Freshwater diatom biogeography and the genus *Luticola*: An extreme case of endemism in Antarctica

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Abstract Historic views on levels of endemism in the Antarctic region have characterized the region as a frozen desert with little diversity and low endemism. More recent studies have uncovered that endemism does exist in this region and may be much greater than previously expected in several groups. For microbes, assessing levels of endemism in the Antarctic region has been particularly important, especially against a backdrop of debate regarding the possible cosmopolitan nature of small species. In order to assess the degree of endemism of the freshwater diatom genus *Luticola* in the Antarctic region we synthesized the results of a modern high-resolution taxonomy for species in Continental Antarctica, Maritime Antarctica and islands in the sub-Antarctic, as well as southern areas of South America. The diatom genus *Luticola* has one of the highest percentages of endemism in Antarctica of any known diatom genus, in terms of total number of species (treated here as taxon endemism) as well as a percentage of the entire genus (phylogenetic endemism). We examined recent and historical taxonomic treatments of freshwater diatoms, and compiled data for the number of endemic species and their distributions. Of the over 200 species of *Luticola* currently known worldwide, nearly 20% (43) occur in freshwater habitats in the Antarctic region. Of these 43 species, 42 are endemic to the overall Antarctic region, with Maritime Antarctic localities having the largest number of species and sub-regional endemics (28, 23, respectively), followed by Continental Antarctica (14, 9 respectively) and the sub-Antarctic islands (8, 6, respectively). Thus, 38 of the 42 Antarctic endemics are found in a single sub-region only. These numbers of endemics for *Luticola* are compared with other groups of terrestrial and freshwater organisms, and the genus has one of the highest, if not the highest, levels of endemicity in Antarctica. The timing of the diversification of *Luticola* has not been established, but the oldest known fossils of the genus date only to the Holocene, suggesting that diversification processes in this genus are rapid, and that single or multiple invasions of the region may have occurred over a very short geologic timescale. Understanding the origin and evolution of endemic species in Antarctica will help us better assess and interpret the baseline and impacts during a time of large-scale environmental change in southern latitudes.

Keywords Antarctica, aquatic, Bacillariophyta, continental, diatoms, endemism, *Luticola*, maritime, sub-Antarctic islands

Introduction

Terrestrial and freshwater aquatic habitats of the Antarctic region include the sub-Antarctic islands, Maritime Antarctica and Continental Antarctica (Cande et al*.,* 2000; Chown & Convey, 2007; Convey, 2013). This region has been the focus of numerous studies addressing the impacts of glacial geology (Ruddell, 2006; Sugden et al., 2006), changes in climate (Convey 2003; Convey et al., 2009), and biogeography (Brundin, 1966; Mortimer et al., 2011) across the Southern Hemisphere. Convey et al. (2014) have produced an excellent summary of the physical and chemical factors that play important roles in structuring biological communities in the Antarctic region including light, temperature, wind, and availability of water.

Antarctica has in the past been described as a biologically barren, cold desert with few unique species and low overall richness (Benninghoff, 1987; Convey 2010). For some groups, that statement is clearly true. However, for other groups, a variety of methods including morphological and molecular analyses have begun to suggest that the Antarctic region is more diverse (and, in particular, more unique) than has been widely assumed in the past (Convey et al., 2008, 2009).

For microbes, there has been controversy over the past two decades regarding whether they may exhibit biogeographic patterns at all (Finlay & Clarke 1999; Finlay 2002; Finlay & Fenchel 2004), and if so, the extent to which they exist and what we can learn from them. The controversy has included responses from those working with a variety of groups of microbial organisms, including freshwater diatoms (Kociolek & Spaulding

2000; Vyverman et al. 2007; Vanormelingen et al. 2008). The Antarctic region along with the resource of a high-resolution modern taxonomy of the genus *Luticola* in this area (see Table 1) offers an unique opportunity to explore the level of endemism in this relatively pristine habitat, and to assess this not only with regard to the species present (taxon diversity) but also related to monophyletic groups (phylogenetic diversity).

Diatoms are a large (> 64,000 described taxa; Fourtanier & Kociolek, 2011) and diverse group of photosynthetic, eukaryotic microbes, inhabiting almost every place where there is or has been water (Kociolek 2007). Many published studies have supported the idea that freshwater diatom species are not all cosmopolitan, and in fact many (perhaps most) species have limited distributions (e.g., Kociolek & Spaulding 2000). Limitations on their distributions can be seen as focused on a single place, such as individual lakes (i.e., Kulikovskiy et al. 2012; Hamsher et al. 2014), areas (e.g., many of the works by Lange-Bertalot and colleagues in the series *Iconographia Diatomologica*, now up to 27 volumes, fall into this category), or regions (Potapova & Charles 2002). The Antarctic region demonstrates endemism for many groups of diatoms (e.g., Van de Vijver 2004, 2011; Kopalová et al. 2009, 2011), but for *Luticola* the case for endemism in Antarctica is even stronger.

The diatom genus *Luticola* (Round et al. 1990) is composed of mostly small, yet easily diagnosed, taxa. Features of the genus include a conspicuous isolated pore, canals running longitudinally along each of the margins and distinctly punctate striae (Figs. 1, 2). The most recent monograph of the genus is that of Levkov et al. (2012), treating almost 200 taxa from all parts of the world. Ecologically, the genus has been characterized as being aerophilous, and its members have been described at the edges of streams, in splash zones of waterfalls, in moist soils, and amongst mosses (Round et al., 1990), though a few species are also estuarine (Hustedt, 1964).

Members of *Luticola* have been recognized since the first collections of microbes were made from Antarctica (Van Heurck, 1909; West & West, 1911). A long history on the treatment of the genus from Antarctica is provided by Kellogg & Kellogg (2002). Hustedt (1964) listed four species associated with Antarctica, while Kellogg & Kellogg (2002) included 14 taxa. Applying LM and SEM tools, and a high-resolution taxonomic approach, a large number of new *Luticola* taxa have been described from this region in recent years (see Figures 1a-b), making the genus one of the most species-rich in the area. Images of representative endemic *Luticola* species described from the Antarctic region are presented in Figs. 2a-i. Most *Luticola* taxa in Antarctica show a preference for aquatic and limno-terrestrial environments such as soils and damp moss habitats (Van de Vijver et al., 2002a; Lowe et al., 2007). No resting stages or spores are known.

Here we review the occurrence and distribution of *Luticola* species from the Antarctic region, derived from samples collected in many parts of the region (Figure 3). We compare the number of endemic species in the region to that characteristic of other groups of organisms. The patterns present in the number and distribution of *Luticola* species in the region lead to important questions regarding their phylogeny and biogeography, possible adaptations for this region, and the fate of these endemics in rapidly changing environmental conditions (Turner et al. 2009).

APPROACH

In comparing levels of endemism, we consider both specific, widely used sub-regions within Antarctica (Continental, Maritime and sub-Antarctic), as well as 'Antarctica' in its entirety (the sum of those three sub-regions). We also distinguish between different 'level of endemism' concepts. The term, 'level of endemism', can be used to indicate the number of species endemic to a specific location relative to the total number of species of that taxon present there (taxon endemism). However, a second and different definition can be the number of taxa endemic to a specific location relative to the total number of taxa known for that group worldwide (phylogenetic endemism or phylodiversity; Laity et al., 2015).

TAXON AND PHYLOGENETIC DIVERSITY OF *LUTICOLA* IN THE ANTARCTIC REGION

On the sub-Antarctic islands, a total of eight taxa have been recognized, six of which are endemic to this region (Van de Vijver et al., 2002, 2011; Levkov et al., 2012). Taxa have been considered from Île de la Possession (Îles Crozet), as well as Îles Kerguelen, Prince Edward Islands and Heard Island. During a recent survey of the Ulu Peninsula on James Ross Island (Maritime Antarctic), 18 different *Luticola* taxa were found and, of those, six were described as new species (Kopalová et al., 2009, 2011).

The geographic distribution of the observed taxa indicates a highly specific *Luticola* flora on James Ross Island (Kopalová et al., 2011). One taxon, *L. austroatlantica* Van de Vijver et al., was previously recorded from both Continental and Maritime Antarctic, whereas *L. gaussii* (Heiden in Heiden & Kolbe) D.G.Mann was previously only known from the Continental Antarctic (Esposito et al., 2008). This is perhaps not surprising considering the close vicinity of the Antarctic Continent, and the fact that James Ross Island has been considered part of the transitory zone on the eastern Antarctic Peninsula between the Maritime and Continental Antarctic regions (Øvstedal & Smith, 2001). Outside James Ross Island, only six other taxa have been reported in the entire Maritime Antarctic region. These species are, at present, only reported from the South Shetland Islands north-west of the Antarctic Peninsula (Van de Vijver et al., 2006, 2011; Van de Vijver & Mataloni, 2008). Six taxa have been found only on the South Shetland Islands, and seem to be absent from the more southerly located James Ross Island.

Detailed light and scanning electron microscopic observations, review of pertinent literature, and examination of historical and type material led to the identification of 14 *Luticola* species in Continental Antarctica (Tables 1, 2). All but one of the *Luticola* species considered (13) in Kohler et al. (2015) show distributions that are restricted to the Antarctic region as a whole, and eight of them are limited in their distribution to Continental Antarctica alone. Three species recognized from Continental Antarctica have also been identified in Maritime Antarctica, one was found in all three Antarctic regions

(*L. muticopsis* (VanHeurck) D.G.Mann), and one (*L. cohnii* (Hilse) D.G.Mann) is a cosmopolitan species (Kohler et al., 2015).

Of the total number of *Luticola* taxa currently known from the entire Antarctic region (43, summarized in Table 1) only one is found beyond that region (*L. cohnii*), one is found in all three regions (*L. muticopsis*), and three are found in both the Maritime and Continental Antarctic regions. No species are found whose distribution includes the sub-Antarctic islands and Continental Antarctica to the exclusion of Maritime Antarctica (Table 1). Thus, 42 of the 43 species (98%) found in the region (taxon endemism) are endemic to the entire Antarctic, and 40 of these are endemic to one of the three recognized sub-regions. Of those species that are endemic, 60.5% are found in Maritime Antarctica alone, 23.7% are found in Continental Antarctica alone, and 15.7% are restricted to the sub-Antarctic. Nearly 20% of the entire genus (Levkov *et al.*, 2012) is endemic (phylodiversity) to the Antarctic region as a whole. 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; Vinocur & Maidana 2010). Though members of *Luticola* are small, it is unlikely this pattern of high endemism is due solely to intensity of sampling and survey work in Antarctica (versus, say, North America, Europe and Japan).

EXTREME ENDEMISM IN ANTARCTICA

The diversity and levels of endemism seen in *Luticola,* with 42 species endemic to the Antarctic region, are unmatched by any other known genus of organisms in Antarctic limno-terrestrial environments. Similar high levels of endemism within Antarctica are known in the marine realm (Clarke & Johnston 2003; Griffiths et al. 2009). For a genus of worldwide distribution (Levkov et al. 2012), that 20% of all *Luticola* species are found only from the Antarctic region is similar to the level for Pycnogonida (sea spiders) reported by Munilla & Membrives (2008). Below, we give an overview of known diversity and levels of endemism in terrestrial and freshwater ecosystems across a wide range of biodiversity in the Antarctic region.

COMPARISON OF *LUTICOLA* ENDEMISM WITH OTHER GROUPS

Flora

The terrestrial biota of Antarctica until recently has been described as relatively depauperate, based mostly on the inspection of the macroscopic flora and fauna. In addition to a reduced flora, there are few apparently endemic taxa. For photosynthetic organisms, higher plants number just two species known from the maritime Antarctic and ca. 200 species from the sub-Antarctic, with most of these not being endemic to Antarctica as a whole (Convey 2007). Specific endemism of bryophytes is subject to ongoing taxonomic uncertainty, but their taxon endemism is thought to be less than 5% out of over 100 species reported from Antarctica (Ochyra et al. 2008). There are 415 species of lichens reported from the region, with estimates of endemism ranging from 24% to 50% (Øvstedal & Smith 2001, 2004). It is not clear if these endemic taxa are grouped within monophyletic groups, hence diversity within lineages is difficult to assess (Ruprecht et al. 2012).

Invertebrates

Pugh & Convey (2008) surveyed the literature and analyzed distributional data for the non-marine Antarctic invertebrate fauna. Out of 520 taxon records for Maritime and Continental Antarctica, they recognized 175 verified, free-living invertebrate taxa, 135 of which are terrestrial and 40 of which are aquatic. The taxonomic groups included nematodes, rotifers, tardigrades, crustaceans, arachnids and hexapods. Several interesting comparisons can be made with *Luticola*. First, the 175 species occur in 140 genera, mirroring the pattern seen in other diatom groups (see below) that there are a few species per genus that are endemic to Antarctica. Second, for a more direct comparison, we should add to the 175 endemics, those that are found in the sub-Antarctic, which include another 43 invertebrate species, giving a total of 218 (Pugh & Convey 2008). When the non-endemic species are added (84 species), the total, free-living invertebrate fauna numbers 302, of which just over 72% are taxon endemics (data from Table 1 of Pugh & Convey 2008). Third, patterns described for invertebrates, wherein species are endemic to a particular region within Antarctica and relatively few species occur across several of these regions, are similar to *Luticola*. Finally, some invertebrates also show a finer scale regionalism being found, for example, in certain sectors of Continental Antarctica, but data are currently lacking for *Luticola* in this regard. Data for specific groups of invertebrates are summarized below.

In earlier studies, a total of 17 springtail species (Collembola) across 13 genera were recognized from the Continental and Maritime Antarctic regions (Wise 1967, 1971), and nine of these were regarded as endemic. Greenslade (1995) reported 25 species of Collembola described from these regions, and also highlighted that only one of these was common between the two regions (*Friesea grisea* Schaeffer, for which subsequent molecular analyses have revealed species-level divergences in the mitochondrial genome; Torricelli et al. 2010). A number of the Maritime species are also known from the sub-Antarctic, but not more widely. Greenslade (2006) also reported 6 endemic genera and that all 10 species found in Victoria Land (Continental Antarctica) are endemic there, while no endemic genera and 6 endemic species are found in other Antarctic regions. Similar patterns, with slightly smaller numbers were reported by Adams et al. (2006). For the group as a whole, it is estimated that there are 8,000 species of springtail worldwide (Bellinger et al. 1996-2015). If there are a total of 25 (9+10+6) endemic species from the Antarctic region, for the group the level of Antarctic phylogenetic endemism is less than 1%.

For tardigrades, Convey & McInnes (2005) list 43 species or taxa having affinities with a named species in 19 genera for the Antarctic region (their Table 3). Another 3 species are indicated as possible new species. No single genus has more than 8 species present in the fauna. A molecular phylogenetic analysis of tardigrades in parts of the Antarctic region (mostly the Continental Antarctic) suggests the presence of 4–6 species, 2 of which may be new to science (Czechowski et al. 2012). Another new species representing a genus previously not reported from the Antarctic region was described recently (Giudetti et al.

2014). The well-known ability of tardigrades to withstand a wide range of extreme physical and chemical conditions (Jönsson & Bertolani 2001) contributes to the number of endemic species present.

Chironomids have been suggested to be the "…most diverse and most widely distributed group of holometabolous insects" in the Antarctic and sub-Antarctic regions (Cranston 1985, p. 35). While 32 species in 18 genera are reported in the entire region, only 2 occur in Maritime Antarctica (one of which is endemic) and none in Continental Antarctica (Cranston 1996; Convey & Block 1996). Although Antarctica may have been a corridor for the dispersal of Gondwandan chironomids (Brundin 1966), the present day fauna is extremely limited in the Antarctic Continent and Maritime Antarctic regions.

Perhaps the group with the most species reported from Antarctica is the Acari or mites, with 528 species catalogued (Pugh 1993). This number, however, includes free-living, marine, and parasitic species reported from sea birds, seals and other mammals. It is not clear from the work of Pugh & Convey (2008), how many of the 175 free-living, endemic invertebrates, are mites. Most of the mites in the sub-Antarctic region have been reported as primarily cosmopolitan, being carried by host waterfowl (Pugh 1993).

For rotifers, Dartnall (1983) reported 70 species present in the Antarctic region. The group comprises two major subgroups, the Bdelloidea and the Monogononta. Of the bdelloids, 36 species have been reported, 5 of which are considered endemic as determined through morphological observations (Velasco-Castrillón et al. 2014).

However, these workers, using the COI gene, also suggest much higher levels of endemic lineages in Antarctica, perhaps as high as 26 endemic taxa, a conclusion supported by the recent study of Iakovenko et al. (2015). Fontaneto et al. (2015) suggest there are latitude and habitat differences in the diversity of rotifers in the Antarctic region, as determined by a review of over one hundred years of research on the group in Antarctica. Despite this long history, more work is necessary to sort out patterns of diversity in the two major subgroups in the region.

Invertebrates are a large and disparate set of taxa and their representation in the Antarctica fauna in terms of number of species and levels of endemism varies. The invertebrates also show regionalization within Antarctica, with endemics being located in either the sub-Antarctic, Maritime or Continental regions, and only small numbers of species overlapping across regions. This is the same pattern found among the species of *Luticola*.

Soil and Aquatic Microbes

Komárek (2013) has reviewed the long history of research on terrestrial and freshwater Cyanobacteria from Antarctica. Though no synopsis of diversity is presented by Komárek or in other overviews (e.g. Zakhia et al. 2008), summary statements suggested the Cyanobacteria flora comprises a mix of cosmopolitan and endemic taxa, but detailed molecular analysis is wanting. Current research does not seem to suggest that Cyanobacteria, which are found in nearly every type of extreme environment on Earth that receives sunlight, shows remarkable endemism in Antarctica.

A molecular study of freshwater coccoid green algae by De Wever et al. (2009) showed that 14 distinct taxa from lacustrine environments in maritime and continental Antarctica were distributed across the Chlorophyceae, Trebouxiophyceae and Ulvophyceae of the Chlorophyta or Green Algae. Many of these 14 Antarctic species had sister taxa from outside the region, suggesting several dispersal events to the Antarctic Continent. The Antarctic representatives were highly divergent from their non-Antarctica relatives. Moniz et al. (2012) suggested significant cryptic diversity in the green algal genus *Prasiola* (Prasiolales, Trebouxiophyceae). Schmidt et al. (2010) however, found that there were similar taxa in both the Dry Valleys of Antarctica and the high Himalayas, and that the same taxa adapted to extreme cold and dry conditions existed in these similar, but physically remote habitats. Though no estimates of diversity or endemism were presented, the work of Pichrtová et al. (2013) and Thangaraj (2015) suggest members of the Zygnematales can withstand high light intensity and ultraviolet radiation. Vyverman et al. (2010) suggested that the number of endemics of other algal groups, namely of Cyanobacteria, Chlorophyta and Bacillariophyta (diatoms), might be high.

Analyses of the soil bacteria community suggest endemism might be high in the Antarctic. For example, Lee et al. (2011) studied the heterotrophic bacteria from microbial mats in wet habitats. Molecular data suggested nearly 37% of the phylotypes, from 5 major phyla, determined with 16S rRNA are known only from Antarctica. These authors concluded that for these organisms "…in Antarctica, both cosmopolitan taxa and taxa with limited dispersal and a history of long-term isolated evolution occur". Similar results were recorded by Peeters et al. (2012). Chong et al. (2013) suggest the levels of bacterial endemism in Antarctica may be more modest (ca. 25%), but noted regional distribution of genera (versus a homogenous flora). Both species and genera have been thought to be endemic to Antarctica (see references in Vyverman et al. 2010).

Other Freshwater Diatoms

For freshwater diatoms in the Antarctic, a number of groups have been detailed over the last 25 years, and endemics have been described in several genera, including *Gomphonema*, *Stauroneis*, and *Orthoseira*. For example, Kociolek & Jones (1995) described a new *Gomphonema* species from Signy Island. However, the genus *Gomphonema* contains over 800 taxa (Fourtanier & Kociolek 2011). Van de Vijver et al. (2004) reported 18 endemic taxa of *Stauroneis* from sub-Antarctic islands, most of them newly discovered. Like *Gomphonema*, *Stauroneis* is a large genus (> 500 taxa), suggesting the level of Antarctic endemism of *Stauroneis* taxa to be just over 3% of the global diversity. More than 47 species of *Pinnularia* have been described from the Antarctic Region (Van de Vijver 2008; Van de Vijver et al. 2002, 2012b; Van de Vijver & Zidarova 2011; Zidarova et al., 2012). However, like *Gomphonema* and *Stauroneis*, *Pinnularia* is a very large genus (Fourtanier & Kociolek, 2011) and the overall level of Antarctic endemism relative to global diversity is modest (less than 5%). Forthcoming work on the genus *Nitzschia* (Hamsher et al. 2016) will mirror the examples of *Gomphonema*, *Stauroneis* and *Pinnularia*. Van de Vijver & Kopalová (2008), Van de Vijver et al. (2002), Lowe et al. (2013) and Van de Vijver & Crawford (2014) each described a new species of *Orthoseira* from sub-Antarctic islands. This genus is much smaller, ca. 15 species (Fourtanier & Kociolek, 2011), and correspondingly the rate of endemism is much higher (ca. 10%).

A genus that approaches the level of endemism seen in *Luticola* in Antarctica is *Muelleria* (J. Frenguelli) J. Frenguelli. Van de Vijver et al. (2014) have summarized previous work (e.g. Spaulding & Stoermer 1997; Spaulding et al. 1999; Van de Vijver et al. 2010) and presented new observations and species descriptions of members of this genus. Of the 35 *Muelleria* species currently recognized, 24 occur in Antarctica, and four of those occur elsewhere; two of these four also occur in South America and two others occur in South Africa. Thus the total number of *Muelleria* species endemic to Antarctica (20) results in taxon endemism lower than *Luticola*, but the genus has a higher proportion of species that are endemic to the region, and phylogenetic endemism (20/35 = 57%).

PHYLOGENETIC RELATIONSHIPS AND MONOPHYLY OF *LUTICOLA* SPECIES IN THE ANTARCTIC REGION

While there is no phylogenetic analysis of the genus *Luticola* (its position in the diatom tree of life is not well understood), the number and types of features shared by members of the genus suggest the genus is a natural group. We cannot establish, however, whether the 42 endemic species of *Luticola* from the Antarctic region are monophyletic. In other groups of Antarctic diatoms, populations (= species?) from the region of taxa such as *Hantzschia amphioxys* and *Pinnularia borealis* are more closely related to each other than they are to populations outside the Antarctic region (Souffreau et al. 2013). If the

Luticola species in the Antarctic region are monophyletic, additional questions arise about their origin, and tempo and mode of evolution in the region, such as whether they have been in Antarctica a long time, and whether the flora today is the result of an extended process, or if they are the result of a rapid, adaptive radiation associated with extreme conditions. How lineages like these might adapt to rapidly changing environmental conditions like those seen in recent decades in parts of the Antarctic region (Turner et al. 2009), is also an important area of research.

In terms of phylogenetic affinities of the *Luticola* species in the Antarctic region with species from areas of close proximity, the many endemic species from South America, (although mostly from Amazonia), and from Tierra del Fuego (Frenguelli, 1924) may be key sources. Maidana et al. (2005) studied diatom communities along a transect from southern Santa Cruz province and Tierra del Fuego province in Argentina to the South Shetland Islands and the Antarctic Peninsula. They showed similarity in the diatom flora along this transect, and suggested southern South America as a source of species for Antarctica. In terms of other potential sources of species of *Luticola* for Antarctica, a single endemic has been described from South Africa (*L. kraeusellii* (Cholnoky) Metzeltin & Lange-Bertalot; Cholnoky, 1954), however no endemics have yet been described from New Zealand (Foged, 1979; Cassie, 1989), Tasmania (Vyverman et al., 1995) or Australia (Foged, 1978; Vyverman et al., 1995; Hodgson et al., 1997). The only species found in these regions that also occurs in Antarctica are *L. cohnii*, a cosmopolitan taxon, and *L. muticopsis*, and reports of the latter require more detailed work to validate its report from New Zealand (Foged, 1979).

CONCLUSIONS

In summary, while the larger-sized biota of Antarctica has are represented by few species and few endemics, in smaller animal, plant, fungal, algal and bacterial groups, as well as other genera of freshwater diatoms, there are a large number of species present in the Antarctic region and some of these are endemic. In nearly every case surveyed, however, the number of endemic species is modest in the context of being a part of relatively species-rich genera.

The freshwater-terrestrial diatom genus *Luticola* is an important exception. *Luticola* demonstrates remarkable levels of endemism in Antarctica, with nearly 98% taxon endemicity, and nearly 20% phylogenetic endemicity. Unlike most groups in Antarctica, including other freshwater diatoms, where there is high number of endemics relative to the number of species present (taxon endemicity) but a low percentage of endemics relative to the total number of species (phylogenetic endemism) in a genus, *Luticola* has high percentages of both types of endemism. Factors that might explain the high levels of endemism in *Luticola*, and especially its success in harsh terrestrial environments have not yet been identified. Hypotheses about the ability to produce oil as an anti-freeze, withstand challenging freeze-thaw cycles and withstand high light and UV intensities for these Antarctica endemic species (relative to others in the genus) await testing.

Perhaps even more remarkable is that the genus has a very short temporal span, with the earliest known fossils coming from the Holocene in Antarctica (Björck et al., 1996).

Thus, its diversification and high levels of endemism in Antarctica may have occurred in a very rapid time frame. While the genus appears monophyletic, it is currently unknown whether the *Luticola* species presently found in Antarctica are descended from one or multiple immigration events.

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Table 1. Summary of the numbers of *Luticola* species in different Antarctic regions.

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sub-Antarctic: total number of taxa: 8; number endemic to the sub-Antarctic: 6

Maritime Antarctic: total number of taxa: 28; number endemics to the maritime Antarctic: 23

Continental Antarctic: total number of taxa: 14; number endemics to the continental Antarctic: 9

Table 2. Listing of *Luticola* species identified from the Antarctic region. C= Cosmopolitan, CA=continental Antarctic, MA= maritime Antarctica, SA=sub-Antarctic. Adapted from Kohler et al. (2015).

TAXON	Distribution	References
Luticola cohnii (Hilse) D.G.Mann	C	Van de Vijver et al., 2011; Levkov et al., 2012
Luticola dolia S.A.Spaulding & Esposito	CA	Esposito et al., 2008; Kopalová et al., 2011
Luticola elegans (West & West) Kohler & Kopalová	CA	Kohler et al., 2015
Luticola laeta S.A.Spaulding & Esposito	CA	Esposito et al., 2008
Luticola macknightiae Kohler & Kopalová	CA	Kohler et al., 2015
Luticola murrayi (West & West) D.G.Mann	CA	West & West, 1911
Luticola pseudomurrayi Van de Vijver & Tavernier	CA	Van de Vijver et al., 2012
Luticola spainiae Kohler & Kopalová	CA	Kohler et al., 2015
Luticola bradyi Kohler	CA	Kohler et al., 2015
Luticola transantarctica Kohler & Kopalová	CA	Kohler et al., 2015
Luticola adelae Van de Vijver & Zidarova	MA	Van de Vijver et al., 2011
Luticola amoena Van de Vijver, Kopalová, Zidarova & Levkov	MA	Levkov et al., 2012

Luticola australomutica Van de Vijver	MA	Van de Vijver & Mataloni, 2008
Luticola bogaertsiana Zidarova, Levkov & Van de Vijver	MA	Zidarova et al., 2014
Luticola caubergsii Van de Vijver	MA	Van de Vijver & Mataloni, 2008
Luticola contii Zidarova, Levkov & Van de Vijver	MA	Zidarova et al., 2014
Luticola delicatula Van de Vijver, Zidarova, Kopalová & Levkov	MA	Levkov et al., 2012
Luticola desmetii Kopalová & Van de Vijver	MA	Kopalová et al., 2011
Luticola doliiformis Kopalová & Van de Vijver	MA	Kopalová et al., 2011
Luticola evkae Kopalová	MA	Kopalová et al., 2011
Luticola gigamuticopsis Van de Vijver	MA	Van de Vijver & Mataloni, 2008
Luticola higleri Van de Vijver, Van Dam & Beyens	MA	Van de Vijver et al., 2006
Luticola katkae Van de Vijver & Zidarova	MA	Van de Vijver et al., 2011
Luticola neglecta Zidarova, Levkov & Van de Vijver	MA	Zidarova et al., 2014
Luticola nelidae Van de Vijver	MA	Van de Vijver & Mataloni, 2008
Luticola olegsakharovii Zidarova, Levkov & Van de Vijver	MA	Zidarova et al., 2014

Luticola pusilla Van de Vijver, Kopalová, Zidarova & Levkov	MA	Levkov et al., 2012
Luticola quadriscrobiculata Van de Vijver	MA	Van de Vijver & Mataloni, 2008
Luticola raynae Zidarova & Van de Vijver	MA	Van de Vijver et al., 2011
Luticola tomsui Kopalová	MA	Kopalová et al., 2011
Luticola truncata Kopalová & Van de Vijver	MA	Kopalová et al., 2009
Luticola vandevijveri Kopalová, Zidarova & Levkov	MA	Levkov et al., 2012
Luticola vermeulenii Van de Vijver	MA	Van de Vijver et al., 2011
Luticola austroatlantica Van de Vijver, Kopalová, S.A.Spaulding & Esposito	MA/CA	Esposito et al., 2008
Luticola gaussii (Heiden) D.G.Mann	MA/CA	Van de Vijver et al., 2012; Kopalová et al., 2013
Luticola permuticopsis Kopalová & Van de Vijver	MA/CA	Kopalová et al., 2011
Luticola muticopsis (Van Heurck) D.G.Mann	MA/CA/SA	Van de Vijver & Mataloni, 2008
Luticola beyensii Van de Vijver & Ledeganck & Lebouvier	SA	Van de Vijver et al., 2002
Luticola crozetensis Van de Vijver, Kopalová, Zidarova & Levkov	SA	Levkov et al., 2012

Luticola ledeganckii Van de Vijver	SA	Van de Vijver et al., 2002
Luticola robusta Van de Vijver, Ledeganck & Beyens	SA	Van de Vijver et al., 2002
Luticola subcrozetensis Van de Vijver, Kopalová, Zidarova & Levkov	SA	Levkov et al., 2012
Luticola suecorum (Carlson) Van de Vijver	SA	Carlson, 1913; Van de Vijver et al., 2002

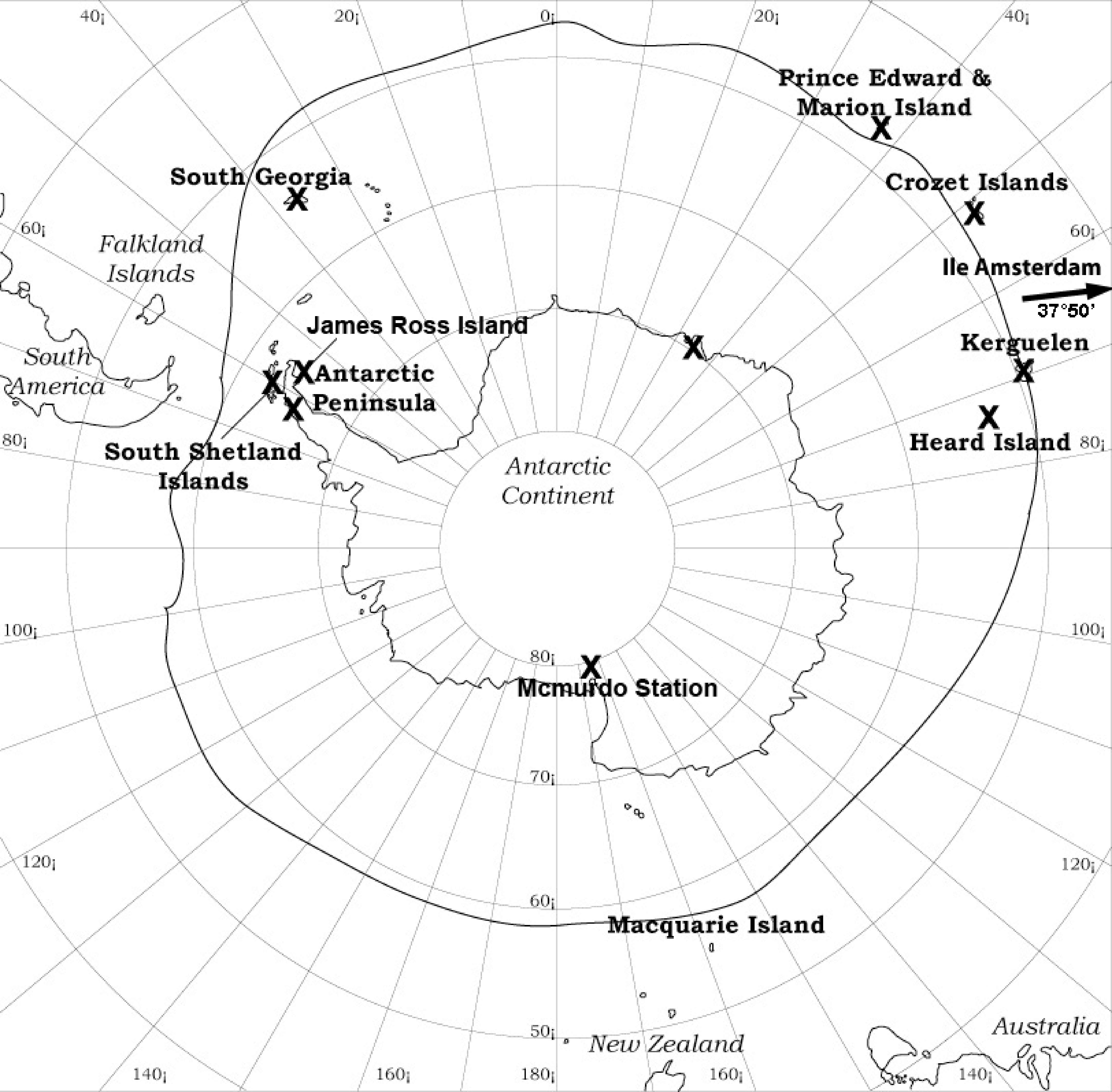
Figure Legends

Figure 1a. SEM observations of external features of *Luticola* species. The valve has distinctly punctate striae (S), with a distinct raphe system (R) positioned in the middle of the valve. A small isolated pore (IP) is present. Internally, the raphe (R) is central and the isolated pore opening (IP) is obvious in the central area. Longitudinal canals (LC) run the length of the valve near the valve face:mantle junction. Areolae have hymenate (H) occlusions over them. Scale bar represents 10 µm.

Figure 1b. SEM observations of internal features of *Luticola* species. The raphe (R) is central and the isolated pore opening (IP) is obvious in the central area. Longitudinal canals (LC) run the length of the valve near the valve face:mantle junction. Areolae have hymenate (H) occlusions over them. Scale bar represents 10 µm.

Figures 2a-i. SEM images of some *Luticola* species that are endemic to the Antarctic region. Fig. 2a. *L. permuticopsis*, Fig. 2b. *L. higleri*, Fig. 2c. *L. pusilla*, Fig. 2d. *L. vermeulenii*, Fig. 2e. *L. amoena*, Fig. 2f. *L. quadriscrobiculata*, Fig. 2g. *L. ledeganckii*, Fig. 2h. *L. muticopsis*, Fig. 2i. *L. desmetii*. Scale bars represent 10 µm.

Figure 3. Map of the Antarctic region showing the origins of samples on which the high resolution taxonomic studies are based.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James Ross Island
Kerguelen
South
America
Antarctic
Peninsula
Heard Island
80¡
80¡
South Shetland
Islands
Antarctic
Continent
100¡
100¡
80¡
Mcmurdo Station
70¡
120¡
120¡
60¡
Macquarie Island
Australia
50¡
New Zealand
140¡
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180¡
160¡
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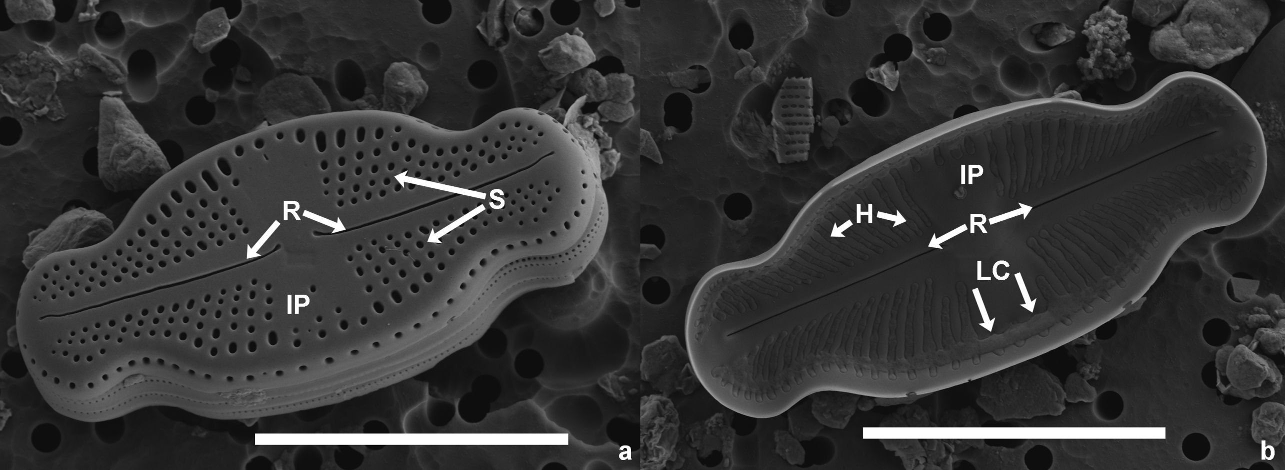
S
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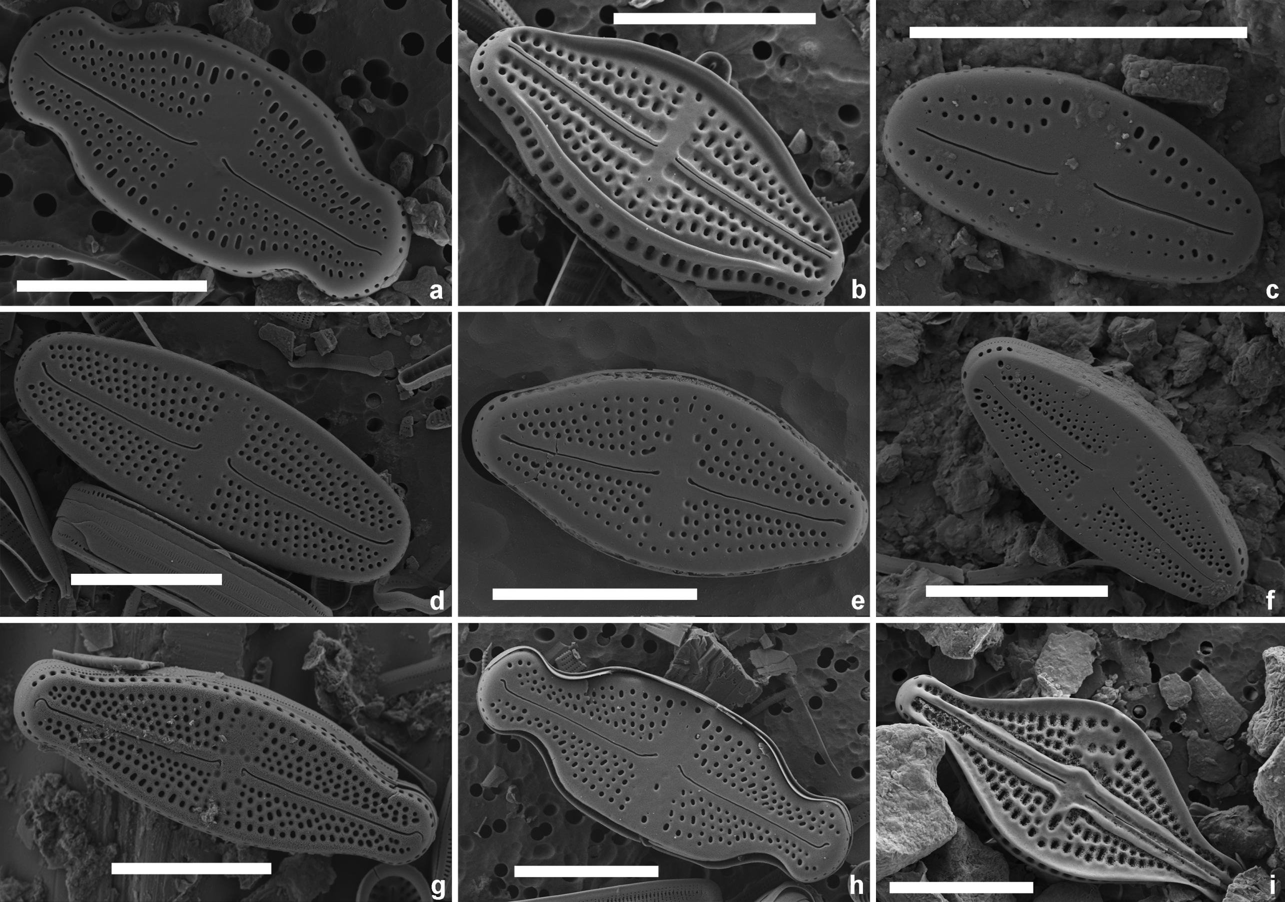
LC
b



a
b
c
d
e
f
g
h
i