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To cite this article: J. P. Kociolek (2018) A worldwide listing and biogeography of freshwater diatom genera: a phylogenetic perspective, *Diatom Research*, 33:4, 509-534, DOI: [10.1080/0269249X.2019.1574243](https://doi.org/10.1080/0269249X.2019.1574243)

To link to this article: <https://doi.org/10.1080/0269249X.2019.1574243>



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Published online: 25 Mar 2019.



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A worldwide listing and biogeography of freshwater diatom genera: a phylogenetic perspective

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A listing of the accepted freshwater diatom genera worldwide is presented, indicating the distribution of the genera by continent. Out of a total of 249 genera, 63 (25%) of those genera are endemic to a single continent. The continent with the largest number of endemic genera is Asia, hosting 35 endemic genera. While Asia is also the continent with the most reported genera, a regression analysis showed there is no relationship between the continental richness of genera and generic endemism. Disjunct genera, those found on two continents, represent distributions found in other groups of organisms such as in higher plants, including North America–Europe, North America–Asia and Southern Hemisphere disjunctions. There are certain lineages of freshwater diatoms where the endemic genera are restricted to specific continents: both thalassiosiroid and cymbelloid diatoms have endemics in Asia, while eunotioids have endemics in South America. Future research is suggested combining distributions over space and time related to phylogenetic relationships of diatoms.

Keywords: *freshwater, genera, Bacillariophyta, biogeography, endemism, continents, disjuncts*

Background

While historically there have been researchers who identified and described biogeographic patterns of freshwater diatoms (e.g. Ehrenberg 1849, Skvortzow 1937, Hustedt 1938–1939), ideas about rampant dispersal and wide variation within species (such as those espoused by Lotsy 1916 on ‘syngameons’), the dogma of ‘Everything is Everywhere’ developed in Bacteriology by Baas-Becking (1934) and rekindled by Finlay and colleagues (Finlay 2002, Finlay & Estaban 2007, Fenchel & Finlay 2003, 2004a, b, see Williams’ 2011 review of this in relation to diatoms) kept a strong grip on the thinking about freshwater diatom distributions. That grip was perhaps most pronounced in the development of the now classic ‘Süßwasserflora von Mitteleuropa’ and the way species concepts in that work were developed (Krammer & Lange-Bertalot 1986). The concept was a self-fulfilling prophecy, since research projects in areas without detailed taxonomic works began to ‘shoe-horn’ forms into European taxon names, since these floras were the only ones available.

Beginning in 2000, a series of papers (Kociolek & Spaulding 2000, Vanormelingen et al. 2007, Vyverman et al. 2007) started to analyse and summarize the literature on freshwater diatom distributions, concluding that endemism was found at different levels of taxonomic hierarchy amongst the freshwater diatoms around the world. The model that endemism exists and can be (has been!) applied to a substantial number of taxa around the world, has been adopted by most workers. Molecular methods

have supported the splitting of morphologically similar entities at the level of species, suggesting shoe-horning of taxa into names whose valve morphology was quite different was not justified. The morphological measures for splitting out forms may actually be too conservative relative to the genetic differences identified, as ‘pseudo-cryptic’ and ‘cryptic’ species have been documented (Vaneslander et al. 2009, Poulícková et al. 2010, Lundholm et al. 2012, Vanormelingen et al. 2013).

The diatom tree of life

Nearly three centuries of work with light, scanning and transmission electron microscopy has yielded the description of over 75,000 diatom taxa (Kociolek et al. 2018), and there have been numerous attempts to organize that diversity into groupings that reflect evolutionary relationships. Williams (2007) has documented many of the systems that emerged from those observations and proposals, with most of them choosing a single idea on which to base a system (modes of sexual reproduction; ability for active movement; size and number of chloroplasts, etc.). More integrative systems were proposed, ranging from ‘ideas’ (inexplicit review of certain facts) to formal analyses across the entire diatom group. The morphology-based descriptions were fully resolved but not repeatable (Round & Crawford 1981, 1984, Simonsen 1987, Round et al. 1990), and formal analyses of morphological data across broad taxonomic scales yielded unresolved polytomies

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Associate editor: Eileen Cox

(Received 22 April 2018; accepted 6 December 2018)

(e.g. Cox & Williams 2006). Explicit, formal analyses of the overall diatom tree of life were ushered in with the development of molecular techniques, yielding evidence-based, testable hypotheses. Sometimes the evidence was not always retrievable (Theriot 2008, Journal of Phycology 2009, 2010, Kaczmarska & Medlin 2009), branching patterns of the trees have differed based on taxon sampling and/or genes sequenced and analysed (Sörhannus et al. 1995, Sörhannus 2004, Sims et al. 2006, Theriot et al. 2010), and there have been vigorous discussions about how evolutionary trees can be converted into classifications (see discussions about the value of monophyly towards that end; Williams & Kociolek 2007, 2010a, b). A 2015 paper by Theriot et al. focused on the information content of molecular data, yielded a tree of over 200 terminal taxa based on sequence data from seven genes. Based on this analysis, a phylogenetic analysis of the overall diatom tree of life could be developed, like the one in Fig. 1a and b, which here includes only those clades with freshwater genera.

Endemism of freshwater diatom genera

Several analyses of endemism have centred on the taxonomic level of genus. Kociolek & Spaulding (2000) and Khursevich & Kociolek (2012) provided reviews of endemic freshwater diatom genera, based on over a century of reports. Vyverman et al. (2007), using genera as the finest taxonomic category, assuming data in their analysis of over 600 lakes worldwide would be consistent at this level of taxonomic hierarchy. From that study, Vyverman et al. (2007, p. 1924) concluded that ‘At regional to global scales, historical factors explain significantly more of the observed geographic patterns in genus richness than do contemporary environmental conditions.’ It is clear that different authors have viewed the level ‘genus’ of the Linnaean hierarchy differently (and not just in diatoms, see Laurin 2010), the monophyly of many diatom genera has yet to be verified (Kociolek & Williams 2015), and there might be other rationales for comparisons (those lineages

of the same age, lineages with similar number of taxa, etc. see Avise & Johns 1999, Avise & Mitchell 2007). However, reflecting the current state of knowledge for the group, it seems that the level of genus may be the best place to start for the freshwater diatoms.

How many endemic freshwater genera are there, and where do you find them?

Tables 1 and 2 provide the first comprehensive listing of currently recognized and used freshwater diatom genus names worldwide, both fossil and recent, and the distribution of those genera by continent. In Table 1 the genus names are listed within broad phylogenetic groupings, indicated in the phylogeny illustrated in Fig. 1a and b, while in Table 2 they are presented alphabetically. These tables are derived from summaries provided in Fourtanier & Kociolek (1999) and Kociolek et al. (2018), and listed individual papers.

In several cases, there are genera that have disjunct distributions between two continents. If a genus has a distribution across three continents, it is listed as ‘widely distributed’, and if it has been reported across four or more continents it listed as ‘cosmopolitan’. These are conservative summaries, since in other groups, an organism’s distribution across an entire continent might be considered ‘cosmopolitan’. In Table 3 those genera endemic to, or with disjunct distributions between, two continents are presented by continent.

A total of 249 genera are presented in the overall listing. Several groups, notably the eunotioids and cymbelloids, are almost exclusively freshwater, and the thalassiosiroids have a majority of freshwater genera, while all the other main groups of diatoms have a significantly larger representation (at the level of genus) in brackish or marine waters. Of those that are not endemic or disjunct, most are considered cosmopolitan. Twenty-seven (just over 10%) genera are considered ‘widely distributed’.

With respect to generic endemism, 63 freshwater diatom genera have distributions restricted to a single

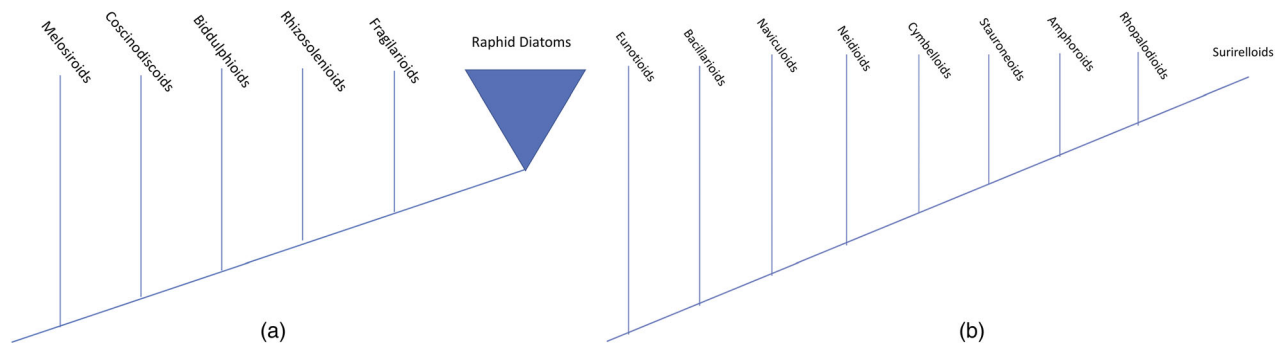


Fig. 1. Showing the phylogenetic relationships of major groups of freshwater diatoms. Fig. 1a. Overall relationships of non-raphid diatom groups with freshwater representatives. After Theriot et al. (2015). Fig. 1b. Overall relationships of raphid diatom groups with freshwater representatives. After Theriot et al. (2015).

Table 1. A worldwide listing of recognized freshwater diatom genus names in use, including fossil and recent taxa, listed within major clades as outlined in Fig. 1 and their distributions.

Taxa	Distribution
MELOSIRALES (12 genera; 4 endemics; 2 disjuncts)	
<i>Alveolophora</i> Moisseeva & Nevretdinova 1990	Widely Distributed (fossil)
* <i>Melosira</i> C.A.Agardh 1824	Cosmopolitan
<i>Brevisira</i> K.Krammer 2001	North America, Europe
<i>Eoseira</i> Wolfe & Edlund 2005	North America (fossil)
<i>Ferocia</i> Van de Vijver & Houk 2017	Antarctica
<i>Aulacoseira</i> G.H.K. Thwaites 1848	Cosmopolitan
<i>Pseudoaulacosira</i> Lupikina & Khursevich 1991	Asia (fossil)
<i>Orthoseira</i> G.H.K. Thwaites 1848	Cosmopolitan
<i>Cavernosa</i> Stidolph 1990	Australasia, Antarctica
<i>Guarreraea</i> Kociolek et al. 2018	S. America
<i>Ellerbeckia</i> R.M. Crawford 1988	Cosmopolitan
<i>Arcanodiscus</i> Maidana et al. 2017	S. America, Antarctica
COSCINODISCALES (4 genera; 3 endemics)	
* <i>Actinocyclus</i> Ehrenberg 1837	Widely distributed (fossil)
<i>Fideliacyclus</i> Siver et al. 2016	North America (fossil)
<i>Lobodiscus</i> Lupikina & Khursevich 1991	Asia (fossil)
<i>Undatodiscus</i> Lupikina 1984	Asia (fossil)
BIDDULPHIALES (5 Genera; 1 endemic)	
<i>Hydrosirella</i> Hustedt 1952	North America
<i>Pleurosira</i> (G. Meneghini) Trevisan 1848	Cosmopolitan
<i>Stoermeria</i> Kociolek et al. 1996	Widely distributed
<i>Terpsinoe</i> Ehrenberg 1843	Cosmopolitan
<i>Hydrosera</i> Wallich 1858	Cosmopolitan
Thalassiosiroids (27 genera; 11 endemics)	
<i>Concentrodiscus</i> Khursevich et al. 1989	Asia (fossil)
<i>Conticribra</i> Stachura-Suchoples & D.M.Williams 2009	Cosmopolitan
<i>Spicaticribra</i> Johansen et al. 2008	Cosmopolitan
* <i>Thalassiosira</i> P.T. Cleve 1873	Cosmopolitan
* <i>Skeletonema</i> R.K.Greville 1865	Cosmopolitan
<i>Cribrionella</i> Jovanovska et al. 2016	Europe (fossil)
<i>Cyclotella</i> (Kützing) de Brébisson 1838	Cosmopolitan
<i>Cyclostephanopsis</i> Loginova 1993	Asia (fossil)
<i>Cyclostephanos</i> F.E.Round ex Theriot et al. 1987	Cosmopolitan
<i>Cyclotubicoalitus</i> Stoermer et al. 1990	North America, Asia
<i>Dimidialimbus</i> H.Tanaka & Nagumo 2013	Asia (fossil)
<i>Discostella</i> Houk & Klee 2004	Cosmopolitan
<i>Edtheriotia</i> Kociolek et al. 2016	Asia
<i>Lindavia</i> (F. Schütt) G.B.DeToni & A.Forti 1900	Cosmopolitan
<i>Mesodictyon</i> Theriot & Bradbury 1987	Cosmopolitan (fossil)
<i>Mesodictyopsis</i> Khursevich et al. 2004	Asia (fossil)
<i>Pantocsekiella</i> Kiss & Acs 2016	Cosmopolitan
<i>Pliocaenicus</i> F.E.Round & H.Hakansson 1992	Widely Distributed
<i>Praestephanos</i> Tuji et al. 2014	North America, Asia
<i>Strelnikoviella</i> Kociolek et al. 2014	North America (fossil)
<i>Stephanocostis</i> Genkal & Kuzmin 1985	Widely Distributed
<i>Stephanodiscus</i> Ehrenberg 1845	Cosmopolitan
<i>Stephanopsis</i> Khursevich et al. 2000	Asia (fossil)
<i>Tertiarius</i> H.Hakansson & Khursevich 1997	Widely distributed (fossil)
<i>Tertiariopsis</i> Khursevich & Kociolek 2002	Asia (fossil)
<i>Ectodictyon</i> Khursevich & Cheriaeva 1989	Asia (fossil)
<i>Thalassiobeckia</i> Khursevich & Fedenya 2005	Asia (fossil)
<i>Cleoparvus</i> Woodbridge et al. 2010	Asia
RHIZOLENIALES (3 genera)	
<i>Urosolenia</i> F.E.Round & R.M. Crawford 1990	Cosmopolitan
<i>Acanthoceros</i> Honigmann 1910	Cosmopolitan
* <i>Chaetoceros</i> Ehrenberg 1844	Cosmopolitan

(Continued).

Table 1. Continued.

Taxa	Distribution
FRAGILARIALES (25 genera; 4 endemics)	
<i>Asterionella</i> Hassall 1850	Cosmopolitan
<i>Ctenophora</i> (Grunow) Williams & Round 1986	Cosmopolitan
<i>Fragilaria</i> Lyngbye 1819	Cosmopolitan
<i>Hannaea</i> R.M.Patrick 1966	Cosmopolitan
<i>Tabularia</i> (Kützing) Williams & Round 1986	Cosmopolitan
<i>Tibetiella</i> Li et al. 2013	Asia
<i>Ulnaria</i> (Kützing) P.Compère 2001	Cosmopolitan
<i>Popovskayella</i> Kulikovskiy et al. 2015	Asia
<i>Pseudostaurosira</i> D.M.Williams & F.E.Round 1988	Cosmopolitan
<i>Pseudostaurosiropsis</i> Morales 2002	North America
<i>Punctastriata</i> D.M.Williams & F.E.Round 1988	Cosmopolitan
<i>Sarcophagodes</i> Morales 2001	North America
<i>Stauroforma</i> Flower et al. 1996	Cosmopolitan
<i>Staurosira</i> Ehrenberg 1843	Cosmopolitan
<i>Staurosirella</i> D.M.Williams & F.E.Round 1988	Cosmopolitan
<i>Williamsella</i> Graeff et al. 2013	North America, Asia
<i>Diatoma</i> Bory 1824	Cosmopolitan
<i>Distrionella</i> Williams 1990	Cosmopolitan
<i>Fragilariforma</i> D.M.Williams & F.E.Round 1988	Cosmopolitan
<i>Meridion</i> C.A.Agardh 1824	Cosmopolitan
<i>Odontidium</i> Kützing 1844	Cosmopolitan
<i>Oxyneis</i> F.E.Round 1990	Widely Distributed
<i>Synedra</i> Ehrenberg 1830	Cosmopolitan
<i>Tabellaria</i> Ehrenberg ex Kützing 1844	Cosmopolitan
<i>Tetracyclus</i> Ralfs 1843	Cosmopolitan
EUNOTIALES (15 genera; 7 endemics; 2 disjuncts)	
<i>Actinellopsis</i> Taylor et al. 2007	Africa, North America (fossil)
<i>Peronia</i> de Brebisson & Arnott ex Kitton 1868	Cosmopolitan
<i>Pseudoperonia</i> Manguin 1964	South America
<i>Sinoperonia</i> Liu et al. 2017	Asia
<i>Actinella</i> F.W.Lewis 1864	Cosmopolitan
<i>Amphicampa</i> (Ehrenberg) Ralfs 1861	North America, Australasia
<i>Amphorotia</i> D.M.Williams & G.Reid 2006	Widely Distributed
<i>Bicudoa</i> Wetzel et al. 2012	South America
<i>Burliganiella</i> Wetzel & Kociolek 2018	South America
<i>Eunotia</i> Ehrenberg 1837	Cosmopolitan
<i>Eunotioforma</i> Kociolek & Burliga 2013	South America
<i>Semiorbis</i> R.M.Patrick 1966	Widely Distributed
<i>Desmogonium</i> Ehrenberg 1848	Cosmopolitan
<i>Eunophora</i> Vyverman et al. 1998	Australasia
<i>Perinotia</i> Metzeltin & Lange-Bertalot 2007	South America
BACILLARIALES (11 genera; 1 disjunct)	
<i>Bacillaria</i> Gmelin 1788	Cosmopolitan
<i>Cylindrotheca</i> Rabenhorst 1859	Cosmopolitan
<i>Cymbellonitzschia</i> Hustedt 1924	Cosmopolitan
<i>Denticula</i> Kützing 1844	Cosmopolitan
<i>Gomphonitzschia</i> Grunow 1867	Africa and Asia ¹
<i>Grunowia</i> Rabenhorst 1864	Cosmopolitan
<i>Hantzschia</i> Grunow 1877	Cosmopolitan
<i>Nitzschia</i> Hassall 1845	Cosmopolitan
<i>Psammodictyon</i> D.G.Mann 1990	Cosmopolitan
<i>Simonsenia</i> Lange-Bertalot 1979	Cosmopolitan
<i>Tryblionella</i> W.Smith 1853	Cosmopolitan
CYMBELLALES (35 genera; 9 endemics; 4 disjuncts)	
<i>Adlafia</i> Moser et al. 1998	Cosmopolitan
<i>Angusticopula</i> Van de Vijver, nom. prov.	Antarctica

(Continued).

Table 1. Continued.

Taxa	Distribution
<i>Brebissonia</i> Grunow 1860	Cosmopolitan
<i>Celebesia</i> Kasputin et al. 2017	Asia
<i>Crucicostulifera</i> J.C.Taylor & Lange-Bertalot 2010	Africa, Antarctica
<i>Cymbella</i> C.A.Agardh 1830	Cosmopolitan
<i>Cymbellafalsa</i> Lange-Bertalot & Metzeltin 2009	Widely Distributed
<i>Cymbellopsis</i> Krammer 1997	South America, Africa
<i>Cymbopleura</i> Krammer 1999	Cosmopolitan
<i>Delicata</i> Krammer 2003	Cosmopolitan
<i>Didymosphenia</i> M. Schmidt 1899	Cosmopolitan
<i>Encyonema</i> Kützing 1833	Cosmopolitan
<i>Encyonopsis</i> Krammer 1997	Cosmopolitan
<i>Geissleria</i> Lange-Bertalot & Metzeltin 1996	Cosmopolitan
<i>Gomphocymbellopsis</i> Krammer 2003	Europe, N. America
<i>Khursevichia</i> Kulikovskiy et al. 2012	Asia, Europe
<i>Kozhowia</i> Kulikovskiy et al. 2012	Asia
<i>Kurtkammeria</i> Bahls 2015	Cosmopolitan
<i>Navicymbula</i> Krammer 2003	Cosmopolitan
<i>Ochigma</i> Kulikovskiy et al. 2012	Asia
<i>Oricymba</i> Jüttner et al. 2010	Asia
<i>Placoneis</i> Mereschkowsky 1903	Cosmopolitan
<i>Pseudencyonema</i> Krammer 1997	Cosmopolitan
<i>Pseudocymbopleura</i> Pomazkina & Rodionova 2014	Asia
<i>Reimeria</i> Kociolek & Stoermer 1987	Cosmopolitan
<i>Yasnitskya</i> Pomazkina & Rodionova 2014	Asia
<i>Antiquonema</i> Karthick et al. nom. prov.	Asia
<i>Gomphocymbella</i> O. Müller 1899	Africa
<i>Gomphoneis</i> Cleve 1894	Cosmopolitan
<i>Gomphonema</i> Ehrenberg 1832	Cosmopolitan
<i>Gomphopleura</i> Reichelt ex Tempere 1894	Europe, Asia (fossil)
<i>Gomphosinica</i> Kociolek et al. 2015	Asia, North America
<i>Rexlowea</i> Kociolek & Thomas 2010	Widely Distributed
<i>Gomphosphenia</i> Lange-Bertalot 1995	Cosmopolitan
<i>Rhoicosphenia</i> Grunow 1860	Cosmopolitan
ACHNANTHIDIALES (15 Genera; 1 endemic)	
<i>Achnanthes</i> Bory 1822	Cosmopolitan
<i>Cocconeis</i> Ehrenberg 1837	Cosmopolitan
<i>Crenotia</i> Wojtal 2013	Europe
<i>Achnanthidium</i> Kützing 1844	Cosmopolitan
<i>Anorthoneis</i> Grunow 1868	Cosmopolitan
* <i>Astartiella</i> Witkowski et al. 1998	Cosmopolitan
<i>Eucoconeis</i> P.T.Cleve ex Meister 1912	Cosmopolitan
<i>Gliwiczia</i> Kulikovskiy et al. 2013	Widely Distributed
<i>Karayevia</i> F.E.Round & Bukhtiyarova 1998	Cosmopolitan
<i>Lemnicola</i> F.E.Round & Basson 1997	Cosmopolitan
<i>Planothidium</i> F.E.Round & Bukhtiyarova 1996	Cosmopolitan
<i>Platessa</i> Lange-Bertalot 2004	Cosmopolitan
<i>Psammothidium</i> F.E.Round & Bukhtiyarova 1996	Cosmopolitan
<i>Rossithidium</i> F.E.Round & Bukhtiyarova 1996	Cosmopolitan
<i>Skabitschewskia</i> Kulikovskiy & Lange-Bertalot 2015	Cosmopolitan
NAVICULALES (82 genera; 17 endemics; 7 disjuncts)	
<i>Altana</i> Kulikovskiy et al. 2012	Asia
<i>Amphipleura</i> Kützing 1844	Cosmopolitan
<i>Aneumastus</i> Mann & Stickle 1990	Cosmopolitan
<i>Anomoeoneis</i> Pfitzer 1871	Cosmopolitan
* <i>Berkeleya</i> Greville 1827	Cosmopolitan
<i>Biremis</i> Mann & Cox 1990	Widely Distributed
<i>Boreozonacola</i> Lange-Bertalot et al. 2010	Widely Distributed
<i>Brachysira</i> Kützing 1836	Cosmopolitan

(Continued).

Table 1. Continued.

Taxa	Distribution
<i>Brevilinea</i> Siver et al. 2007	North America, Europe
<i>Buryatia</i> Kulikovskiy et al. 2012	Asia
<i>Caloneis</i> P.T.Cleve 1894	Cosmopolitan
<i>Capartogramma</i> Kufferath 1956	Cosmopolitan
<i>Cavinula</i> Mann & Stickle 1990	Cosmopolitan
<i>Chamaepinnularia</i> Lange-Bertalot & Krammer 1996	Cosmopolitan
<i>Cholnokyella</i> Taylor & Lange-Bertalot 2013	Africa
<i>Corbellia</i> Maidana & Round 1999	South America
<i>Cosmioneis</i> Mann & Stickle 1990	Cosmopolitan
<i>Craticula</i> Grunow 1867	Cosmopolitan
<i>Decussata</i> (Patrick) Lange-Bertalot 2000	Cosmopolitan
<i>Diadesmis</i> Kützing 1844	Cosmopolitan
<i>Diatomella</i> Greville 1855	Cosmopolitan
* <i>Diploneis</i> Ehrenberg ex Cleve 1894	Cosmopolitan
<i>Diprora</i> Main 2003	Australasia
<i>Eileenxcoxia</i> Blanco & Wetzel 2016	Australasia
<i>Envekadea</i> Van de Vijver et al. 2009	Widely Distributed
<i>Eolimna</i> Lange-Bertalot & W. Schiller 1997	Cosmopolitan
<i>Fallacia</i> Stickle & Mann 1990	Cosmopolitan
<i>Fistulifera</i> Lange-Bertalot 1997	Cosmopolitan
<i>Frankophila</i> Lange-Bertalot 1997	Cosmopolitan
<i>Frustulia</i> Rabenhorst 1853	Cosmopolitan
<i>Genkalia</i> Kulikovskiy et al. 2012	Asia, Europe
<i>Germainiella</i> Lange-Bertalot & Metzeltin 2005	Widely Distributed
<i>Gyrosigma</i> Hassall 1845	Cosmopolitan
<i>Haslea</i> Simonsen 1974	Cosmopolitan
<i>Hippodonta</i> Lange-Bertalot et al. 1996	Cosmopolitan
<i>Humidophila</i> Lowe et al. 2006	Cosmopolitan
<i>Hygropetra</i> K.Krammer & Lange-Bertalot 2000	North America, Europe
<i>Kobayasiella</i> Lange-Bertalot & Genkal 1999	Cosmopolitan
<i>Krasskella</i> Ross & Sims 1978	Widely Distributed
<i>Krsticiella</i> Levkov 2007	Europe, Asia
<i>Lacustriella</i> Lange-Bertalot et al. 2012	Asia
<i>LeCohuia</i> Lange-Bertalot 2000	S. America, Antarctica
<i>Luticola</i> Mann 1990	Cosmopolitan
<i>Luticolopsis</i> Levkov et al. 2013	Asia
<i>Mayamaea</i> Lange-Bertalot 1997	Cosmopolitan
* <i>Mastogloia</i> Thwaites 1856	Cosmopolitan
<i>Michelcostea</i> Van de Vijver et al. 2017	Antarctica
<i>Microcostatus</i> Johansen & Sray 1998	Cosmopolitan
<i>Microfissurata</i> Lange-Bertalot et al. 2009	Europe, Antarctica
<i>Muelleria</i> (J.Frenguelli) Frenguelli 1945	Cosmopolitan
<i>Navicula</i> Bory 1822	Cosmopolitan
<i>Naviculonema</i> Graeff et al. 2013	North America
<i>Navigiolum</i> Lange-Bertalot et al. 2003	North America, Europe
<i>Neidiomorpha</i> Lange-Bertalot & Cantonati 2010	Widely Distributed
<i>Neidiopsis</i> Lange-Bertalot & Metzeltin 1999	Widely Distributed
<i>Neidium</i> Pfitzer 1871	Cosmopolitan
<i>Ninastrelnikovia</i> Lange-Bertalot & Fuhrmann 2014	Africa, Asia
<i>Nupela</i> Vyvrman & Compere 1991	Cosmopolitan
<i>Okhaphkinia</i> Kulikovskiy et al. 2018	Asia
<i>Paraplaconeis</i> Kulikovskiy et al. 2012	Europe, Asia
<i>Petroplacus</i> Pomazkina 2016	Asia
<i>Pinnularia</i> Ehrenberg 1843	Cosmopolitan
<i>Pinnunavis</i> Okuno 1975	Widely Distributed
<i>Plagiotropis</i> Pfitzer 1871	Cosmopolitan
<i>Playaensis</i> Spaulding & Kociolek 2002	North America
<i>Pleurosigma</i> W.Smith 1852	Cosmopolitan
<i>Porosularia</i> Skvortzow 1976	Asia

(Continued).

Table 1. Continued.

Taxa	Distribution
<i>Prestauroneis</i> Bruder & Medlin 2008	Widely Distributed
<i>Proschkinia</i> Karayeva 1978	Widely Distributed
<i>Pseudofallacia</i> Liu et al. 2012	Cosmopolitan
<i>Pulchella</i> Krammer 2000	Cosmopolitan
* <i>Scoliopleura</i> Grunow 1860	Cosmopolitan
<i>Seminavis</i> Mann 1990	Cosmopolitan
<i>Sellaphora</i> Mereschkowsky 1902	Cosmopolitan
<i>Sichuaniella</i> et al. 2013	Asia
<i>Skvortzovia</i> Kulikovskiy et al. 2012	Asia
<i>Stauroneis</i> Ehrenberg 1843	Cosmopolitan
<i>Stauronella</i> Mereschkowsky 1901	Europe, Asia
<i>Staurophora</i> Mereschkowsky 1903	Widely Distributed
<i>Trifonovia</i> Kulikovskiy et al. 2012	Asia
* <i>Tursiocola</i> Holmes et al. 1993	S. America
<i>Veigaludwigia</i> Lange-Bertalot 2000	S. America, Australasia
THALASSIOPHYCIDALES (2 genera)	
<i>Amphora</i> Ehrenberg ex Kützing 1844	Cosmopolitan
<i>Halamphora</i> (Cleve) Levkov 2009	Cosmopolitan
RHOPALODIALES (3 genera; 1 endemic)	
<i>Epithemia</i> Kützing 1844	Cosmopolitan
<i>Rhopalodia</i> O.Müller 1895	Cosmopolitan
<i>Tetralunata</i> Hamsher et al. 2014	Asia
SURIRELLALES (9 genera; 2 endemics)	
<i>Entomoneis</i> (Ehrenberg) Ehrenberg 1845	Cosmopolitan
<i>Campylodiscus</i> Ehrenberg ex Kützing 1844	Cosmopolitan
<i>Cymatopleura</i> W.Smith 1851	Cosmopolitan
<i>Iconella</i> Jurilj 1949	Cosmopolitan
<i>Klinodiscus</i> Jurilj 1949	Europe
<i>Scoliodiscus</i> Jurilj 1954	Europe
<i>Stenopterobia</i> de Brébisson ex Van Heurck 1896	Cosmopolitan
<i>Spirodiscina</i> Blanco & Wetzel 2016	Cosmopolitan
<i>Surirella</i> Turpin 1828	Cosmopolitan

Notes: 249 Genera recognized. Endemic: restricted to one continent; Disjunct: restricted to two continents; Widely Distributed: found across three continents; Cosmopolitan: found on four or more continents. *Indicates genera that have nearly all of their species found in marine waters.

¹North American records are deformed *Nitzschia* species.

continent (25% of the total number of genera) and another 27 are found disjunct between two continents (a total of 90 genera being limited to one or two continents, over 36% of all the recognized genera). If we exclude genera that have the vast majority of their species in marine systems (the 11 genera indicated by an asterisk in Table 1), the overall percentages of endemics (26%) and endemics + genera that are disjuncts (37%) increase only slightly, relative to the freshwater genera.

Nearly all the major groups of diatoms have a least one endemic genus, the exceptions being the non-thalassiosiroid biddulphioids, and amphoroids. There are some very large groups, such as the bacillarioids, the gomphonemoids, those diatoms in a morphological grade with a single raphe system ('monoraphids'), and the 'fragilaroid' diatoms, that have few endemic genera. It is possible that treatment of these groups with finer taxonomic circumscription might yield interpretable biogeographic patterns or reveal endemism (see below).

Are endemic genera evenly distributed across the globe?

Put another way, we can ask, 'Based on current knowledge, which continents have the greatest number or greatest percentage of endemic freshwater diatom genera?' Table 3 summarizes the number and percent of those genera with limited distributions.

The data from Table 4 show that 56% of the endemic genera of freshwater diatoms are found in Asia, and the remaining 44% are found elsewhere around the world. Asia has four times the number of endemic genera of South America and North America, the continents with the second highest levels of generic endemism (eight and seven genera, respectively). The high level of endemism in Asia is driven in part by the number of endemic genera described from Lake Baikal. That long-lived (ca. 30 million years) water body has 13, living and fossil, genera that are endemic to the lake. While other genera were described

Table 2. Overall genus listing_ alphabetical by continent.

Genera/Continents	North America	Europe	South America	Asia	Australasia	Africa	Antarctica
<i>Acanthoceros</i>	X	X	X	X	X		
<i>Achnanthes</i>	X	X	X	X	X	X	X
<i>Achnanthidium</i>	X	X	X	X	X	X	X
<i>Actinella</i>	X	X	X	X	X	X	
<i>Actinellopsis</i>	X					X	
<i>Actinocyclus</i>	X	X	X	X	X		
<i>Adlafia</i>	X	X	X	X	X	X	X
<i>Altana</i>				X			
<i>Alveolophora</i>	X	X		X			
<i>Amphicampa</i>	X	X			X		
<i>Amphipleura</i>	X	X	X	X	X	X	
<i>Amphora</i>	X	X	X	X	X	X	
<i>Amphorotia</i>	X	X		X			
<i>Aneumastus</i>	X	X		X			
<i>Angusticopula</i>							X
<i>Anomoeoneis</i>	X	X	X	X	X	X	X
<i>Anorthoneis</i>	X		X			X	
<i>Antiquonema</i>				X			
<i>Arcanodiscus</i>			X				X
<i>Astartiella</i>	X	X	X	X			
<i>Asterionella</i>	X	X	X	X	X	X	X
<i>Aulacoseira</i>	X	X	X	X	X	X	
<i>Bacillaria</i>	X	X	X	X	X	X	
<i>Berkeleya</i>	X	X	X		X		
<i>Bicudoa</i>			X				
<i>Biremis</i>	X	X		X			
<i>Boreozonacola</i>	X	X		X			
<i>Brachysira</i>	X	X	X	X	X	X	X
<i>Brebissonia</i>	X	X	X	X			
<i>Brevilinea</i>	X	X					
<i>Brevisira</i>	X	X					
<i>Burliganiella</i>			X				
<i>Buryatia</i>				X			
<i>Caloneis</i>	X	X	X	X	X	X	X
<i>Campylodiscus</i>	X	X		X	X	X	X
<i>Capartogramma</i>	X	X	X		X	X	
<i>Cavernosa</i>					X		X
<i>Cavinula</i>	X	X	X	X	X	X	
<i>Celebesia</i>				X			
<i>Chaetoceros</i>	X	X		X		X	
<i>Chamaepinnularia</i>	X	X	X	X	X	X	X
<i>Cholnokyella</i>						X	
<i>Clipeoparvus</i>				X			
<i>Cocconeis</i>	X	X	X	X	X	X	X
<i>Concentrodiscus</i>				X			
<i>Contricribra</i>	X	X	X	X			
<i>Corbellia</i>			X				
<i>Cosmioneis</i>	X	X		X			
<i>Craticula</i>	X	X	X	X	X	X	
<i>Crenotia</i>		X					
<i>Cribronella</i>		X					
<i>Crucicostulifera</i>						X	X
<i>Ctenophora</i>	X	X	X	X	X	X	X
<i>Cyclostephanopsis</i>				X			
<i>Cyclostephanos</i>	X	X	X	X	X	X	
<i>Cyclotella</i>	X	X	X	X	X	X	X
<i>Cyclotubicoalitus</i>	X			X			
<i>Cylindrotheca</i>	X	X	X	X			
<i>Cymatopleura</i>	X	X	X	X	X	X	

(Continued).

Table 2. Continued.

Genera/Continents	North America	Europe	South America	Asia	Australasia	Africa	Antarctica
<i>Cymbella</i>	X	X	X	X	X	X	X
<i>Cymbellafalsa</i>	X	X		X			
<i>Cybellonitzschia</i>	X	X		X		X	
<i>Cymbellopsis</i>			X			X	
<i>Cymbopleura</i>	X	X	X	X		X	X
<i>Decussata</i>	X	X	X	X			
<i>Delicata</i>	X	X		X			
<i>Denticula</i>	X	X	X	X	X	X	X
<i>Desmogonium</i>	X		X	X		X	
<i>Diadesmis</i>	X	X	X	X	X	X	
<i>Diatoma</i>	X	X	X	X	X	X	X
<i>Diatomella</i>	X	X	X	X	X		X
<i>Didymosphenia</i>	X	X	X	X	X		
<i>Dimidialimbus</i>				X			
<i>Diploneis</i>	X	X	X	X	X	X	X
<i>Diprora</i>					X		
<i>Discostella</i>	X	X	X	X	X	X	
<i>Distrionella</i>	X	X					
<i>Ectodictyon</i>				X			
<i>Edtheriotia</i>				X			
<i>Eileencoxia</i>					X		
<i>Ellerbeckia</i>	X	X	X	X			
<i>Encyonema</i>	X	X	X	X	X	X	X
<i>Encyonopsis</i>	X	X	X	X		X	X
<i>Entomoneis</i>	X	X	X	X	X	X	
<i>Envekadea</i>	X			X		X	
<i>Eolimna</i>	X	X	X	X		X	X
<i>Eoseira (fossil)</i>	X						
<i>Epithemia</i>	X	X	X	X	X	X	X
<i>Eucocconeis</i>	X	X	X	X			
<i>Eunophora</i>					X		
<i>Eunotia</i>	X	X	X	X		X	X
<i>Eunotioforma</i>			X				
<i>Fallacia</i>	X	X	X	X	X	X	
<i>Ferocia</i>							X
<i>Fideliacyclus (fossil)</i>	X		X				
<i>Fistulifera</i>	X	X		X		X	X
<i>Fragilaria</i>	X	X	X	X	X	X	X
<i>Fragilariforma</i>	X	X	X	X	X	X	
<i>Frankophila</i>	X		X		X		X
<i>Frustulia</i>	X	X	X	X	X	X	X
<i>Geissleria</i>	X	X	X	X	X	X	X
<i>Genkalia</i>		X		X			
<i>Germainiella</i>		X	X	X			
<i>Gliwiczia</i>	X	X		X			
<i>Gomphocymbella</i>						X	
<i>Gomphocymbellopsis</i>	X	X					
<i>Gomphoneis</i>	X	X	X	X	X	X	X
<i>Gomphonema</i>	X	X	X	X	X	X	X
<i>Gomphonitzschia</i>	X			X		X	
<i>Gomphopleura</i>	X	X		X			
<i>Gomphosinica</i>	X			X			
<i>Gomphosphenia</i>	X	X	X	X		X	
<i>Grunowia</i>	X		X	X		X	
<i>Guarreraea</i>			X				
<i>Gyrosigma</i>	X	X	X	X	X	X	X
<i>Halamphora</i>	X	X	X	X	X	X	X
<i>Hannaea</i>	X	X	X	X			

(Continued).

Table 2. Continued.

Genera/Continents	North America	Europe	South America	Asia	Australasia	Africa	Antarctica
<i>Hantzschia</i>	X	X	X	X		X	X
<i>Haslea</i>	X	X	X	X			
<i>Hippodonta</i>	X	X	X	X		X	X
<i>Humidophila</i>	X	X	X	X	X	X	X
<i>Hydrosera</i>	X	X	X	X			
<i>Hydrosirella</i>	X						
<i>Hygropetra</i>	X	X					
<i>Iconella</i>	X	X	X	X	X	X	X
<i>Karayevia</i>	X	X	X	X	X		X
<i>Khursevichia</i>		X		X			
<i>Klinodiscus</i>		X					
<i>Kobayasiella</i>	X	X	X	X	X	X	X
<i>Kozhowia</i>				X			
<i>Krasskella</i>	X	X	X				
<i>Krsticiella</i>		X		X			
<i>Kurtkammeria</i>	X	X	X			X	
<i>Lacustriella</i>				X			
<i>LeCohuia</i>			X				X
<i>Lemnicola</i>	X	X	X	X	X	X	
<i>Lindavia</i>	X	X	X	X	X	X	
<i>Lobodiscus</i>				X			
<i>Luticola</i>	X	X	X	X	X	X	X
<i>Luticolopsis</i>				X			
<i>Mastogloia</i>	X	X	X	X	X	X	X
<i>Mayamaea</i>	X	X	X	X		X	X
<i>Melosira</i>	X	X	X	X	X	X	X
<i>Meridion</i>	X	X	X	X	X	X	X
<i>Mesodictyon</i>	X		X	X		X	
<i>Mesodictyopsis</i>				X			
<i>Michelcostea</i>							X
<i>Microcostatus</i>	X	X		X			X
<i>Microfissurata</i>		X					X
<i>Muelleria</i>	X	X	X	X			X
<i>Navicula</i>	X	X	X	X	X	X	X
<i>Naviculonema</i>	X						
<i>Navicymbula</i>	X	X		X		X	
<i>Navigiolum</i>	X	X				X	
<i>Neidiomorpha</i>	X	X		X			
<i>Neidiopsis</i>	X	X		X			
<i>Neidium</i>	X	X	X	X	X	X	X
<i>Ninastrelnikovia</i>				X		X	
<i>Nitzschia</i>	X	X	X	X	X	X	X
<i>Nupela</i>	X	X	X	X	X	X	X
<i>Ochigma</i>				X			
<i>Odontidium</i>	X	X	X	X			
<i>Okhapkinia</i>				X			
<i>Oricymba</i>				X			
<i>Orthoseira</i>	X	X	X	X		X	X
<i>Oxyneis</i>	X	X		X			
<i>Pantocsekiella</i>	X	X	X	X	X	X	
<i>Paraplaconeis</i>		X		X			
<i>Perinotia</i>			X				
<i>Peronia</i>	X	X	X	X			
<i>Petroplacus</i>				X			
<i>Pinnularia</i>	X	X	X	X	X	X	X
<i>Pinnunavis</i>		X		X			X
<i>Placoneis</i>	X	X	X	X	X	X	X
<i>Plagiotropis</i>	X	X	X	X			
<i>Planothidium</i>	X	X	X	X	X	X	X

(Continued).

Table 2. Continued.

Genera/Continents	North America	Europe	South America	Asia	Australasia	Africa	Antarctica
<i>Platessa</i>	X	X	X	X			
<i>Playaensis</i>	X						
<i>Pleurosigma</i>	X	X	X	X	X	X	
<i>Pleurosira</i>	X	X	X	X	X	X	
<i>Pliocaenicus</i>	X	X		X			
<i>Popovskayella</i>				X			
<i>Porosularia</i>				X			
<i>Praestephanos</i>	X			X			
<i>Prestauroneis</i>	X	X		X			
<i>Proschkinia</i>	X	X		X			
<i>Psammodictyon</i>	X	X	X				
<i>Psammothidium</i>	X	X	X	X		X	
<i>Pseudoaulacosira</i>				X			
<i>Pseudencyonema</i>				X			
<i>Pseudocymbopleura</i>				X			
<i>Pseudofallacia</i>	X	X	X	x	X	X	
<i>Pseudoperonia</i>			X				
<i>Pseudostaurosira</i>	X	X	X	X	X	X	X
<i>Pseudostaurosiropsis</i>	X						
<i>Pulchella</i>	X		X	X			
<i>Punctastriata</i>	X	X		X			X
<i>Reimeria</i>	X	X	X	x	X	X	X
<i>Rexlowea</i>	X	X		X			
<i>Rhoicosphenia</i>	X	X	X	X	X	X	X
<i>Rhopalodia</i>	X	X	X	X	X	X	X
<i>Rossithidium</i>	X	X	X	X	X		
<i>Sarcophagodes</i>	X						
<i>Scoliodiscus</i>		X					
<i>Scoliopleura</i>	X	X	X	X			
<i>Sellaphora</i>	X	X	X	X	X	X	X
<i>Seminavis</i>	X	X		X		X	
<i>Semiorbis</i>	X	X		X			
<i>Sichuaniella</i>				X			
<i>Simonsenia</i>	X	X	X	X		X	
<i>Sinoperonia</i>				X			
<i>Skabitschewskia</i>		X		X			
<i>Skeletonema</i>	X	X		X		X	
<i>Skvortzowia</i>				X			
<i>Spicaticribra</i>	X		X	X		X	
<i>Spirodiscina</i>	X	X		X			
<i>Stauroneis</i>	X	X	X	X	X	X	X
<i>Stauronella</i>		X		X			
<i>Stauroforma</i>	X	X	X	X			X
<i>Staurophora</i>	X	X			X		
<i>Staurosira</i>	X	X	X	X	X	X	X
<i>Staurosirella</i>	X	X	X	X	X	X	X
<i>Stenopterobia</i>	X	X	X	X	X	X	
<i>Stephanocostis</i>	X	X		X			
<i>Stephanodiscus</i>	X	X	X	X	X	X	
<i>Stephanopsis</i>				X			
<i>Stoermeria</i>	X	X			X		
<i>Strelnikoviella</i>	X						
<i>Surirella</i>	X	X	X	X	X	X	X
<i>Synedra</i>	X	X	X	X	X	X	
<i>Tabellaria</i>	X	X	X	X	X	X	X
<i>Tabularia</i>	X	X	X	X	X	X	X
<i>Terpsinoë</i>	X		X				
<i>Tertiariopsis</i>				X			
<i>Tertiarius</i>	X	X		X			

(Continued).

Table 2. Continued.

Genera/Continents	North America	Europe	South America	Asia	Australasia	Africa	Antarctica
<i>Tetracyclus</i>	X	X	X	X			
<i>Tetralunata</i>				X			
<i>Thalassiobeckia</i>				X			
<i>Thalassiosira</i>	X	X	X	X	X	X	
<i>Tibetiella</i>				X			
<i>Trifonovia</i>				X			
<i>Tryblionella</i>	X	X	X	X	X	X	
<i>Tursiocola</i>			X				
<i>Ulnaria</i>	X	X	X	X		X	X
<i>Undatodiscus</i>				X			
<i>Urosolenia</i>	X	X	X	X	X	X	
<i>Veigaludwigia</i>			X		X		
<i>Williamsella</i>	X			X			
<i>Yasnitzkya</i>				X			
TOTALS	176	172	137	194	110	95	80

from Lake Baikal, (Kulikovskiy et al. 2012, 2015), some of them have newly-proposed representatives outside the lake. Another five genera (all fossil) have been described from sediments from the Baikal region, if not from the lake itself. Even if we were to exclude the Baikal genera, Asia would still have nearly twice the number of endemics found in the more heavily-studied regions of either North America or Europe.

Generic endemism and genus richness

Would we expect a proportional number of endemic genera to be related to the overall number of genera for a continent? In Table 5, genus richness and generic endemism are listed by continent. With the information currently in hand, we can estimate the number of genera in the most studied areas of the world. For example, of the most studied regions, North America and Europe have 176 and 172 freshwater diatom genera in their respective floras. For the North American flora, with eight endemic genera, and Europe with four endemic genera, there is a very low percentage of endemism (ca. 4.5% and 2.0%, respectively) at the level of genus. Based on the work of Kulikovskiy et al. (2016) and Kociolek et al. (Accepted), we can total the number of freshwater diatom genera in Asia to be 194. This yields a level of endemism at the rank of genus at ca. 18%. Ninetyfive freshwater diatom genera comprise the Australasian flora, making the level of endemism (3%) similar to that of Europe (2%) and Africa (2%), but lower than South America (5.8%) and Antarctica (3.8%) (Table 5, 2 and 3). Thus, based on the total number of genera, the level of endemism in freshwater diatom genera in Asia is more than four times greater than any other continent in the world, and more than three times greater as a percent of the total number of genera.

A simple regression analysis of the number of endemic genera versus the total number of genera by continent ($p > .11$) suggests that, at the 95% confidence level, we

cannot reject the null hypothesis. That is, there is no statistical relationship between the number of endemic genera and generic richness by continents.

Comparing endemism in diatoms to other organisms

We can compare the levels of endemism, and areas of higher endemism, to other groups of organisms. For other groups of freshwater organisms, a collection of papers from *Hydrobiologia* in 2008 was published called, 'Freshwater Animal Diversity Assessment' (Balian et al. 2008), which, among other things, looked at the number of genera and species of a wide range of taxonomic groups, and the levels of endemism, across geographic realms (Palearctic, Nearctic, Neotropical, Afrotropical, Oriental and Australasian); nearly the same as the continental approach taken in the present report. In this volume, we can see groups that have very low generic endemism (rotifers have only 10 endemic genera out of a total of 128; nine of the 10 genera are monotypic; Segers 2008), while in freshwater amphipods nearly all of the 293 genera are endemics (Vainola et al. 2008). The freshwater amphipods, like the diatoms, have most of their diversity (genera and species) represented in marine systems, and the freshwater forms, like the freshwater diatoms, do not form a monophyletic group. 'Genus level inter-continental distributions are rare even in the less strictly continental groups' in freshwater amphipods (Vainola et al. 2008, p. 251), versus the 23% generic endemism seen in the freshwater diatoms.

For Angiosperms, Brummitt (2005) reported that areas with 'highest genus richness only had moderate degrees of generic endemism' (p. 549), suggesting no relationship between the two, an outcome echoed by freshwater diatoms. Areas with Angiosperm endemism greater than 10% of the species include: Southern Africa (29%), Western Indian Ocean (29%) and Australia (35%); Malesia (10.8%), Mexico (11.8%), Caribbean (12.6%), Western South America (10.8%), Brazil (15.7%) and Southern

Table 3. Endemic and disjunct freshwater diatom genera listed by continent.

North America (8 endemics + 11 disjuncts)	
<u>Endemics</u>	<u>Disjuncts:</u>
<i>Eoseira</i> (fossil)	<i>Actinellopsis</i> (fossil)
<i>Fideliacyclus</i> (fossil)	<i>Amphicampa</i>
<i>Hydrosirella</i>	<i>Anorthoneis</i>
<i>Naviculonema</i>	<i>Brevilinea</i>
<i>Playaensis</i>	<i>Brevisira</i>
<i>Pseudostaurosiropsis</i>	<i>Cyclotubicoalitus</i>
<i>Sarcophagodes</i>	<i>Gomphocymbellopsis</i>
<i>Strelnikoviella</i> (fossil)	<i>Gomphosinica</i>
	<i>Hygropetra</i>
	<i>Praestephanos</i> (fossil)
	<i>Williamsella</i>
South America (8 endemics + 4 disjuncts)	
<u>Endemics</u>	<u>Disjuncts</u>
<i>Bicudoa</i>	<i>Arcanodiscus</i>
<i>Burliganiella</i>	<i>Cymbellopsis</i>
<i>Corbellia</i>	<i>LeCohuia</i>
<i>Eunotioforma</i>	<i>Veigaludwigia</i>
<i>Guarreraea</i>	
<i>Perinotia</i>	
<i>Pseudoperonia</i>	
<i>Tursiocola</i>	
Europe (4 endemics + 12 disjuncts)	
<u>Endemics</u>	<u>Disjuncts</u>
<i>Crenotia</i>	<i>Brevilinea</i>
<i>Cribronella</i> (fossil)	<i>Brevisira</i>
<i>Klinodiscus</i>	<i>Genkalia</i>
<i>Scoliodiscus</i>	<i>Gomphocymbellopsis</i>
	<i>Gomphopleura</i>
	<i>Hygropetra</i>
	<i>Khursevichia</i>
	<i>Krsticiella</i>
	<i>Microfissurata</i>
	<i>Paraplaconeis</i>
	<i>Skabitschewskia</i>
	<i>Stauronella</i>
Africa (2 endemics + 6 disjuncts)	
<u>Endemics</u>	<u>Disjuncts</u>
<i>Cholnokiyella</i>	<i>Actinellopsis</i>
<i>Gomphocymbella</i> (<i>Afrocybella</i>)	<i>Anorthoneis</i>
	<i>Crucicostulifera</i>
	<i>Cymbellopsis</i>
	<i>Gomphonitzschia</i>
	<i>Ninastrelnikovia</i>
Asia (35 endemics + 13 disjuncts)	
<u>Endemics</u>	<u>Disjuncts</u>
<i>Altana</i>	<i>Cyclotubicoalitus</i>
<i>Antiquonema</i>	<i>Genkalia</i>
<i>Buryatia</i>	<i>Gomphonitzschia</i>
<i>Celebesia</i>	<i>Gomphopleura</i>
<i>Clipeoparvus</i>	<i>Gomphosinica</i>
<i>Concentrodiscus</i> (fossil)	<i>Khursevichia</i>
<i>Cyclostephanopsis</i> (fossil)	<i>Krsticiella</i>
<i>Dimidialimbus</i> (fossil)	<i>Ninastrelnikovia</i>
<i>Ectodictyon</i> (fossil)	<i>Paraplaconeis</i>
<i>Edtheriotia</i>	<i>Praestephanos</i> (fossil)
<i>Kozhowia</i>	<i>Skabitschewskia</i>
<i>Lacustriella</i>	<i>Stauronella</i>

Continued.

Table 3. Continued.

<i>Lobodiscus</i> (fossil)	<i>Williamsella</i>
<i>Luticolopsis</i>	
<i>Mesodictyopsis</i> (fossil)	
<i>Ochigma</i>	
<i>Okhaphkinia</i>	
<i>Oricymba</i>	
<i>Petroplacus</i>	
<i>Popovskayella</i>	
<i>Porosularia</i>	
<i>Pseudoaulacosira</i> (fossil)	
<i>Pseudencyonema</i>	
<i>Pseudocymbopleura</i>	
<i>Sichuaniella</i>	
<i>Sinoperonia</i>	
<i>Skvortzowia</i>	
<i>Stephanopsis</i> (fossil)	
<i>Tertiariopsis</i> (fossil)	
<i>Tetralunata</i>	
<i>Thalassiobeckia</i> (fossil)	
<i>Tibetiella</i>	
<i>Trifonovia</i>	
<i>Undatodiscus</i> (fossil)	
<i>Yasnitzkya</i>	
Australasia (3 endemics + 3 disjunct)	
<u>Endemics</u>	<u>Disjuncts</u>
<i>Diprora</i>	<i>Amphicampa</i>
<i>Eileencoxia</i>	<i>Cavernosa</i>
<i>Eunophora</i>	<i>Veigaludwigia</i>
Antarctica (3 endemics + 5 disjunct)	
<u>Endemics</u>	<u>Disjuncts</u>
<i>Angusticopula</i>	<i>Arcanodiscus</i>
<i>Ferocia</i>	<i>Cavernosa</i>
<i>Michelcostea</i>	<i>Crucistulifera</i>
	<i>LeCohuia</i>
	<i>Microfissurata</i>

Table 4. Listing of continents with the number of endemic genera versus the total number of endemic genera (63), and the percentage of endemic genera.

	Number of endemics per continent	Percent of all endemics
Asia	35	56%
North America	8	13%
South America	8	13%
Africa	2	3%
Europe	4	6%
Australasia	3	5%
Antarctica	3	5%
Total	63	100%

South America (13.6%). Across freshwater animals, we can find groups with the greatest generic endemism in the Palaearctic (amphipods Vainola et al. 2008, Bryozoans, Massard & Geimer 2008), Nearctic (mussels, Bogan 2008), Neotropical (Odonates, Boxshall & Defaye 2008, Kalkman et al. 2008), Afrotropical (Ostracods; Martens et al. 2008),

Australasian (Isopods, Wilson 2008) and Oriental (freshwater crabs, Yeo et al. 2008) regions. None of the groups surveyed showed highest generic endemism in the Antarctic region.

An analysis of the freshwater animal data published in Balian et al. (2008) by Collen et al. (2014) drew the interesting conclusion that ‘Pairwise analysis of geographical distribution between taxa showed that no single species group exhibited a consistent pattern of congruence with other taxa.’ This suggests that a group’s evolutionary history may have more to do with their distributions than environmental or ecological conditions, echoing the conclusions by Vyverman et al. (2007) for freshwater diatoms.

Disjunct taxa

Numbers of disjunct taxa are small (27 genera of the 249, or nearly 11%, have disjunct distributions), however, some patterns between disjuncts have been described for diatoms (Tables 3 and 6) and for a wide variety of other organisms. The greatest number of disjuncts is found between Europe and Asia, North America and Asia, and North America and Europe. Antarctica has connections via disjuncts with South America, Africa and Australasia, and these would seem biologically realistic given the proximity of these continents to Antarctica *sensu lato* (the definition we are using here). Likewise, some disjuncts across the southern hemisphere were reported earlier by Williams (1996), Williams & Reid (2006a, b, 2009) and Williams & Kociolek (2017). Disjunct distributions between North America and Asia have been reported for mosses (Crum 1972), freshwater invertebrates (Ross 1967, de Moor & Ivanov 2008), lichens (Sheard et al. 2017) and higher plants (e.g. Wen 1999, Qian 2002). Ehrenberg (1849) noted the similarities between western North America and Asian diatom floras. And the disjunct distributions between North America and Europe have been noted at the species level of diatoms, as well as a wide range of other organisms (e.g. Sanmartin et al. 2001, Milne 2006, Reisch 2008, Garnica et al. 2011).

Phylogenetics and endemism in freshwater diatom genera

The concept of endemism of lineages is well known to students of biogeography of other organisms. There are many examples of this phenomenon, including the placental mammals of Australia (Holt et al. 2013), southern beeches (*Nothofagus*) for the flora of Australasia and South America (Veblen et al. 1996, Hill 2001) and the honeycreepers of Hawaii (Lerner et al. 2011). However, any analysis of endemism of lineages in diatoms is hindered by a still-primitive understanding of the phylogenetic relationships of large swaths of diatom groups that have freshwater representatives. For example, there is still tremendous work to do on the ‘naviculoids’. So, while lineages such as

the Stauroneidaceae (Davidovich et al. 2017) have been well-established, the group of biraphid diatoms is, overall, extremely large and the number of taxa included in modern analyses is still relatively few. Therefore, an understanding of any phylogenetic context for endemism in the group is still rather primitive. That being said, there are some trends in the data presented in Tables 1 and 2 that can be discussed.

For example, within the thalassiosiroid diatoms, 11 of the 27 genera (over 40%) are endemics, and of those 11 endemics, nine are found in Asia. Of the Asian endemics, eight of the nine genera are exclusively fossil. Thus nearly 30% of the genera occur as fossils in Asia. The fossil endemic taxa overall, and particularly in Asia, are almost all of Miocene age (Khursevich & Kociolek 2012). Using fossil representatives Julius and colleagues have attempted to reconstruct the phylogeny of certain branches of this evolutionary lineage (e.g. Julius & Tanimura 2001, Tuji et al. 2014), but for the group overall no attempts have been made to incorporate fossils into phylogenetic reconstructions based on molecular data (Alverson et al. 2007). And given the important history of the lineage in Asia, it is surprising that no Asian freshwater representatives have been used in the molecular research.

Within the cymbelloids, (defined here as the freshwater cymbelloid and gomphonemoid diatoms *sensu* Kociolek & Stoermer 1988), seven of the 35 genera of this group (20%) are endemic to Asia. It is the only continent where endemic members of the group have thus far been documented, except for *Angusticopula* nom. prov., a genus soon to be described from Antarctica. Also, in this group is the genus *Geissleria* Lange-Bertalot & Metzeltin (Kulikovskiy et al. 2014), and many species of this genus have been described from Lake Baikal. Bukhtiyarova & Pomazkina (2013) described nearly 50 new species with features found in *Geissleria* and segregated them into nine new genera. These have not yet been included in this analysis, pending further review of their approach, but it points to the importance of Asia in the evolution of lineages within the freshwater cymbelloid diatoms.

The Miocene was a time of tremendous climate disruption in Asia, with the establishment of the monsoonal climate in the southcentral part of the country (Sun & Wang 2005, Favre et al. 2015). Such changes are suggested to help account for the establishment and diversity of the unique angiosperm flora of China (Lu et al. 2018) when 66% of the flora became established. Environmental changes in the late Miocene in the Baikal region were also documented with diatoms from long cores taken from the lake (Williams et al. 1997, BDP Members 2000). Uplift of the Tibetan Plateau in the Oligocene, around 40 mya, may have initiated changes in climate patterns across the northern hemisphere (Raymo & Ruddiman 1992), and accounted for the tremendous increase in continental freshwater ecosystems, productivity and taxon turnover (e.g. Bradbury et al. 1994, Bradbury & Krebs 1995, Khursevich

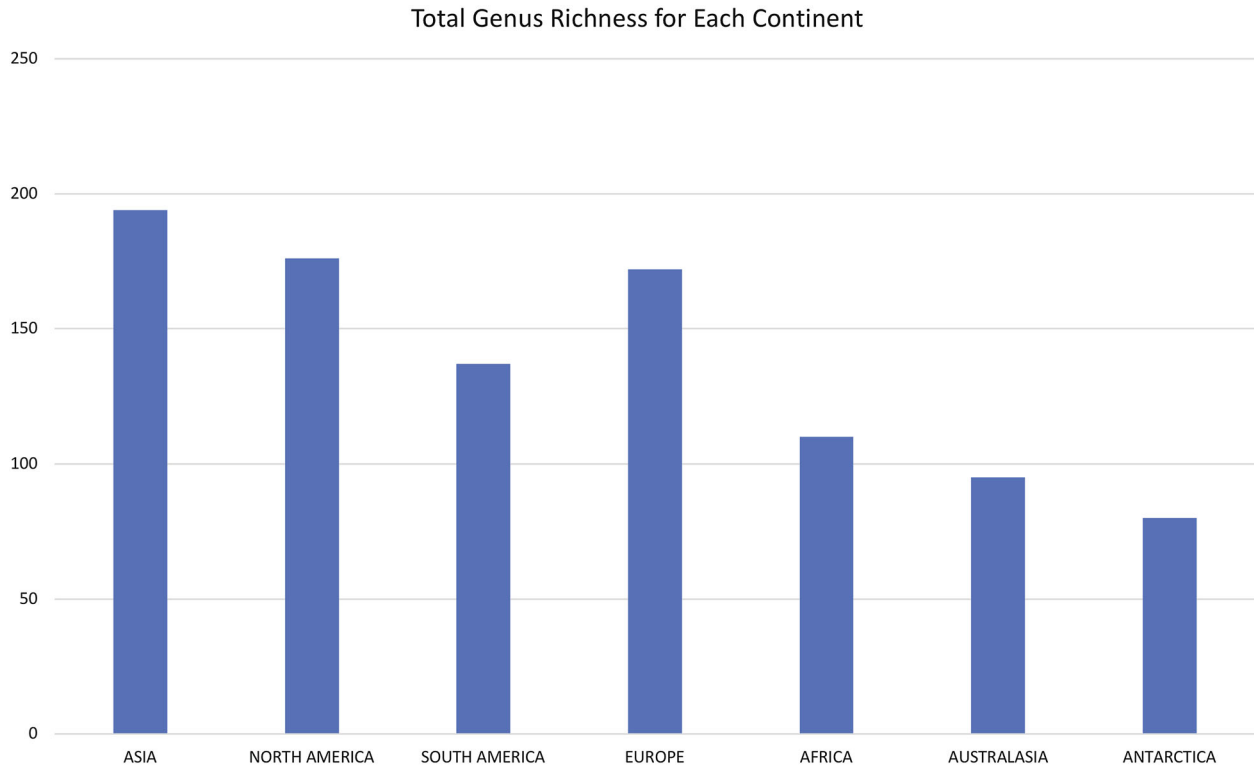


Fig. 2. Graph showing total genus richness for each continent.

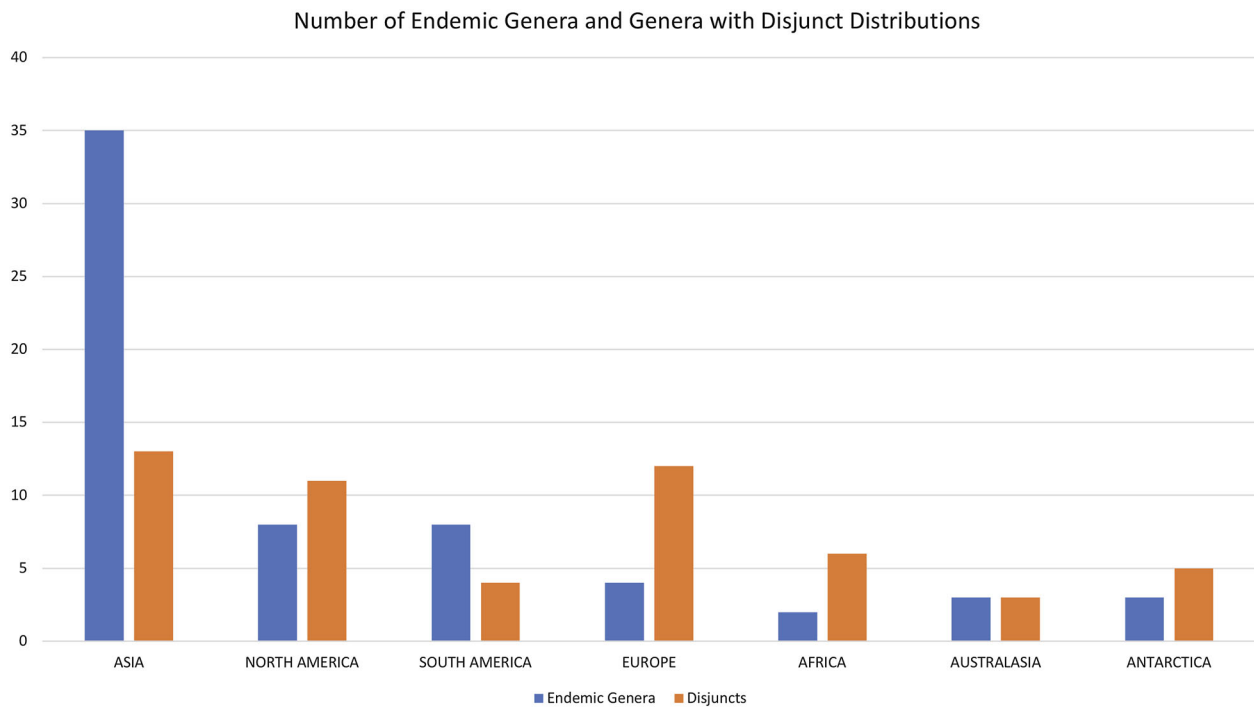


Fig. 3. Graph showing number of endemic genera and genera with disjunct distributions by continent.

Table 5. Listing of endemic genera in relation to the total number of genera reported for each continent (with percent indicated).

	Number of endemic genera	Number of disjuncts*	Total number of genera (percent endemics) (percent endemics + disjuncts)		
Asia	35	13	194	18%	24.7%
North America	8	11	176	4.5%	10.8%
South America	8	4	137	5.8%	8.6%
Europe	4	12	172	2%	9.3%
Africa	2	6	110	2%	7.2%
Australasia	3	3	95	3%	6.3%
Antarctica	3	5	80	3.8%	10.0%
Totals	63	48	(*24 taxa are disjunct)		

Table 6. Most common disjunctions between genera.

Continents	Number of genera with disjunctions
Europe + Asia	5
North America + Asia	4
North America + Europe	4
South America + Antarctica	2

2006). De Bruyn et al. (2014) describe Indochina and Borneo as major evolutionary hotspots for a wide range of groups, including plants, invertebrates and vertebrates, the result of several different geological collision events.

Another lineage that shows a high degree of endemism is the eunotioids of South America. This group has the highest proportion of endemism overall, with nine of 15 genera (60%) being either endemic or disjunct. There are seven endemic genera in the eunotioid lineage, and five of them occur in South America. Thus, 33% of the lineage (at the level of genus) is found only in South America. Williams & Reid (2006a) showed a Pan-Pacific distribution for *Amphorotia* Williams & Reid.

On a finer taxonomic scale, the Orthoseiraceae has two of the three genera occurring as disjuncts, either between South America + Antarctica (*Guarreraea* Kociolek et al.), or between Australasia + Antarctica (*Cavernosa* S.R.Stidolph).

Extinctions and endemics

Fossil genera represent important proportions of endemics in certain lineages. For example, except for *Actinocyclus normanii* f. *subsalsa* (Juhlin-Dannfelt) Hustedt, all of the freshwater members of the genus are fossil. This was documented in North America by the work of Bradbury & Krebs (1995). In addition, the three other genera that are representatives of the coscinodiscoids are also fossil. Fossil endemic genera can be found in North America (*Fideliacyclus* Siver et al.) and Asia (*Lobodiscus* Lupikina & Khursevich and *Undatodiscus* Lupikina).

A total of ten of the 11 endemic genera of the thalassiosiroids are known only as fossils. Conditions in which this group evolved in the Mio-Pliocene must have

occurred where lacustrine systems were developed. Krebs et al. (1987) suggested these formed a pattern of substitution (not necessarily evolution) in western North America. Khursevich and colleagues (Khursevich et al. 2000, 2002) described a sequence of genera in the sediments of Lake Baikal, where the pattern of substitution may have also been a pattern of evolutionary divergence and change.

In terms of continents, 43% of the endemic genera found in North America (three of seven) are fossils, while for Europe it is 25% (one of four) and for Asia nearly a third (11 of 34) are fossil endemics. While freshwater diatomites are known from every continent (Flower in Elias & Mock 2003), the insufficient study of these sediments from a taxonomic point of view is likely the primary reason that no fossil endemic genera have been recorded from other continents.

Surprises

Islands are wonderful natural laboratories on which to observe and describe evolutionary and ecological processes. One of these processes is adaptive radiation, in which many descendants within a geographically-restricted monophyletic group exploit available niches (e.g. Givnish & Sytsma 1997, Ricklefs & Bermingham 2007, Grant & Grant 2007, Emlen et al. 2007). For diatoms, this phenomenon has not been documented for islands to any great degree, and certainly not at the level of genus. While many new taxa of a wide range of organisms have been described from the 'island continent' of Madagascar (Goodman & Benstead 2003), there are relatively few studies on the freshwater diatoms from Madagascar (Manguin 1941, 1952, Spaulding & Kociolek 1998, Metzeltin & Lange-Bertalot 2002). These studies have yielded no new or endemic genera. The total number of samples examined from this region, though, is likely less than 100, and the island has an area of over 575,000 km². None of the largest rivers of the island have been sampled for diatoms. Similarly, the island of New Caledonia has perhaps been best studied, based on the works of Maillard (1978), Manguin (1962) and Moser et al. (1995, 1998). Despite this effort, this 'Island of endemics' has yielded only one genus (*Eileencoxia* Blanco & Wetzel), though

many new species have been recognized. The Hawaiian Islands have an endemic genus (*Diprora* Main), described from aerophilous environments (Main 2003), but currently, no other endemic freshwater diatom genera are recognized from these islands. In Tasmania and New Zealand, *Eunophora* Vyverman et al. was described as an endemic (Vyverman et al. 1998), though John (2009a, b, 2012a, b, c, 2015) subsequently reported it from Australia. *Celebesia* Kasputin et al. is known only from the island of Celebes (Kasputin et al. 2017). It is surprising given what we know of islands for other organisms, there has not been the divergence of freshwater diatoms, at the genus level, on islands to any great degree.

Can endemism of taxa/lineages give us new perspectives on phylogeny?

Phylogeography is the study of how history (evolutionary history through population genetics and phylogenetics) can lead to an understanding of the current spatial distribution of species and lineages (Avice 2000). This discipline demonstrates how phylogeny can help us interpret biogeographic patterns. We could, however, flip this relationship and pose the question, ‘How does the distribution of organisms affect our understanding of phylogeny?’ For example, if major families or groups that are endemic to certain places were absent from a dataset, would we recover the same groupings across that group’s overall tree of life? In other words, does including biogeographically-limited taxa in the overall tree of life give us new perspectives on, or understanding of, the entire tree? For example, in the phylogeny of Theriot et al. (2015), of the 207 freshwater terminal taxa, less than 1% are from Asia. Yet endemic Asian genera represent 13% of all freshwater diatom genera. Would including endemics from Asia give us new perspectives on the overall phylogeny of the diatoms?

Challenges of this type of analysis, and some directions for the future

This analysis is a summary of our current knowledge, of both the listing of genera with freshwater representatives, and the number of endemic genera and genera that appear to have disjunct distributions. There are biases in these data based on the levels of collection and taxonomic effort for different areas and approaches to taxonomic practice. There is also a heavy bias in the studies on recent freshwater versus fossil taxa. These will all have some effect on the data at hand, though the impacts of each is more a matter of speculation than being data-driven at the current time. Despite this, trends related to areas of endemism and phylogeography have been identified and are worthy of future research.

In freshwaters, estimates of the size of continental floras have ranged into the thousands of species (Kociolek 2005), yet worldwide there are a mere 248 genera. Thus,

while ecologists have raised concerns about the increasing number of new taxa being recognized, diatom taxonomists have still been fairly (too?) conservative in recognizing genera (Kociolek & Williams 2015), compared to other groups of organisms. With a finer dissection of taxa at the level of genus, we should expect to see a greater number of genera that are endemic. Some areas of research that might start looking to divide up genera include:

1. Large genera that have not yet been broken up. Places to start might include *Pinnularia* Ehrenberg (over 3500 taxa), *Eunotia* Ehrenberg (almost 2400 taxa), *Gomphonema* Ehrenberg (nearly 2000 taxa), *Stauroneis* Ehrenberg (about 1200 taxa), *Diploneis* Ehrenberg ex Cleve and its relatives (around 1000 taxa) (taxon estimates from Kociolek et al. 2018). Several morphological groups are recognized within each of these genera (documented in *Pinnularia* by Patrick & Reimer 1966 and Krammer 2000, in *Gomphonema* by Kociolek & Kingston 1999, Kociolek et al. 2016, in *Stauroneis* by Hustedt 1964, and *Diploneis* by Pennesi et al. 2017).
2. Even though there was a major revision of *Fragilaria* Lyngbye and *Synedra* Ehrenberg in the late 1980s as well as work on other ‘araphid’ groups (Williams & Round 1986, 1987, Williams 1990), resulting in seven new genera from freshwaters, almost all of them are cosmopolitan. It is possible that finer-scale distributional patterns will be found within these groups.
3. With at least 3500 described species and subspecific taxa, the Bacillariales is one of the most species-rich taxonomic orders of diatoms (Kociolek et al. 2018), comparable to the entire Class Mammalia of metazoans. But whereas extant mammals are classified among some 1200 extant genera, Bacillariales are divided among less than 20 genera; there are only 11 genera found in freshwaters (the case is even more extreme if you include extinct taxa). Only two freshwater genera have been proposed within the Bacillariales over about the last 100 years, and all the freshwater genera except *Gomphonitzschia* Grunow are either widely distributed or cosmopolitan. This partly reflects the lack of formal treatment of the systematics of this group for almost 140 years (Cleve & Grunow 1880). While taxon sampling has been limited, initial phylogenetic analyses of this group with molecular data have yielded results that suggest some of the bacillarioid genera are non-monophyletic (Lundholm et al. 2002).
4. Recent phylogenetic studies by Ruck using morphology (Ruck & Kociolek 2004) and molecular data (Ruck & Theriot 2011) shed new light on

relationships within the surirelloid diatoms, indicating that several of the commonly recognized genera are paraphyletic. Some endemic genera in this group (described by Jurilj 1949, 1954 from Lake Ohrid) have been resurrected (Ruck et al. 2016). However, a finer dissection of the group might point to additional endemics and disjunct distributions.

- Although the monoraphid diatoms are not a natural group (Thomas et al. 2016), the 13 monoraphid genera found in freshwaters, are all either cosmopolitan or widely distributed. Given that the groups have been revised relatively recently, albeit in a piecemeal fashion and devoid of phylogenetic context (Round & Bukhtiyarova 1996, Round 1998), the biogeography of the genera suggests finer taxonomic distinctions might be forthcoming.

Conclusions

Endemic freshwater diatom genera comprise nearly a quarter of all genera in freshwaters across the globe. The number of endemic genera is not statistically related to the overall number of genera for a continent. Certain lineages of freshwater diatoms, including the cymbelloids and thalassiosiroids, have a significant number of endemics in Asia, while eunotioid diatoms have a large number of genera that are endemic to South America. Integrating phylogenetic information with levels of generic endemism can help identify research agendas for the study on freshwater diatoms, from phylogeny reconstruction to generic revisions. Genera with large numbers of species and subspecific taxa, usually coupled with cosmopolitan distributions, may be places to focus research. Revisionary studies of these groups can be hypothesis-based, including the evolutionary history of characters, taxa and biogeography, so that practitioners are not seen as focused on minute details and detached from broader studies of evolutionary biology, systematics and questions related to space and time (and the myriad of other questions correlated with these factors). These types of studies can lead to comparisons with other organisms and provide research questions related to distributions and endemism (Rosauer et al. 2009, Rosauer & Jetz 2015) as well as dispersal and the evolutionary ecology of food web interactions (e.g. Mathews & Heins 1987, Bohanak & Jenkins 2003).

Acknowledgments

I am indebted to Dr. Silvia Sala, Facultad de Ciencias Naturales y Museo Universidad Nacional de La Plata, Argentina, for her help with literature, thoughts and a careful reading of the manuscript, as well as Drs David Williams, Life Sciences Department, The Natural History Museum, London, U.K., Maxim Kulikovskiy, Papanin's Institute for Biology of Inland Waters Russian Academy of Sciences, Borok, and Institute of Plant Physiology, Russian Academy of Sciences, Botanical Street 35,

127276, Moscow, Russia, and Rex Lowe, Bowling Green State University and University of Wisconsin, Madison, for their critical reading of the manuscript and helpful suggestions. Bart Van de Vijver, Botanical Garden, Meise, Belgium, kindly provided a list of genera from the Antarctic region.

Disclosure statement

No potential conflict of interest was reported by the author.

Supplemental data

Supplemental data for this article can be accessed at <https://doi.org/10.1080/0269249X.2019.1574243>. References marked with an asterisk are cited in the supplemental data.

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