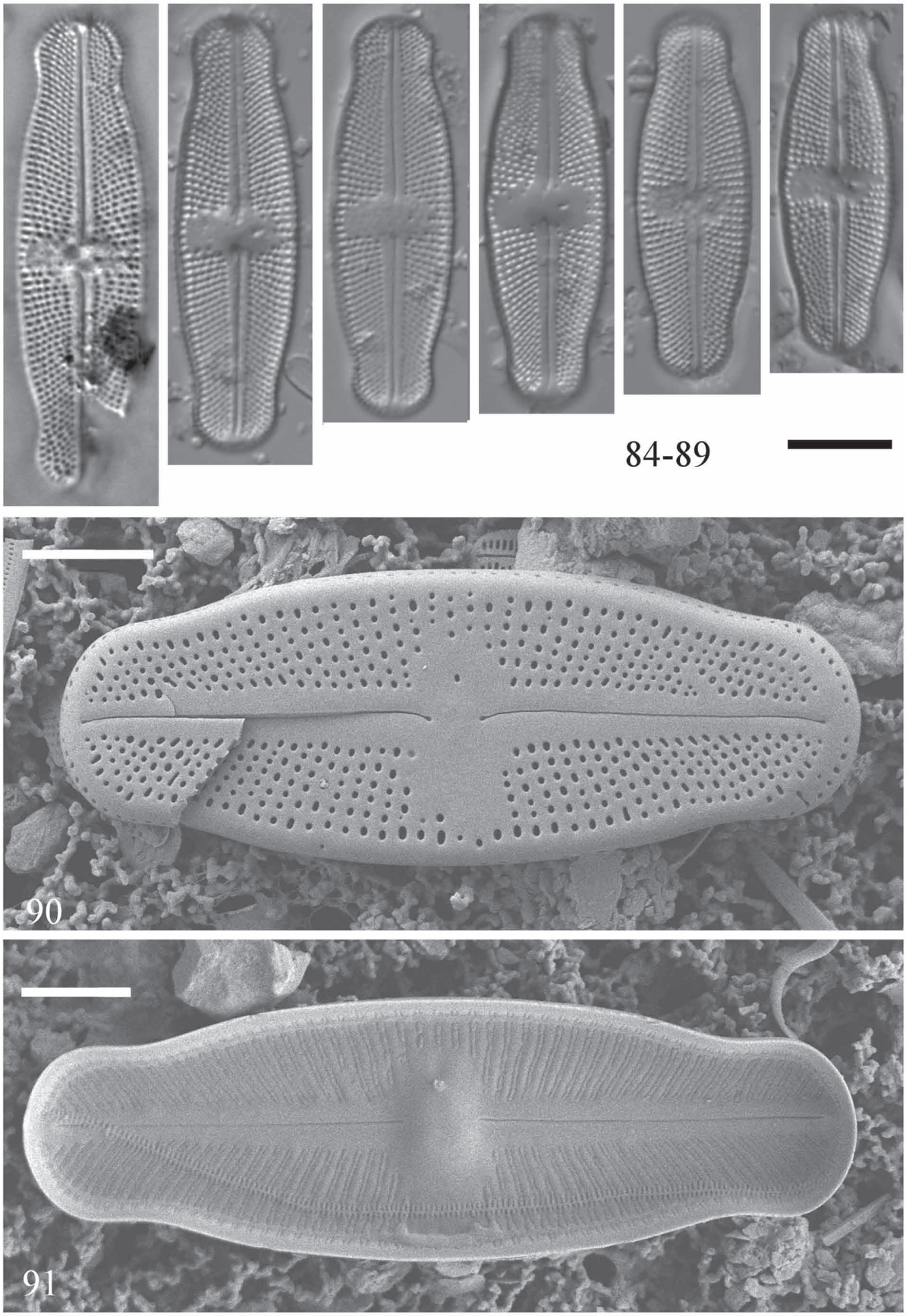
***Luticola bradyi* Kohler, *sp. nov*. (Figs. 84–91)**

LM observations (Figs. 84–89): Valves elliptical to elliptical-lanceolate with convex margins. Apices broadly rounded, rostrate to sub-capitate. Valve dimensions (n=16): length 28.3–44.8 µm, width 10.5–12.5 µm. Axial area linear, slightly widening towards the valve center. An isolated pore present in the central area, located halfway between the valve center and valve margin. Central area asymmetric, varying from elliptic to an acute-angled sub-fascia, bordered by shortened striae on both sides, wider opposite the isolated pore. Raphe branches straight, deflected away from the isolated pore at both proximal and distal ends. Transapical striae radiate throughout, more widely spaced in the central portion of the valve, 16–18 in 10 µm. SEM observations (Figs. 90–91): Externally, (Fig. 90), striae composed of 5–7 areolae, 2–4 areolae at apices. Areolae rounded, slightly elongated along the axial and marginal areas and near poles, not extending past distal raphe endings. Isolated pore rounded, slightly elongated, Central area bordered by irregular, shortened striae comprised of 3–5 rows of five rounded areolae on isolated pore side, 1–2 rows on opposite side. Proximal raphe endings deflected opposite the isolated pore, resolving into small drop-like pores. Distal raphe endings slightly deflected opposite isolated pore, terminating into small pores or fissures on the valve face. Clear separation between valve face and margins with rounded mantle areolae interrupted at apices. A single row of rounded areolae present along entire valve mantle, interrupted at apices. Internally (Fig. 91), central nodule thickened. Both, proximal and terminal raphe endings straight. Distal raphe ends terminating onto very small helictoglossae. Marginal canal visible, interrupted at apices. Areolae covered by hymens, forming continuous strip along striae. Isolated pore opening covered by solid silica flap.

Type:—ANTARCTICA. McMurdo Dry Valleys: Taylor Valley, Commonwealth Glacier, cryconite hole, Sample CC-9, *A. Mass*, *10 January 2014* (holotype INSTAAR! #2657A, illustrated in Fig. 88, isotypes BM! 101776, BR! 4405).

Etymology:—This species is named for Brady Kohler (Cheney, Kansas, USA), brother and best friend of the first author.

Habitat, ecology and distribution:—*Luticola bradyi* has at present only been observed from the McMurdo Sound Region, Antarctic continent. A large population of *L. bradyi* was observed during a survey of the Commonwealth Glacier cryoconite holes collected during the austral summer 2013–14. This population was found among other common cryoconite species (Stanish *et al*. 2013) such as *Muelleria supra* Spaulding & Esposito in Esposito *et al*. (2008: 1384, figs. 42–49), *M. cryoconicola* Stanish & Spaulding in Van de Vijver *et al*. (2010: 26, figs. 27–35), *Humidophila spp*. Lowe *et al*. (2014: 357), and *L. gaussii* (Levkov *et al*. 2013: 117, pl. 127, figs. 1–19). Aside from this population, single valves have been recovered from Cape Royds, the Onyx River in Wright Valley, and streams in the Fryxell Basin, Taylor Valley.



FIGURES 84–91. *Luticola bradyi* Kohler *sp. nov*. Light (LM) and scanning electron micrographs (SEM). 84–89. Specimens from Commonweath Glacier, Taylor Valley, the type population, LM. 90. External valve view, type population, SEM. 91. Internal valve view, type population, SEM. LM scale bar = 10 µm. SEM scale bars = 5 µm.

INSTAAR herbarium:—Lake Fryxell 390; Canada Stream 436, 527, 618, 666–667, 670, 676, 683, 689, 691, 693–694, 696–697; Green Creek 512; Relict Channel 638, 640, 739, 751, 757; Von Guerard Stream 440–441; Commonwealth Stream 888; Coast Lake 2467; Commonwealth Glacier 2657.

Observations:**—**Previously referred to as *L. cohnii* var. *#1* (Esposito *et al*. 2008: 1381), this taxon was thought to be an initial cell of an unknown diatom due to its large size and scarcity. However, since a large population was found in a cryoconite hole on the Commonwealth Glacier, it is possible that this species is not rare, and is instead occasionally transported from the glaciers into streams. In valve dimensions and outline, *L. bradyi* most resembles *L. wulffii* (Peterson 1924: 312, fig. 2) Levkov *et al*. (2013: 259, pl. 126, figs. 19–29) which is an arctic species reported from Canada and Russia. However, *L. wulffii* has a very narrow rectangular to bow-tie shaped central area, while the central area in *L. bradyi* is broadly rectangular or elliptic. The shortened striae in *L. wulffii* are composed of 1–2(3) areolae (Levkov *et al*. 2013), while the shortened striae in *L. bradyi* may number 3–5 on the side of the isolated pore. Striae in *L. bradyi* terminate more irregularly in the axial area than *L. wulffii*, which exhibits straight striae. Lastly, apices in *L. bradyi* are subcapitate at the largest sizes and become rostrate as valves become smaller. Apices in *L. wulffii* remain subcapitate, contricted where the apices meet the body, throughout the size range as illustrated in Levkov *et al*. (2013). These differences, along with opposite polar distributions, are sufficient to separate these two species from each other. *Luticola magellanica* (Frenguelli 1924: 95, pl. 6, fig. 37) Levkov *et al*. (2013: 153, pl. 41, figs. 12–19), described from Tierra del Fuego, is also similar in outline, but has denser striae (14–18 in 10 µm) and never develops constrictions at the apices; the apices are rounded.

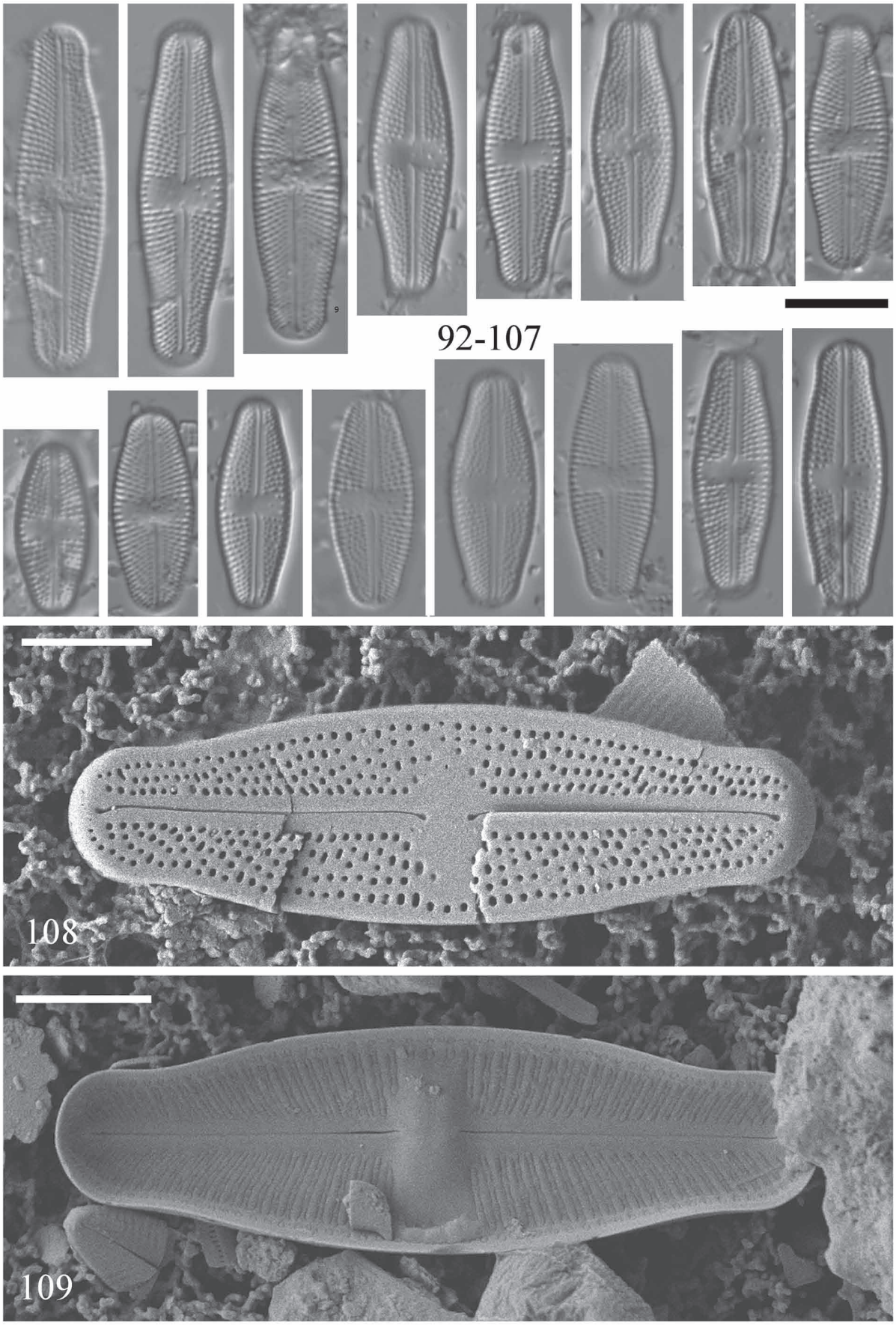
In Antarctica, *L. vermeulenii* is similar in valve length and width range (24–50 µm, 9.5–14.0 µm), though slightly longer than our observed population of *L. bradyi*. *Luticola vermeulenii* also has denser striae (14–17 in 10 µm *vs*. 17–21 in 10 µm) and differs in valve outline, never forming constrictions at the apices like the subcapitate endings in *L. bradyi* at the upper size ranges. Another species that bears some resemblance based on valve outline and valve length, is *L. vandevijveri* Kopalová, Zidarova & Levkov in Levkov *et al*. (2013: 247, pl. 10, figs. 1–24), described from James Ross Island. The latter is however narrower (maximal width 9.0 µm) giving it a more slender outlook, and has a lower number of areolae per stria. In the McMurdo Sound Region, *L. bradyi* is most similar to *L. spainiae* and *L. laeta*, which are also common cryoconite species (Stanish *et al*. 2013). However, most differences between these two species are found with respect to valve size. *Luticola bradyi* is generally much larger in length and width compared to *L. spainiae* and *L. laeta*, as well as most other *Luticola*. Lastly, the apices of *L. bradyi* are broadly rostrate, becoming subcapitate at larger size ranges. This differs from the apices of *L. laeta*, which are always more narrow and never become constricted where they meet the central area.

Luticola spainiae Kohler & Kopalová, *sp. nov*. (Figs. 92–109)

LM observations (Figs. 92–107): Valves elliptical to elliptical-lanceolate with two convex margins. Apices rounded at the lower size range (Figs. 100–101), broadly rostrate to sub-capitate at upper sizes (Figs. 92–99). Valve dimensions (n=22): length 12.1–33.6 µm, width 6.4–8.7 µm. Axial area linear, slightly widening towards the central area. An isolated pore present in the central area, located halfway between the valve center and valve margin. Central area bow-tie shaped to almost rectangular, bordered on both sides by shortened striae. Raphe branches straight, deflected away from the isolated pore at both proximal and distal ends. Transapical striae irregular, radiate throughout entire valve, 19–22 in 10 µm. SEM observations (Figs. 108–109): Externally (Fig. 108), striae composed of 4–5 areolae, 2–4 at apices. Areolae rounded, becoming slightly elongated near axial area and at poles, extending beyond distal raphe endings. Isolated pore small, rounded. Central area bordered by 2–3 rows of four rounded areolae on isolated pore side, and a single row of four on opposite side. Proximal and distal raphe endings open drop-like pores and deflect away from isolated pore. Distal raphe endings terminate on the valve face. Clear separation between valve face and margins. Internally (Fig. 109), central nodule thickened. Both proximal and distal raphe endings straight. Distal raphe endings terminating onto very small helictoglossae. Marginal canal visible, interrupted at apices. Areolae covered by hymenes, forming a continuous strip along each stria. Isolated pore opening covered by solid silica flap.

Type:—ANTARCTICA. McMurdo Dry Valleys: Fryxell Lake Basin, Commonwealth Glacier, cryconite hole, Sample CC-9, *A. Mass*, *10 January 2014* (holotype INSTAAR! #2657A, illustrated in Fig. 95, isotypes BM! 101777, BR! 4406).

Etymology:—*Luticola spainiae* is named in honor of our friend and colleague, Rae Spain, whose years as the Lake Hoare camp manager have facilitated decades of research in the McMurdo Dry Valleys in addition to providing visitors a home away from home.



FIGURES 92–109. *Luticola spainiae* Kohler & Kopalová, *sp. nov*. Light (LM) and scanning electron micrographs (SEM). 92–107. Specimens from Commonwealth Glacier, Taylor Valley, the type population, LM. 108. External valve view, type population, SEM. 109. Internal valve view, type population, SEM. LM scale bar = 10 µm. SEM scale bars = 5 µm.

Habitat, ecology and distribution:—*Luticola spainiae* is at present known only from the Commonwealth Glacier cryoconite holes, Taylor Valley, Antarctic continent. Found alongside *L. bradyi* as well as other common cryoconite species, such as *Muelleria supra*, *M. cryoconicola*, *M. peraustralis* (W. & G.S.West 1911: 284) Spaulding & Stoermer in Spaulding & Stoermer (1997), *Humidophila* spp., and *L. gaussii* (Stanish *et al*. 2013). Due to similarities with *L. laeta*, *L. mutica*, and *L. bradyi*, this species may be under-reported from the McMurdo Sound Region.

INSTAAR herbarium:—Commonwealth Glacier 2657

Observations:**—**If observed at all, the smaller size range of this species has probably been identified as *L. mutica* or *L. cohnii*, which may be a complex similar to *L. muticopsis* in Antarctica (Van de Vijver & Mataloni 2008). Like the lower size range of *L. spainiae*, *L. mutica* is oval-shaped, but the latter has eccentric proximal raphe endings terminating in hooks (Levkov *et al*. 2013: 284, pl. 2, figs. 1–8), which is visible under SEM. Furthermore, at the upper size ranges, *L. spainiae* has distinctly rostrate apices not present in *L. mutica*, and reaches a greater upper size (*vs*. 28 µm for *L. mutica*). *Luticola cohnii* is another diatom reported from the Antarctic continent that resembles *L. spainiae* in valve outline, especially at lower size ranges. However, *L. cohnii* is in general longer (19–40 µm) and wider (8.5–11.0 µm) than *L. spainiae* (Levkov *et al*. 2013: 91). Furthermore, *L. cohnii* is always oval in outline even at large sizes, while valve apices become rostrate in *L. spainiae*. Furthermore, the eccentric distal raphe endings in *L. cohnii* terminate on valve margins, whereas in *L. spainiae*, they terminate on the valve face (Levkov *et al*. 2013: 292, pl. 6, figs. 1–8).

Other Antarctic diatoms such as *L. vermeulenii* (Van de Vijver *et al*. 2011: 145, figs. 16–29) may be similar in valve outline, but have a greater length and width range (24–50 µm, 9.5–14.0 µm). *Luticola vermeulenii* also has denser striae (14–17 in 10 µm *vs*. 19–22 in 10 µm) and differs in valve outline, never forming constrictions at the apices like the subcapitate endings in *L. spainiae* at upper size ranges. In the MDVs, *L. spainiae* is very similar in valve outline to *L. bradyi*, which is found in the same cryoconites. The major difference between these species is the width of valves. The upper end of the *L. spainiae* width range is 8.7 µm, while the lower width range of observed *L. bradyi* is 10.5 µm. Distal and proximal raphe pores are much larger in this species than in *L. bradyi*, which actually has a proximal raphe that resolves into slits. Also very similar is *L. laeta*, and it is possible that confusion between these two species has taken place in the past, as they are almost identical in their length/width ratios. However, *L. spainiae* has much broader, more rostrate apices than *L. laeta*, and has more areolae per striae, especially with regard to the shortened striae near the isolated pore in the central area, which only numbers 1–2 in *L. laeta*.

Luticola elegans* (W. & G.S.West) Kohler & Kopalová, *comb. nov. stat. nov. (Figs. 110–120, Fig. 110 is original illustration by West & West (1911))

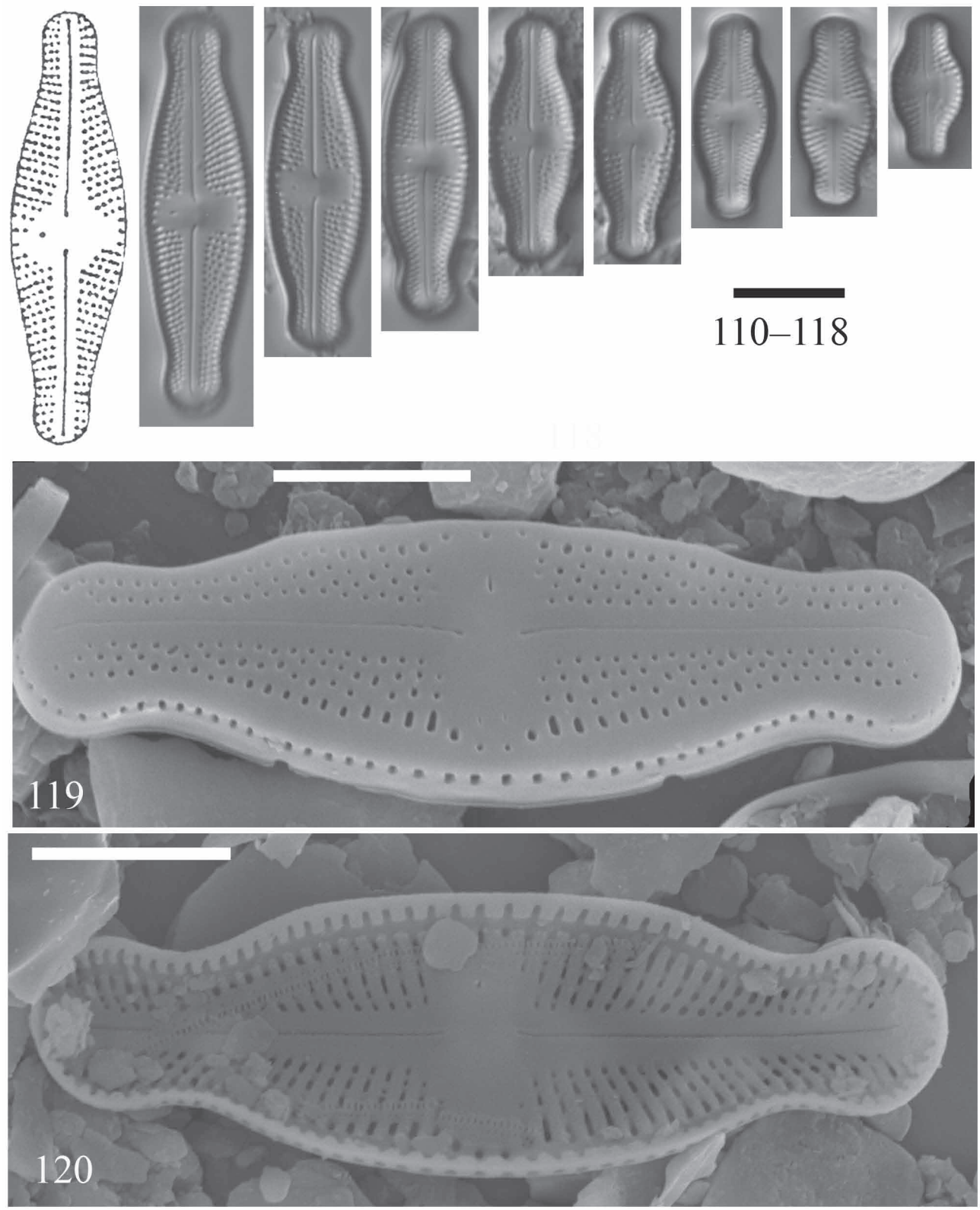
Basionym: *Navicula (Pinnularia) murrayi* var. *elegans* W. & G.S.West (1911) *British Antarctic Expedition 1907–1909*, *vol. 1*., *Biology*, *Part VII*, p. 285, pl. XXVI, fig. 130).

LM observations:—(Figs. 111–118) Valve lanceolate to elliptical-lanceolate with two convex margins. Apices capitate to sub-capitate in middle size ranges (Figs. 112–115), becoming rostrate in smaller and greater size range (Figs. 111, 116–118). Valve dimensions (n=10): length 12.9–35.8 µm, width 6.4–9.5 µm. Axial area linear, widening slightly towards central area. An isolated pore is present in the central area, located halfway between the valve margin and valve center. Central area broadly rectangular to round, bordered by shortened striae on both sides. Raphe branches straight, both proximal and distal raphe endings deflected away from the isolated pore. Transapical striae irregular, radiate throughout, 16–20 in 10 µm.

SEM observations:—(Figs. 119–120) Externally (Fig. 119), striae composed of 3–4 areolae, 2–3 at apices. Areolae rounded throughout, becoming elongated at margins near central area, extend to the distal raphe ending. Isolated pore elongated, slit-like. Central area bordered by a single row of 3–4 rounded areolae on both sides, positioned closer to the valve margin than other striae. Distal raphe endings deflect away from isolated pore on a valve face, resolving into slits. Proximal raphe ending terminates in slightly opened pore, deflected away from isolated pore. Clear separation between valve face and margins, with open area at apices around terminal raphe endings. A single row of areolae visible in a shallow depression along entire valve mantle. Internally (Fig. 120), structures difficult to discern due to specimen corrosion and small sample size.

Habitat, ecology and distribution:—*Luticola elegans* is known only from Cape Royds and the McMurdo Dry Valleys. Since this species has probably been identified as both *L. muticopsis* and *L. austroatlantica* due to similarities in morphology and extensive varieties present in *L. muticopsis* (*i.e*. Ko-Bayashi 1963, 1965), its distribution may be more widespread than currently known. Sakaeva (2014) report it from many of the upland ponds from both Cape

Royds and the MDVs, and we can confirm its presence in at least Wales and Crescent streams. The basionym, *Navicula murrayi* var. *elegans*, has been reported from Graham Land (Carlson 1913), Ongul Islands (Ko-Bayashi 1963), and South Shetland Islands (Carlson 1913), though these distributions should be interpreted with caution.



FIGURES 110–120. *Luticola elegans* (W. & G.S.West) Kohler & Kopalová, *comb. et stat. nov.* 109. Original illustration from West & West (1911: pl. 26, fig. 130). Light (LM) and scanning electron micrographs (SEM). 111–118. Specimens from Green Lake, Cape Royds, LM. 119. External valve view of a specimen from Green Lake, SEM. 120. Internal valve view of a specimen from the Nussbaum Riegal, SEM. LM scale bar = 10 µm. SEM scale bars = 5 µm.

INSTAAR herbarium:—Green Lake 2475; Spaulding Pond 2495–2496; Blue Lake 2497–2499; Clear Lake 2501; McMurdo Hut Ridge 2664–2665; Picture Pond 2666–2668, 2670; Nussbaum Regal Pond (unofficial name) 2671; Upland Pond 2677–2678; Hughes Glacier Pond (unofficial name) 2679.

Observations:—West & West (1911) described *Navicula murrayi* var. *elegans* from presumably one large valve measuring 31 µm long, 8.1 µm wide, and with 15 striae per 10 µm. Later, Ko-Bayashi (1963: pl. 8, figs. 3–4) published images of what may be this diatom under the name *N. muticopsis* var. *elegans*, but it has been seldom reported since. In our survey of recent material at Cape Royds, we found a species that we argue belongs to *N. murrayi* var. *elegans* due to the strong morphological resemblance of the upper size range to the original illustration, as well as the locality from which our samples were taken. As a result, we here elevate the Cape Royds taxon to a species of *Luticola*. Levkov *et al*. (2013) report a species that may be conspecific from Cape Royds as *L. murrayi*, and has a length 16–35 µm, width 6.5–8.5 µm, and 15–17 striae in 10 µm. The authors also report initial cells up to 45 µm long and 12 µm wide. While we did not measure any initial cells of this length when analyzing the Mt. Erebus Moraine slides (including the lectotype, BM 34126), we did photograph one initial cell from BM 34124, and have included it as Fig. 57 for reference.

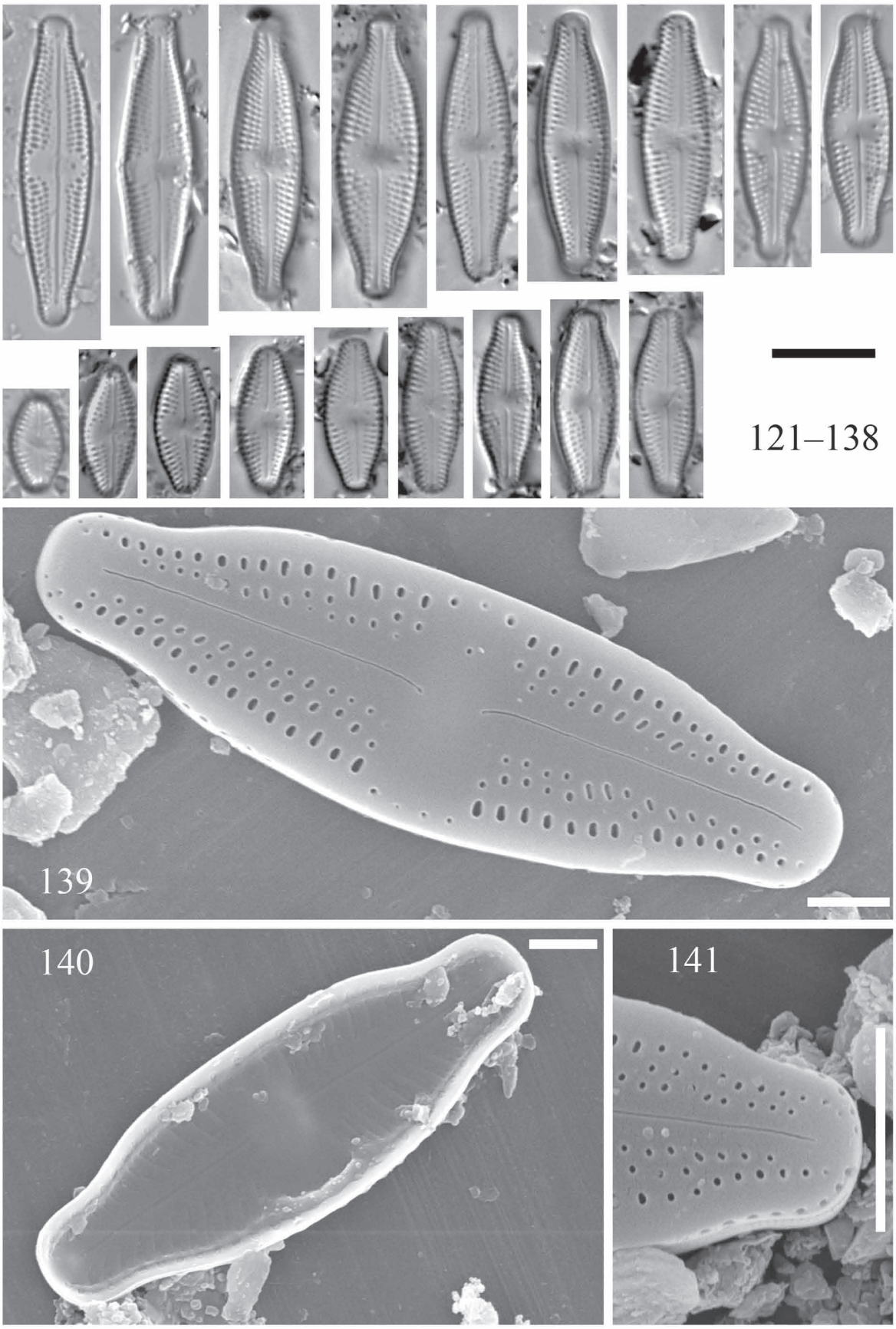
The upper size range of this species may be confused with *L. murrayi*, and is probably why this species was initially described as a variety. However, when a size diminution series of each species is observed and compared, they can be easily separated into two morphologically distinct groups. The morphology of *L. elegans* includes strongly capitate ends at intermediate size range, becoming more rostrate at the upper and lower size ranges. Apices of *Luticola murrayi* on the other hand never become capitate nor rostrate at upper or lower size ranges, and remain obtuse and rounded in all cells. Furthermore, the center of the valve remains rounded and convex in *L. elegans*, conforming well to the description of *Navicula murrayi* var. *elegans* reported by West & West (1911: fig. 130), while the widest part of *L. murrayi* is directly in the center of the cell. Lastly, the central stauros in *L. elegans* can be rounded (though it can also be rectangular) unlike *L. murrayi*, and is clearly illustrated in the original West & West (1911: fig. 130) illustration.

Luticola elegans may be confused with *L. austroatlantica*, which is very similar in valve outline at intermediate side ranges. However, *L. austroatlantica* is more narrow in width (5.6–8.2 µm vs. 6.4–9.5 µm), and has fewer areolae per striae (2–3 *vs*. 3–4). *Luticola elegans* additionally is less constricted between the capitate apices and the valve center compared to *L. austroatlantica*, and apices are generally wider. At the upper size range, *L. elegans* is more rostrate, while *L. austroatlantica* is more capitate. Conversly, *L. austroatlantica* is more rostrate at lower size ranges, while *L. elegans* has sub-capitate apices even at the smallest sizes. *Luticola elegans* may also resemble *L. gaussii*, and the two are often found in the same habitats, especially at Cape Royds. However, *L. gaussii* differs in valve outline, having a more rounded central portion while *L. elegans* is more elongate. In general, *L. gaussii* is wider and shorter than *L. elegans*, and *L. gaussii* additionally has more dense (19–23 in 10 µm), patterned striae organized into three longitudinal rows not present in *L. elegans*.

Luticola macknightiae **Kohler & Kopalová, *sp. nov*. (Figs. 121–141)**

LM observations (Figs. 121–138): Valves linear-lanceolate to elliptical-lanceolate, with convex, sometimes slightly undulate margins (Figs. 122–123). Apices irregular protracted, nearly round, truncate to rostrate at smaller sizes (Figs. 130–138). Valve dimensions (n=24): length 6.7–29.5 µm, width 4.3–7.8 µm. Axial area linear, widening towards the central area. An isolated pore present in the central area, located halfway between valve margin and valve center. Central area broadly elliptical, bordered on both sides by shortened striae. Raphe branches straight, with proximal and distal endings deflected opposite the isolated pore. Distal raphe endings short, terminating on the valve face well before apices. Transapical striae radiate throughout, 16–21 in 10 µm. SEM observations (Figs. 139–141): Externally (Fig. 139), striae composed of 2–3 areolae, 1–2 at apices. Areolae rounded, elongated near valve margin, extend well past distal raphe endings before terminating almost on valve margin (Fig. 141). Isolated pore rounded. Central area bordered on both sides by a single row of 3–4 rounded areolae positioned closer to the valve margin than other striae. Proximal raphe endings deflected opposite side of isolated pore, terminating into small open pores. Distal raphe endings straight, slightly deflected away from isolated pore, terminating into small fissures on the valve face distinctly before apices. Clear separation between valve face and margin, with clear open area at apices. A single row of rounded areolae visible along entire valve mantle. Internally (Fig. 140), central nodule thickened. Marginal canal well developed, clearly visible in central area, interrupted at the apices. Areolae covered by hymenes, forming continuous a strip along each stria. Isolated pore opening covered by solid silica flap.

Type:—ANTARCTICA. McMurdo Dry Valleys: Taylor Valley, Wormherder Creek microbial mat, Sample WHC11-2, *T.J. Kohler*, *10 January 2012* (holotype INSTAAR! #958A, illustrated in Fig. 125, isotypes BM! 101778, BR! 4407).



FIGURES 121–141. *Luticola macknightiae* Kohler & Kopalová, *sp. nov*. Light (LM) and scanning electron micrographs (SEM). 121–138. Specimens from Wormherder Creek, Taylor Valley, the type population, LM. 139. External valve view of a specimen from Canada Stream, Taylor Valley, SEM. 140. Internal valve view of a specimen from Canada Stream, SEM. 141. Detail of apices from Canada Stream specimen, SEM. LM scale bar = 10 µm. SEM scale bars = 2 µm for inside/outside, 5 µm for detail of external apice.

Etymology:—*Luticola macknightiae* is named in honor of our advisor, colleague, and friend, Dr. Diane McKnight (University of Colorado, Boulder, USA), who has promoted a better understanding of freshwater ecosystems through her research in the McMurdo Dry Valleys.

Habitat, ecology and distribution:—At present, *L. macknightiae* is only known from the McMurdo Dry Valleys. As it has been previously been identified as *L. muticopsis* f. *evoluta* (Esposito *et al*. 2006, 2008, Spaulding *et al*. 2010, Stanish *et al*. 2011, 2012), its distribution is known to be widespread throughout the MDVs, occupying stream microbial mats and mosses. It is especially abundant in the Lake Bonney Basin streams, where it sometimes comprises half of the communities by relative abundance (Stanish *et al*. 2012).

INSTAAR herbarium:—Aiken Creek 900, 2227; Von Guerard Stream 906–907, 911–912, 916–917, 919, 923–926; Harnish Creek 928; Bowles Creek 933, 936, 938, 940; Commonwealth Stream 945, 948; Wormherder Creek 955, 958; Priscu Stream 960–961; Bohner Stream 963–966; McKay Creek 975, 977; Wharton Creek 979–980, 982; Delta Stream 983–984, 986–987, 990–992; Onyx River 995–996, 999; Canada Stream 1003, 1011, 2257; Green Creek 1018–1019, 1021–1022, 1025, 1027; Lawson Creek 1030, 1032–1033; Miers Stream 1049; Adams Stream 1051–1054, 1064; Relict Channel 1068, 1070, 1077–1081, 1084, 1087; Little Sharpe (unofficial name) 2340; Lyons Stream tributary 2349–2351; Spaulding Pond 2495–2496; Blue Lake 2498; Clear Lake 2501; McMurdo Hut Ridge 2665; Picture Pond 2667–2670; Nussbaum Regal Pond (unofficial name) 2671, Upland Pond 2677–2678.

Observations:—The identification of *L. macknightiae* as *N. muticopsis* f. *evoluta* probably originates with the publication by Ko-Bayashi (1965: pl. 31), where a small *Luticola* with almost rostrate apices is depicted as this form. Since there is no illustration of *N. muticopsis* f. *evoluta* in West & West (1911), and the original description is limited to "Cells are slightly elongated, slightly below the pole, each distinct but slightly constricted; striae 13–14 in 10 µm" (translated from Latin, West & West 1911: 283), it is entirely impossible to match this form with any extant species. Because of this, *N. muticopsis f. evoluta* has previously been identified as what is the current concept for *L. austroatlantica* (Kellogg 1980: 176, pl. 1, fig.11), *L. pseudomurrayi* (Ko-Bayashi 1963: pl. 8, figs. 1–2), and the reduced form of various unknown diatoms (Ko-Bayashi 1965: pl. 29). Furthermore, in our investigation of the recent Cape Royds material, as well as the original slides from Shackleton's expedition, we found no valves resembling *L. macknightiae*, although West & West (1911: 284) stated that *N. muticopsis* f. *evoluta* was "…common over the whole area in which collections were made". Because of its absence, we conclude the two are not conspecific, and we describe *L. macknightiae* as a new species.

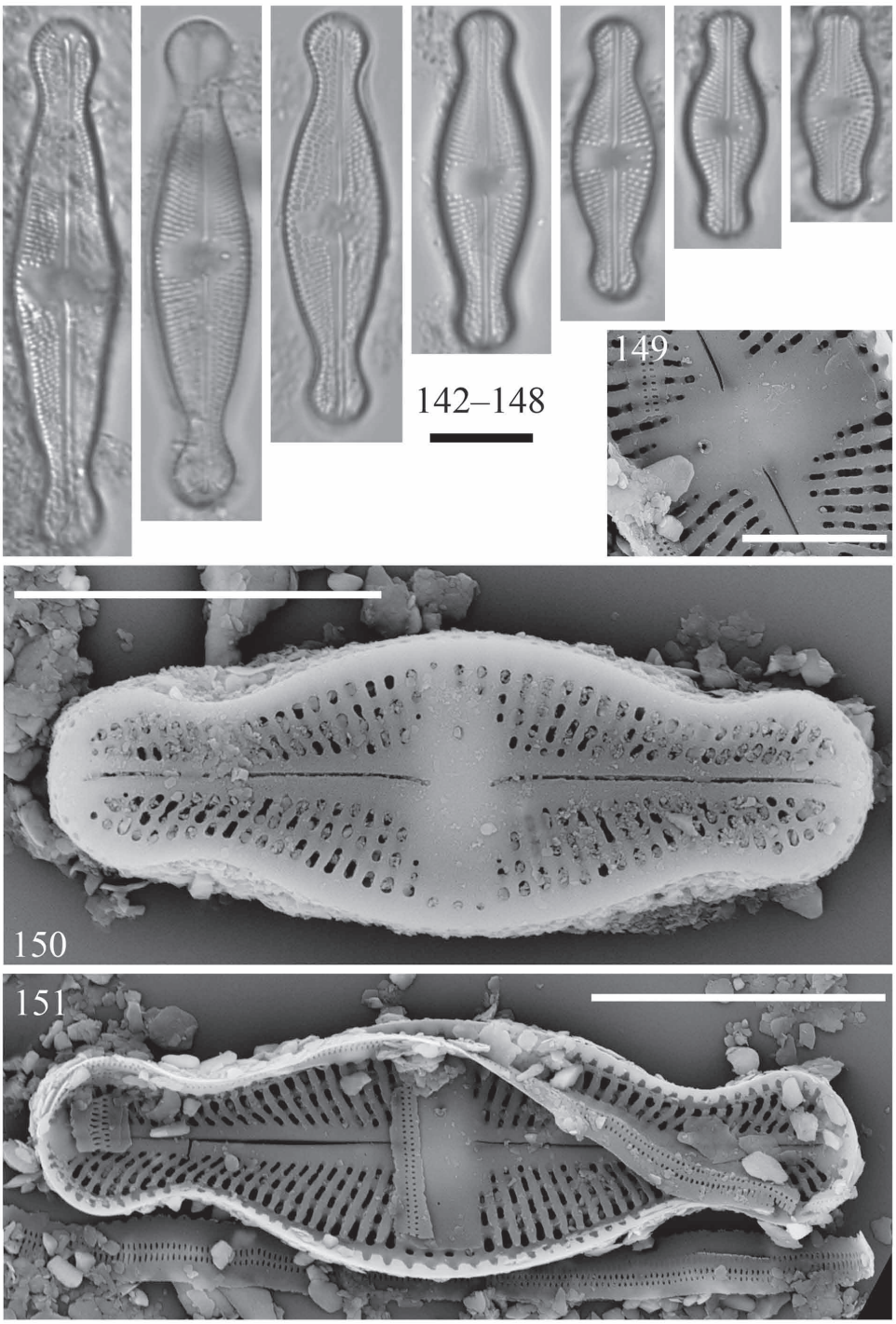
Luticola macknightiae most resembles *L. vesnae* Levkov in Levkov *et al*. (2013: 254, pl. 15, figs. 5–6, and pl. 157, figs. 13–21) valve outline. Described from Macedonia, *L. vesnae* is similar in size, measuring 17–34 µm long and 5.3–8.0 µm wide (Levkov *et al*. 2013). However, it has more dense striae (22–24 in 10 µm), more areolae per stria (3 or 4), and external distal raphe endings continue onto valve mantle, whereas in *L. macknightiae* the raphe terminates at or before the last row of areolae. Among Antarctic taxa, *L. macknightiae* shares similarities to *L. delicatula* Van de Vijver, Kopalová, Zidarova & Levkov in Levkov *et al*. (2013: 99, pl. 53, figs. 21–26, pl. 54, fig. 6), though this species is wider (7.0–9.0 µm), has more coarse striae (15–16 in 10 µm), and is generally widest in the center of the valve tapering to rounded apices. This is in contrast to *L. macknightiae* which has two convex margins and rostrate apices. *Luticola macknightiae* may also resemble *L. pusilla* Van de Vijver, Kopalová, Zidarova & Levkov in Levkov *et al*. (2013: 203, pl. 50, figs. 1–16, pl. 51, figs. 1–7) in dimensions; *L. pusilla* is 12–28 µm long, 4.5–7.5 µm wide, and has 18–21 striae in 10 µm composed of 2–3 areolae. It differs from *L. macknightiae* in having more rounded apices and a more oval shaped intermediate size range. Furthermore, *L. pusilla* has a widened distal end of the raphe not present in *L. macknightiae* (Levkov *et al*. 2013).

On continental Antarctica, *L. macknightiae* may only be confused with *L. austroatlantica* because both taxa have convex margins and at intermediate size ranges exhibit rostrate apices. However, *L. austroatlantica* has distinctly capitate apices at upper size ranges and are more parallel where they meet the central are in intermediate size ranges resulting in distinct "shoulders". In *L. macknightiae*, apices are rostrate at intermediate sizes, and are never fully capitate at upper size ranges. In addition, the areolae of *L. macknightiae* are more sparsely distributed within striae (2–3) compared with *L. austroatlantica* (3–4). Lastly, *L. macknightiae* is consistently narrower than *L. austroatlantica* at any given length, making comparisons between populations straightforward.

Luticola transantarctica Kohler & Kopalová, *sp. nov*. (Figs. 142–151)

LM observations (Figs. 142–148): Valves elliptic-lanceolate, becoming slightly rhombic in larger specimens (Figs. 142–143). Margins symmetrical, convex and rounded in central area. Apices broadly rounded, capitate, becoming slightly rostrate in smaller specimens (Fig. 148). Valve dimensions (n=25): length 16.0–50.9 µm, width 7.1–10.6 µm. Axial area narrow,

expanding towards central area. An isolated pore present in central area, located halfway between valve center and valve margin. Central area rectangular to elliptical, bordered by shortened striae on both sides. Raphe branches straight with both proximal and distal endings slightly deflecting away from isolated pore. Transapical striae radiate throughout, 18–22 in 10 µm. SEM observations (Figs. 149–151): Externally (Fig. 150), striae composed of 3–5 areolae, 2–3 at apices. Areolae rounded to elongated throughout, extending to the distal raphe endings. Isolated pore appears slightly elongated, but obscured by debris. Central area bordered by 1–2 rows of three rounded areolae on the isolated pore side, and a single row on the opposite side. Proximal and distal raphe endings slightly deflected opposite isolated pore, terminate on valve face. Clear separation between valve face and margins. A single row of rounded areolae visible along valve mantle, interrupted at apices. Internally (Figs. 149, 151), structures difficult to discern due to specimen corrosion and small sample size. Central nodule thickened. Distal raphe endings straight, proximal raphe endings deflect slightly towards isolated pore.



FIGURES 142–151. *Luticola transantarctica* Kohler & Kopalová, *sp. nov*. Light (LM) and scanning electron micrographs (SEM). 142–148. Specimens from the Labyrinth Pond, Wright Valley, the type population, LM. 149. Detail of isolated pore, internal valve view, SEM. 150. External valve view, type population, SEM. 151. Internal valve view, type population, SEM. LM scale bar = 10 µm. SEM scale bars = 10 µm, 4 µm for detail of internal isolated pore.

Type:—ANTARCTICA, McMurdo Dry Valleys, Wright Valley, Labyrinth Pond, Sample #4, *A. Sakaeva*, *07 January 2014* (holotype INSTAAR! #2669A, illustrated in Fig. 145, isotypes BM! 101779, BR! 4408).

Etymology:—The name "*transantarctica*" is in reference to the isolated locality in which the type population was collected from; The Labyrinth, Wright Valley, at the foot of the Transantarctic Mountains.

Habitat, ecology and distribution:—At present, this species is only known from The Labyrinth in Wright Valley, Antarctica, where it comprised over 60% of the diatom community by relative abundance (Sakaeva 2014).

INSTAAR herbarium:—Labyrinth Pond 2669.

Observations:—If observed at all, the lower size range of this taxon may have previously been identified as *L. muticopsis* f. *reducta* because of images published by Kellogg *et al*. (1980), which appear to show the reduced form of *L. gaussii* or other *Luticola* with rounded apices. Like *N. muticopsis* f. *evoluta*, there is no original illustration for *L. muticopsis* f. *reducta*, and the description is limited to "Cells are shorter, poles less drawn out and distinctly truncated, striae 13 in 10 µ" (translated from Latin, West & West 1911: 284). However, since *L. transantarctica* was not was not observed in our survey of Cape Royds, nor in the original West & West (1911) slides, we conjecture that the two are not conspecific. Based on published images, it is also possible that *L. transantarctica* has been observed in the past and identified as *L. murrayi* (Kellogg *et al*. 1980: 176, pl. 1, fig.20) or *Naviula globiceps* f. *amphicephala* (Ko-Bayashi 1963: 13, pl. 4, fig. 3), but these populations should be re-investigated before this can be said for certain.

From the Antarctic continent, *Luticola transantarctica* is most similar in morphology to *L. pseudomurrayi*, described from Langhovde, Lützow Holm Bay, East-Antarctica (Van de Vijver *et al*. 2012). However, *L. transantarctica* differs from *L. pseudomurrayi* by having more capitate apices, with narrower constrictions between the apices and the valve center. Lastly, *L. pseudomurrayi* has a larger upper width range than *L. transantarctica* (7.5–12.0 µm *vs*. 7.1–10.6 µm). From the McMurdo Sound Region, *L. transantarctica* could be confused with *L. elegans*, especially at the lower end of the size range. However, apices in *L. transantarctica* remain capitate at small sizes, whereas in *L. elegans* they become more rostrate at lower as well as greater sizes. *Luticola gaussii* is very similar in valve outline, especially at intermediate lengths. However, *L. gaussii* has a more rounded central area compared to the elliptic central area in *L. transantarctica*, and *L. gaussii* additionally has slitted punta under SEM. Furthermore, the striae of *L. gaussii* are patterned as noted by West & West (1911), with two lines running along the axial area in the valve center and one at the apices. In *L. transantarctica*, striae form no such pattern, are punctate and irregular. Finally, *L. gaussii* is consistently wider than *L. transantarctica* at any given length.

Discussion

Based on the results of this study and recent literature (Table 2), our observations indicate the presence of 43 different *Luticola* taxa confirmed from the Antarctic Region. Following the application of a more fine-grained taxonomy, almost 98 % of all *Luticola* species within this grouping are restricted to the Antarctic Region, with a majority (53 %) confirmed only from the Maritime Antarctic. Furthermore, 21 % are known only from the Antarctic continent, and 14 % are typically present only in the sub-Antarctic region. The results also reveal that less than 10 % of the total number of observed species (*L. austroatlantica*, *L. permuticopsis*, *L. gaussii*, and *L. muticopsis*) is shared between the Antarctic continent and Maritime Antarctic Region (MA/CA, not counting *L. cohnii*). There is no evidence for a species only shared between the sub-Antarctic and the Antarctic continent without being also present in the Maritime Antarctic Region, and there is no species that is shared exclusively between the sub- and Maritime Antarctic. Only one species, *L. muticopsis*, is present across the entire Antarctic Region. These results are in strong contrast to previous reports of the biogeographical features of the Antarctic diatom flora, where a majority of the species was considered to be cosmopolitan (Jones 1996, Van de Vijver & Beyens 1999, Toro *et al*. 2007, Esposito *et al*. 2008, Vinocur & Maidana 2010).

Only *L. cohnii* has a cosmopolitan distribution in our analysis, but it is not clear that records report the genuine *L. cohnii*. Although commonly reported from the entire Antarctic Region, including the continent, we found no valves that could be identified conclusively as *L. cohnii* or the similar *L. mutica*. Like many *Luticola* species previously force-fitted into European taxa, these species may be over-reported due to their typical, rounded valve outlines. Following the MacDonald-Pfitzer rule of size diminution (Round *et al*. 1990), diatoms often lose their defining shape characteristics at their lower size ranges, and some species (such as *L. laeta* and *L. spainiae*) become more rounded as they become smaller. This, along with the application of a too broad species concept, may result in an inability to separate these

reduced valves from familiar European taxa such as *L. mutica* and *L. cohnii*. It follows that caution should be taken in considering *L. cohnii* a cosmopolitan diatom until more studies utilizing SEM for the defining morphological characters, and ultimately molecular approaches, can verify its ubiquity.

In our investigation of both recent and original material derived from Cape Royds, we did not find any species that we would attribute to *Navicula muticopsiforme*, *N. muticopsis* f. *evoluta*, or *L. muticopsis* f. *reducta*, all of which were newly described by West & West (1911). While an illustration for *N. muticopsiforme* is presented in the paper to aid in making an identification, there are unfortunately no illustrations for *N. muticopsis* f. *evoluta* nor *L. muticopsis* f. *reducta*, and only modest descriptions. Furthermore, the latter two formae do not have size ranges, and only include overlapping stria densities (13–14 v*s*. 13 in 10 µm). Because these new forms can neither be identified nor distinguished between each other, we would discourage their use as taxonomic entities, and we conjecture that these likely belong to the smallest cells in the cell cycles of other *Luticola* taxa (Van de Vijver *et al*. 2012, Levkov *et al*. 2013), rather than separate entities in their own right.

Lastly, we failed to observe any specimen of *L. pseudomurrayi* in this survey from the McMurdo Sound Region, although it has previously been documented from other parts of East Antarctica (Ko-Bayashi 1963, Roberts & McMinn 1999, Sabbe *et al*. 2003, Ohtsuka *et al*. 2006, Van de Vijver *et al*. 2012). While this diatom may very well be present in the McMurdo Sound Region, it cannot be verified at this time. However, it is interesting that it is often found amongst other genera that have yet to be observed in the McMurdo Sound Region, such as *Gomphonema*, *Pseudostaurosira*, and *Stauroforma* (Sabbe *et al*. 2003) among others (Roberts & McMinn 1999). Because of this, patterns delineating the Antarctic continent flora may be more complex than the single category adapted from Chown & Convey (2007) suggests. We conclude that the genus *Luticola* is highly endemic in continental Antarctica, distinct from the sub- and Maritime Antarctic Regions, and may serve as a fruitful model organism for studying microbial biogeography.

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