A PHYLOGENETIC CLASSIFICATION OF DIATOMS (BACILLARIOPHYTA)

J.P. Kociolek[1], M.P. Ashworth[2] and Andrew J. Alverson[3]

1 Museum of Natural History and Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, CO 80309

2 UTEX Culture Collection, Department of Molecular Biosciences, The University of Texas at Austin, Austin, Texas 78712

3 Department of Biological Sciences, University of Arkansas, Fayetteville, AR, 72701

Abstract

Diatoms are known for their extraordinary species richness, cornerstone roles in aquatic ecosystems, and immense contributions to the global cycling of carbon, oxygen, and silica. For nearly two centuries, taxonomic classifications of diatoms have been based on interpretations of their feature-rich, silica cell walls. These classifications, in turn, have been used to make broad inferences about diatom ecology and evolution, but decades of molecular phylogenetic research have shown that historical and contemporary classification systems do not reflect evolutionary history, severely limiting their utility and insights. We took advantage of recent advances in our understanding of the diatom phylogeny to develop the first entirely natural classification of diatoms, in which only monophyletic groups are recognized and named. The classification is comprehensive, dividing 431 genera among 68 families, 44 orders, and 10 classes. Among these, 7 classes, 13 orders, 3 families and one genus are proposed as new. Although the new classification includes many areas of overlap with previous systems, one principal departure is the increased number of classes, which reflects that "centric" and "araphid" diatoms are comprised of multiple lineages recognized here as distinct classes. By providing a more accurate representation of phylogenetic relationships, the proposed classification facilitates clearer communication about all aspects of diatom biology.

Key words: classification, diatoms, monophyly, phylogeny

Introduction

Diatoms are set apart from other lineages of eukaryotic algae by their species richness, high abundance in aquatic ecosystems worldwide, contributions to global net primary production, and extraordinary morphological diversity. Although it is difficult to estimate the number of species in hyperdiverse groups, generally accepted estimates of diatom diversity range from tens to hundreds of thousand species (Guiry 2012, Mann and Vanormelingen 2013). Just over 1,000 genera have been named, and some 68,000 diatom names exist at the level of species and below (e.g., named varieties) (Kociolek et al. 2025a). These numbers have grown logarithmically over the past three decades (Fig 1). From years 2020–2025 alone, the number of new species and subspecific taxa grew by 15% (Kociolek et al. 2025a). Despite suggestions of taxonomic conservatism at the genus level (Vigneshwaran et al. 2021), the number of new genera has increased by 25% over the same time period (Fig 1B). Classifications at the genus level and above are based principally on morphological features of the siliceous cell wall, life history, and structure of the plastid. Homoplasy in cell wall features can cause misclassifications (Ruck and Theriot 2011, Kociolek et al. 2019), however, and this problem is exacerbated by coarse terminology systems applied to broadly similar, but in many cases nonhomologous, cell wall structures (Cox and Van de Vijver 2024).

Efforts to develop a higher-level classification system for diatoms date back to the early 1800s (Bory 1822–1831, Agardh 1824). Pre-Darwinian and later post-Darwinian attempts to classify diatoms (e.g. Petit 1877, Pfitzer 1871, Mereschkowky 1902a, Schütt 1896) were guided by purported relationships, but these relationships were based on the limited data (e.g. light microscope observations or focus on a single feature) and limited evolutionary knowledge available at the time. One persistent theme has been the "centric–pennate" divide (Schütt 1896), which dominated the classification of diatoms for the next century (e.g. Karsten 1928; Hustedt 1930a, b; Silva 1962) and continues to influence how we describe and discuss diatom diversity. The systems of Hendey (1964) and Patrick and Reimer (1966) were more granular, subdividing centrics and pennates into major groups of equivalent taxonomic rank. The criteria and justifications underlying these groupings were not altogether clear, however. Williams and Kociolek (2007) provide a detailed history of later pursuits of a phylogenetic classification of diatoms, and the works of Reimer Simonsen were pioneering in this regard. Simonsen (1972, 1979) developed a phylogenetic hypothesis for diatoms, advocated for a "natural" (i.e. phylogenetic) classification but did not fully translate these ideas into his proposed classifications (Williams and Kociolek 2007). The "centric–araphid–raphid" split, originally formulated by Smith (1872) and later championed by Round et al. (1990), continues to see widespread formal and informal usage. Round et al. (1990) provided a comprehensive classification of diatoms, but this effort predated major advances in our understanding of diatom relationships made possible through DNA-based molecular phylogenetics. As a result, the widely adopted classification of Round et al. (1990) was based on a mix of stated and unstated character interpretations.

The introduction of molecular phylogenetics to diatom studies in the early 1990s immediately laid bare the shortcomings of previous classification systems, in particular showing that "centric" and "araphid" diatoms were paraphyletic (Medlin et al. 1993, 1996). Since then, the incorporation of phylogeny into comprehensive classification systems of diatoms has been uneven. The subdivision of diatoms into three taxonomic classes—Coscinodiscophyceae ("radial centrics"), Mediophyceae ("polar centrics"), and Bacillariophyceae ("pennates")—quickly gained widespread usage, perhaps because it was presented alongside a broadly sampled phylogenetic tree (Medlin and Kaczmarska 2004). The phylogeny, however, showed weak support for monophyly of Mediophyceae, and Coscinodiscophyceae was paraphyletic (Medlin and Kaczmarska 2004). Interpretations of other characters in support of this classification were consistent with either monophyly or paraphyly of Coscinodiscophyceae and Mediophyceae (Medlin and Kaczmarska 2004, Sims et al. 2006). Theriot et al. (2015) showed that Bayesian support of a Mediophyceae clade was an analytical artefact and not fully supported by the data. These two classes, Coscinodiscophyceae and Mediophyceae, have been resolved as paraphyletic in subsequent analyses with dense taxon sampling (Nakov et al. 2018a) as well as ones with more limited taxon sampling but based on hundreds of genes (Fig. 2) (Alverson et al. 2025). The most recent efforts to establish a comprehensive classification of diatoms embraced the principles of a natural classification but formally recognized and named paraphyletic groupings based on an amalgamation of phylogenetic data, morphology, and historical inertia (Cox 2015, Adl et al. 2019).

We present a phylogenetic classification of diatoms that recognizes monophyletic groups based on a broadly sampled phylogenomic tree of diatoms (Alverson et al. 2025). We classify a total of 431 genera into 10 classes, 44 orders, and 68 families. The classification provides a new framework to foster interpretation and communication of diatom biology and ecology in a way that reflects their underlying evolutionary history. We discuss opportunities and future challenges in developing a comprehensive phylogenetic classification system for this important group of organisms.

Methods and Materials

Our approach to establishing a phylogenetic classification of diatoms was modeled after the Angiosperm Phylogeny Group's approach to developing a higher-level classification system for flowering plants (APG 2003; 2009; 2016). The classification presented here is based primarily on the phylogeny of diatoms from Alverson et al. (2025), which sampled genome-scale data from a total of 284 taxa (280 diatoms + 4 outgroups) representing 170 distinct diatom genera. Other genera not sampled by Alverson et al. (2025) were superimposed onto this backbone tree using areas of congruence with the 11-gene, 1151-

taxon phylogeny of diatoms from Nakov et al. (2018b), other phylogenetic studies, or putative morphological synapomorphies. This allowed us to place and classify many more genera than would have been possible otherwise. Under each category where genera (or other categories of the Linnaean system) are listed, we list the genus name with the author and date of that genus. We then include genera that have been explicitly included in the analysis of Alverson et al. (2025), followed by taxa within those higher categories not in the analysis of Alverson et al. (2025) but whose placement is supported by another molecular study. These are indicated as "Inferred [group] (DNA)" with the references supporting those assignments in brackets. Genera with placements supported exclusively by morphological data are indicated by "Inferred [group] (Morphology)". An "S" is included for taxa with a documented synapomorphy. If the morphological support does not include a specific synapomorphy, the genus name will have a "G" (reflecting general morphological support) for its inclusion in that group. These are the least certain placements whose classifications largely have been carried forward from previous ones (Round et al. 1990; Cox 2015). Using this approach, our classification prioritizes monophyly as the criterion for formal recognition and naming. Using this approach, we recognized only monophyletic groups as candidates for formal recognition and naming. We focused on the categories of Class, Order and Family, with a small number of new subfamilies and one new genus proposed as well.

Results

A new phylogenetically based higher-level classification system for diatoms, from Division through Family, is presented. The Division Bacillariophyta includes 10 classes, 15 Subclasses, 44 Orders, 2 Suborders, and 68 Families. Just over 20% of these categories are described as new (Appendix 1). A total of 431 genera are classified, including the 170 diatom genera from Alverson et al. (2025). The new classification is a marked departure from previous classifications, mostly for the large number of classes and reorganization of orders required to circumscribe monophyletic groups (Fig. 3). Many of the named groups were recognized previously but with differences in genus composition and taxonomic rank.

DIVISION Bacillariophyta Haeckel 1878

Clade 1
Class: Corethrophyceae, New Class
Subclass: Corethrophycidae Round & Crawford 1990
Order: Corethrales Round & Crawford 1990
Family: Corethraceae Lebour 1930
Genus: ***Corethron*** Castracane 1886

Inferred family (Morphology-G): Micrampullaceae Abe et al. 2022 [Abe et al. 2022]

Genus: ***Praecorethron*** Abe et al. 2021 [Abe et al. 2021]; ***Micrampulla*** Hanna (emend Abe et al. 2022) [Abe et al. 2022]

Clade 2

Class: Leptocylindrophyceae, New Class

Subclass: Leptocylindrophycidae, New Subclass

Order: Leptocylindrales Round & Crawford 1990

Family: Leptocylindraceae Lebour 1930

<u>Genera:</u> ***Leptocylindrus*** Cleve in Petersen 1889; ***Tenuicylindrus*** Nanjappa & Zingrone 2013

Clade 3

Class: Melosirophyceae, New Class

Subclass: Proboscidiphycidae New Subclass

Order: Proboscidiales New Order

Family: Proboscidiaceae Nikolaev & Harwood 2002

<u>Genera</u>: ***Proboscia*** Sundström 1986

<u>Inferred genera (Morphology-G)</u>: ***Pyrgupyxis*** Hendey 1969; ***Kreagra*** Gersonde & Harwood 1990 [Jordan & Ligowski 2004]

Subclass: Melosirophycidae Cox, New Subclass

Order: Melosirales Crawford 1990

Family: Melosiraceae Kützing 1844

<u>Genera</u>: ***Melosira*** C.A.Agardh 1824; ***Aulacoseira*** Thwaites 1848

<u>Inferred genera (Morphology-G)</u>*:* ***Alveolophora*** Moisseeva & Nevretdinova 1990 [Usoltseva & Titova 2019]

Order: Paraliales Crawford 1990

Family Paraliaceae Crawford 1988

<u>Genera</u>: ***Paralia*** Heiberg 1863; ***Endictya*** Ehrenberg 1845; ***Podosira*** Ehrenberg 1840; ***Hyalodiscus*** Ehrenberg 1845

<u>Inferred genera (Morphology-G)</u>: ***Bipalla*** Gleser 1992 [Nikolaev, & Harwood 2002]

Order: Stephanopyxales Nikolaev ex Round et al. 1990

Family: Stephanopyxidaceae Nikolaev ex Round et al. 1990

<u>Genus</u>: ***Stephanopyxis*** (Ehrenberg) Ehrenberg 1845

<u>Inferred genera (Morphology-G)</u>: ***Costopyxis*** Gleser 1984 [Nikolaev & Harwood 2000]; ***Creswellia*** Arnott ex Greville 1857 [Nikolaev & Harwood 2000]; ***Pyxilla*** Greville 1865; ***Systephania*** Ehrenberg 1844 [Nikolaev & Harwood 2000]

Incertae Sedis: ***Ellerbeckia*** Crawford 1988; ***Pseudopodosira*** Jouse 1949 emend Vekschina;

Clade 4

Class: Coscinodiscophyceae, Round & Crawford 1990

Subclass: Coscinodiscophycidae Round & Crawford 1990

Order: Rhizosoleniales Silva 1962

Family: Rhizosoleniaceae De Toni 1890

Genera: ***Guinardia*** H.Peragallo 1892; ***Dactyliosolen*** Castracane 1886 ***Rhizosolenia*** Brightwell 1858; ***Pseudosolenia*** Sündstrom 1986

Order: Coscinodiscales Round & Crawford 1990

Family: Coscinodiscaceae Kützing 1844

Genera: ***Coscinodiscus*** Ehrenberg 1839; ***Aulacodiscus*** Ehrenberg 1844; ***Stellarima*** Hasle & P.A.Sims 1986

Inferred genera (DNA) ***Palmerina*** Hasle 1996 [Nakov et al. 2018a]; ***Asteromphalus*** Ehrenberg 1844 [Nakov et al. 2018a]

Inferred genera (Morphology-G): ***Brightwellia*** Ralfs in Pritchard 1861; ***Craspedodiscus*** Ehrenberg 1844; ***Asterolampra*** Ehrenberg 1844; ***Ehrenbergiopsis*** Lobban 2025 [Lobban & Tharngan 2025];

Family: Hemidiscaceae Hendey ex Hasle 1996

Genera: ***Actinocyclus*** Ehrenberg 1837; ***Actinoptychus*** Ehrenberg 1843

Inferred genera (DNA): ***Hemidiscus*** Wallich 1860 [Gomez et al. 2017]

Inferred genera (Morphology-G): ***Azpeitia*** M.Peragallo in Tempere & Peragallo 1912; ***Roperia*** Grunow ex Pelletan 1889; ***Glorioptychus*** Hanna 1927; ***Lepidodiscus*** Witt 1886; ***Rhaphidophora*** Long, Fuge & Smith 1946

Incertae Sedis: ***Rocella*** Hanna 1930; **Gossleriella** Schütt 1892; ***Ethmodiscus*** Castracane 1886; ***Stictodiscus*** Greville 1861; ***Arachnoidiscus*** Deane ex Shadbolt 1852

Clade 5

Class: Thalassiosirophyceae, New Class

Subclass: Thalassiosirophycidae Round et al. 1990

Order: Thalassiosirales Glezer & Makarova 1986

Family:Thalassiosiraceae Lebour 1930

Genera: ***Porosira*** E.Jorgensen 1905; ***Roundia*** Makarova 1994; ***Cyclotella*** (Kützing) Brébisson; ***Skeletonema*** Greville 1865; ***Thalassiosira*** Cleve 1873; ***Discostella*** Houk & Klee 2004; ***Cyclostephanos*** F.E.Round ex Theriot, Hakansson, Kociolek, Round & Stoermer 1987

Inferred genera (DNA): ***Stephanodiscus*** Ehrenberg 1845 [Nakov et al. 2018a]; ***Carenslabia*** Kociolek et al. 2024 [Kociolek et al. 2025c];

Detonula Schütt ex DeToni 1894 [Nakov et al. 2018a]; ***Bacterosira*** Gran 1900 [Nakov et al. 2018a]; ***Minidiscus*** Hasle 1973 [Nakov et al. 2018a]; ***Planktoniella*** Schütt 1892 [Nakov et al. 2018a]; ***Spicaticribra*** Johansen, Kociolek & R.Lowe 2008 [Downey et al. 2021]; ***Shionodiscus*** Alverson, Kang & Theriot 2006 [Alverson et al. 2006]; ***Conticribra*** Stachura-Suchoples & D.M. Williams 2009; ***Lindavia*** (Schütt) G.B. De Toni & A. Forti 1900 [Nakov et al. 2018a]; ***Coenobiodiscus*** A.R.Loeblich, W.W.Wight & Darley, 1968 [Gomez et al. 2025]; ***Lineaperpetua*** Yu et al. 2023; [Yu, You, Kociolek & Wang 2023]; ***Pantocsekiella*** K.T.Kiss & Acs 2016 [Jovanovska et al. 2022]; ***Praestephanos*** Tuji & M.Julius 2014 [Tuji et al. 2014]; ***Lauderia*** Cleve 1873 [Roberts et al. 2023]

<u>Inferred genera (Morphology-S)</u>: ***Mesodictyon*** Theriot & Bradbury 1987; ***Stephanocostis*** Genkal & Kuzmina 1985; ***Strelikoviella*** Kociolek, Khursevich & Theriot 2014; ***Cyclotubicoalitus*** E.F. Stoermer, Kociolek & W. Cody 1990; ***Concentrodiscus*** Khursevich, Moisseeva & Suchova 1989; ***Tertiarius*** Hakansson & Khursevich 1997; ***Tertiariopsis*** Khursevich & Kociolek in Khursevich, Kociolek & Fedenya 2002; ***Mesodictyopsis*** Khursevich, Iwashita, Kociolek & Fedenya in Khursevich et al. 2004; ***Pliocaenicus*** F.E.Round & Hakansson 1992; ***Edtheriotia*** Kociolek et al. 2016; ***Cribrionella*** Jovanoska et al. 2016; ***Ectodictyon*** Khursevich & Cherniaeva 1989; ***Stephanopsis*** Khursevich & Fedenya, 2000; ***Disymmetria*** Lobban 2023; ***Mediolabrus*** Y. Li 2020

Order: Anaulales Round & Crawford 1990
Family: Anaulaceae (Schütt) Lemmermann 1899
<u>Genus</u>: ***Eunotogramma*** J.F.Weise 1854

<u>Inferred genus (DNA)</u>: ***Anaulus*** Ehrenberg 1844 [Witkowski et al. 2020]

Subclass: Lithodesmiophycidae Round & Crawford 1990
Order: Lithodesmiales Round & Crawford 1990
Family: Lithodesmiaceae Round 1990
<u>Genera</u>: ***Ditylum*** J.W.Bailey ex L.W.Bailey 1861; ***Lithodesmium*** Ehrenberg 1839; ***Helicotheca*** M.Ricard 1987; ***Bellerochea*** Van Heurck 1885

<u>Inferred genera (DNA)</u>: ***Lithodesmioides*** von Stosch 1987 [Nakov et al. 2018a]; ***Mediopyxis*** Medlin & Kühn 2006 [Nakov et al. 2018a]; ***Climacodium*** Grunow 1868 [Gomez et al. 2018]

<u>Inferred genus (Morphology-G)</u>: ***Subsilicea*** von Stosch & Reimann 1970

Subclass: Ardissoniophycidae New Subclass

Order: Ardissoneales F.E.Round 1990, emend Lobban & Ashworth
Family: Ardissoceaceae F.E.Round 1990, emend Lobban & Ashworth
<u>Genera:</u> ***Toxarium*** J.W. Bailey 1854; ***Ardissoneopsis*** Lobban & Ashworth in Lobban et al. 2022

Inferred genera (DNA): ***Ardissonea*** G.De Notaris in G. De Notaris & F. Baglietto 1870 [Medlin et al. 2008]; ***Grunowago*** Lobban & Ashworth in Lobban et al. 2022 [Lobban et al. 2022]; ***Synedrosphenia*** (H.Peragallo) Azpeitia 1911 [Lobban et al. 2022]; ***Climacosphenia*** Ehrenberg 1843 [Lobban et al. 2022]

Order: Trigoniumales New Order

Family: Trigoniumaceae Glezer 2019

Genus: ***Trigonium*** Cleve 1867

Family: Lampriscaceae New Family

Genus: ***Lampriscus*** A.Schmidt 1882

Inferred family (DNA): Chrysanthemodiscaceae Round 1978 [Nakov et al. 2018a]

Genus: ***Chrysanthemodiscus*** Mann 1925

Inferred family (DNA): Isthmiaceae Cleve 1867 [Nakov et al. 2018a]

Genera: ***Biddulphiopsis*** Stosch & R.Simonsen 1984; ***Isthmia*** Agardh 1832

Subclass: Eupodiscaphycidae New Subclass

Order: Cymatosirales Round & Crawford 1990

Family: Cymatosiraceae Hasle, von Stosch & Syvertsen 1983

Genera: ***Cymatosira*** Grunow 1862; ***Brockmaniella*** Hasle, von Stosch & Syvertsen 1983; ***Plagiogrammopsis*** Hasle, von Stosch & Syvertsen 1983; ***Campylosira*** Grunow ex Van Heurck 1885; ***Extubocellulus*** Hasle, von Stosch & Syvertsen 1983; ***Leyanella*** Hasle, von Stosch & Syvertsen 1983; ***Minutocellus*** Hasle, von Stosch & Syvertsen 1983; ***Papiliocellulus*** Hasle, von Stosch & Syvertsen 1983

Inferred genera (DNA) [Dabek et al. 2019]: ***Pierrecomperia*** Sabbe, Vyverman & Ribeiro in Sabbe et al. 2010; ***Lambertocellus*** Dabek, Witkowski & Ashworth 2017

Inferred genus (Morphology-G): ***Cymatosirella*** Dąbek, Witkowski & Sabbe 2013 [Dabek et al 2013]

Inferred family (morphology): Rutilariaceae De Toni 1894 [Witkowski et al. 2011]

Genus: ***Rutilaria*** Greville 1863

Order: Eupodiscales Nikolaev & Harwood 2000

Family: Parodontellaceae Komura 1999

Genera: ***Cerataulus*** Ehrenberg 1843; ***Trieres*** Ashworth & Theriot 2013

Inferred genera (Morphology-G): ***Parodontella*** Komura 1999; ***Acigonium*** Komura 1999; ***Stylorium*** Komura 1999; ***Thamnodiscus*** Komura 1999 [Komura 1999]

Family: Odontellaceae Sims, Williams & Ashworth 2018

Genera: ***Mastodiscus*** J.W.Bailey 1854; ***Amphipentas*** Ehrenberg 1841; ***Pleurosira*** (Meneghini) Trevisan 1848; ***Pseudauliscus*** A.Schmidt 1875; ***Pseudictyota*** P.A.Sims & D.M.Williams 2018; ***Ralfsiella*** P.A.Sims, D.M.Williams & Ashworth 2018; ***Hobaniella*** P.A.Sims & D.M.Williams 2018; ***Odontella*** C.A.Agardh 1832

Inferred genus (DNA)**:** ***Amphitetras*** Ehrenberg 1840 [Nakov et al. 2018a]

Inferred genus (Morphology-G): ***Diommatetras*** Komura 1999 [Komura 1999]

Subclass: Chaetocerotophycidae Round & Crawford 1990

Order: Liparogyrales Danz & Kociolek 2024

Family: Liparogyraceae Danz & Kociolek 2024

Genus: ***Aerophilia*** Danz, Van de Vijver & Kociolek 2024

Inferred genera (DNA): ***Liparogyra*** Ehrenberg 1848 [Xiang et al. Accepted]

Inferred genera (Morphology-G) [Danz et al. 2024]: ***Stephanosira*** Ehrenberg 1848; ***Guarreraea*** Kociolek, Guerrero & Van der Vijver 2018

Inferred Family (Morphology-G) [Danz et al. 2024]: Phycavernosaceae Danz & Kociolek 2024

Genus: ***Phycavernosa*** S. Blanco 2020

Order: Hemiaulales Round & Crawford 1990

Family: Hemiaulaceae Heiberg 1863

Genus: ***Hemiaulus*** Heiberg 1863

Order: Eucampiales New Order

Genera: ***Eucampia*** Ehrenberg 1839; ***Cerataulina*** H. Peragallo ex F. Schütt

Order: Chaetocerotales Round & Crawford 1990

Family: Chaetocerotaceae Ralfs in Pritchard 1861

Genus: ***Chaetoceros*** Ehrenberg 1844

Inferred genus (DNA): ***Bacteriastrum*** Shadbolt 1853 [Nakov et al. 2018a]

Order: Acanthoceratales New Order

Family: Acanthocerataceae Crawford & Round 1990

Genera: ***Acanthoceras*** Honigmann 1910; ***Urosolenia*** Round & R.M. Crawford 1990

Inferred order: Hydroseratales New Order [Nakov et al. 2018a]

Family: Hydroserataceae New Family
Genera: ***Terpsinoë*** Ehrenberg 1843; ***Hydrosera*** G.C. Wallich 1858

Clade 6

Class: Biddulphiophyceae New Class
Subclass: Attheyaphycidae New Subclass
Order: Attheyales New Order
Family: Attheyaceae Crawford & Round 1990
Genus: ***Attheya*** West 1860

Subclass: Biddulphiophycidae Round & Crawford 1990
Order: Biddulphiales Krieger 1954
Family: Biddulphiaceae Kützing 1844
Genera: ***Stoermeria*** Kociolek, Escobar & Richardson 1996; ***Biddulphiella*** Sims & Ashworth in Sims et al. 2023; ***Neobrightwellia*** Ashworth & Sims in Sims et al. 2023

Inferred genus (DNA): ***Biddulphia*** Gray 1821 [Sims et al. 2023]

Inferred genus (Morphology-G): ***Tabulina*** Brun 1889 [Sims et al. 2023]

Clade 7

Class: Striatellaphyceae New Class
Order Striatellales F.E.Round 1990
Family Striatellaceae Kützing 1844
Genera: ***Striatella*** C.A.Agardh 1832; ***Pseudostriatella*** S.Sato, D.G.Mann & Medlin 2008

Clade 8

Class: Plagiogrammaphyceae, New Class
Order: Plagiogrammiales Cox 2015 New Order
Family: Plagiogrammaceae De Toni 1890
Genera: ***Neofragilaria*** T.V.Desikachary, A.K.S.K.Prasad & P.Prema in Desikachary & Prema 1987; ***Dimeregramma*** Ralfs in Pritchard 1861; ***Plagiogramma*** Greville 1859; ***Talaroneis*** Kooistra & De Stefano 2004; ***Orizaformis*** A.Witkowski, C.C.L. Li & Ashworth 2015; ***Psammoneis*** S. Sato, Kooistra & Medlin in Sato et al. 2008

Inferred genera (DNA): ***Glyphodesmis*** Greville 1862 [Li et al. 2015]; ***Psammogramma*** S. Sato & Medlin 2008 [Sato et al. 2008]; ***Coccinelloidea*** Li, Górecka & Witkowski 2020 [Li et al. 2020]

Order: Rhaphoneidales Round 1990
Family: Rhaphoneidaceae Forti 1912
Genera: ***Neodelphineis*** Takano 1982; ***Delphineis*** Andrews 1977

Inferred genus (DNA): ***Rhaphoneis*** Ehrenberg 1844 [Nakov et al. 2018a]

Inferred genera (Morphology-G): ***Diplomenora*** Blazé 1984; ***Perissonoe*** Andrews & Stoelzel 1984; ***Sceptroneis*** Ehrenberg 1844; ***Adoneis*** Andrews & Rivera 1987

Inferred family (Morphology-G): Psammodiscaceae Round & Mann in Round et al. 1990
Genus: ***Psammodiscus*** Round & Mann 1908

Family: Asterionellopsidaceae Medlin 2016
Genus: ***Asterionellopsis*** Round in Round et al. 1990

Inferred genus (DNA): ***Asteroplanus*** C.Gardner & R.M.Crawford 1997 [Nakov et al. 2018a]

Inferred order (DNA): Koernerellales Lobban & Ashworth 2022 [Lobban & Ashworth 2022]
Family: Koernerellaceae Lobban & Ashworth 2022
Genera: ***Bleakeleya*** Round 1990; ***Koernerella*** Ashworth, Lobban & E.C. Theriot 2011; ***Perideraion*** Lobban & R.W. Jordan 2011

Clade 9

Class: Fragilariophyceae Round 1990
Subclass: Staurosirophycidae New Subclass
Order: Staurosirales New Order
Family: Staurosiraceae Medlin 2016
Genera: ***Staurosira*** Ehrenberg 1843; ***Punctastriata*** D.M.Williams & F.E.Round 1988; ***Psammotaenia*** Ashworth, C.Li & A.Witkowski 2016; ***Serratifera*** Ashworth, C.Li & A.Witkowski 2016; ***Nanofrustulum*** F.E.Round, Hallsteinsen & Paasche 1999; ***Opephora*** P.Petit 1888; ***Fragilariforma*** D.M.Williams & F.E.Round 1988, ***Castoridens*** Ashworth, C.Li & A.Witkowski 2016; ***Plagiostriata*** S.Sato & Medlin in Sato et al. 2009

Inferred genera (DNA): ***Hendeyella*** M.P.Ashworth, Witkowski & CL.Li 2016 [Li et al. 2016]**;** ***Pseudostaurosira*** D.M.Williams & F.E.Round 1988 [Nakov et al. 2018a]; ***Staurosirella*** D.M.Williams & F.E.Round 1988 [Nakov et al. 2018a]; ***Pseudostaurosiropsis*** Morales 2001 [Nakov et al. 2018a]; ***Stauroforma*** R.J.Flower, V.J.Jones & Round 1996 [Li et al. 2018]

Subclass: Fragilariophycidae Round 1990
Order: Fragilariales Silva 1962
Family: Thalassionemataceae Round 1990
Genera: ***Thalassionema*** Grunow ex Mereschkowsky 1902; ***Thalassiothrix*** Cleve & Grunow 1880

Inferred genera (DNA) [Sabir et al. 2018]: ***Hyalosynedra*** D.M.Williams & F.E.Round 1986; ***Pteroncola*** R.W. Holmes & D.A. Croll 1984; ***Stricosus*** Sabir & Theriot 2018, ***Divergita*** Sabir & Theriot 2018

Family: Fragilariaceae Greville 1833

Genera: ***Ulnaria*** (Kützing) P. Compère 2001; ***Ctenophora*** (Grunow) D.M.Williams & F.E.Round 1986; ***Tabularia*** (Kützing) D.M.Williams & F.E.Round 1986; ***Grammonema*** C.A.Agardh 1832; ***Synedropsis*** Hasle, Medlin & Syvertsen 1988

Inferred genera (DNA): ***Fragilaria*** Lyngbye 1819 [Kahlert et al. 2019]; ***Synedra*** Ehrenberg 1830 [Nakov et al. 2018a]; ***Catacombas*** D.M. Williams & Round 1986 [Nakov et al. 2018a]

Inferred genera (Morphology-S): ***Tibetiella*** Y.Li, D.M.Williams & Metzeltin 2010 [Li et al. 2010]

Order: Licmophorales Round 1990

Family: Licmophoraceae Kützing 1844

Genera: ***Licmophora*** C.A.Agardh 1827; ***Podocystis*** J.W.Bailey 1854

Inferred genus (Morphology-S): ***Gato*** Lobban & Navarro 2013 [Lobban & Navarro 2013]

Order: Cyclophorales Round & Crawford 1990

Family: Cyclophoraceae Round & Crawford 1990

Genera: ***Cyclophora*** Castracane 1878; ***Lucanicum*** Lobban & Ashworth 2014; ***Florella*** Navarro 1982; ***Astrosyne*** Ashworth & Lobban in Ashworth et al. 2012

Inferred genera (DNA): ***Pseudohimantidium*** Hustedt & Krasske in Krasske 1941 [Nakov et al. 2018a]; ***Protoraphis*** Simonsen 1970 [Nakov et al. 2018a]; ***Neosynedra*** D.M. Williams & Round 1986 [Lobban et al. 2021]

Subclass: Tabellariaphycidae New Subclass

Order: Tabellariales Round 1990

Family Tabellariaceae Kützing 1844

Genera: ***Tabellaria*** Ehrenberg ex Kützing 1844; ***Diatoma*** de Candolle 1805; ***Meridion*** C.A.Agardh 1824; ***Asterionella*** Hassall 1850

Inferred genus (DNA): ***Tetracyclus*** Ralfs 1843 [Nakov et al. 2018a]

Inferred genera (Morphology-S): ***Oxyneis*** F.E.Round in Round et al. 1990;
Distrionella D.M.Williams 1990; ***Odontidium*** Kützing 1844

Order: Rhabdonematales Round & Crawford 1990

Family: Rhabdonemataceae Round & Crawford 1990

Genus: ***Rhabdonema*** Kützing 1844

<u>Inferred genus (DNA)</u>: ***Placosira*** Ashworth & Majewska 2021 [Lobban et al. 2021]

Family: Grammatophoraceae Lobban & Ashworth 2014

<u>Genera</u>: ***Grammatophora*** Ehrenberg 1840; ***Microtabella*** Round 1990

<u>Inferred genera (DNA)</u>: ***Hanicella*** Lobban & Ashworth 2014 [Lobban & Ashworth 2014], ***Hyalosira*** Kützing 1844 [Lobban et al. 2021]

Clade 10

Class: Bacillariophyceae Haeckel 1878

Order: Eunotiales Silva 1962

Family: Eunotiaceae Kützing 1844

<u>Genera:</u> ***Eunotia*** Ehrenberg 1837; ***Actinella*** F.W.Lewis 1864

<u>Inferred genera (Morphology-G)</u>: ***Eunophora*** Vyverman, Sabbe & D.G.Mann in Vyverman et al. 1998; ***Actinellopsis*** J.C.Taylor, B.Karthick & Kociolek 2014; ***Semiorbis*** R.Patrick in Patrick & Reimer 1966; ***Desmogonium*** Ehrenberg in Schomburgk 1848; ***Peronia*** de Brébisson & Arnott ex Kitton 1868; ***Sinoperonia*** Kociolek, Liu, Glushchenko & Kulikovskiy 2018; ***Amphicampa*** (Ehrenberg) J. Ralfs in Pritchard 1861 [Kociolek & Spaulding 2003]; ***Bicudoa*** Wetzel et al. 2012 [Wetzel et al. 2012]; ***Eunotioforma*** Kociolek & Burliga 2013 [Burliga et al. 2013]; ***Burliganiella*** Wetzel & Kociolek 2018 [Wetzel & Kociolek 2018]; ***Torgania*** Canani & Talgatti 2021

Order: Amblyamphorales, New Order

Family: Amblyamphoraceae, New Family

<u>Genus</u>: ***Amblyamphora*** (Cleve) New Genus

Ampblyamphora laevissima (Gregory) comb. nov., *Amblyamphora obtusa* (Gregory) comb. nov.

Order: Bacillariales Hendey 1937

Family: Staurotropidaceae

<u>Genus</u>: ***Staurotropis*** Paddock 1988

Family: Achnanthaceae Kützing 1844

<u>Genera</u>: ***Achnanthes*** Bory de Saint-Vincent 1822; ***Craspedostauros*** E.J.Cox 1999 [Ashworth et al. 2017]

<u>Inferred Genus (DNA)</u>: ***Druehlago*** Lobban & Ashworth 2017 [Sugawara et al. 2024]

Family: Bacillariaceae Ehrenberg 1831

<u>Genera:</u> ***Bacillaria*** Gmelin 1788; ***Nitzschia*** Hassall 1845; ***Denticula*** Kütziing 1844; ***Cylindrotheca*** Rabenhorst 1859; ***Pseudo-nitzschia*** H.Peragallo in Peragallo & Peragallo 1900; ***Fragilariopsis*** Husted in Schmidt et al. 1913; ***Tryblionella*** W.Smith 1853; ***Cymbellonitzschia*** Hustedt in Schmidt et al. 1924; ***Psammodictyon*** D.G.Mann in Round et al. 1990; ***Homoeocladia*** C. Agardh emend Lobban & Ashworth 2022

Inferred genus (DNA): ***Hantzschia*** Grunow 1877 [Mann et al. 2021]

Inferred genera (Morphology-G): ***Grunowia*** Rabenhorst 1864 [Kociolek et al. 2020]; ***Gomphotheca*** Hendey & P.A.Sims 1982; ***Denticulopsis*** Simonsen 1979; ***Simonsenia*** Lange-Bertalot 1979; ***Perrya*** Kitton 1874; ***Nagumoea*** A.Witkowski & Kociolek in Witkowski et al. 2011; ***Archibaldia*** A.Witkowski & Kociolek in Witkowski et al. 2011

Order: Naviculales Bessey 1907

Family Pleurosigmataceae Mereschkowsky 1903

Genera: ***Gyrosigma*** Hassall 1845; ***Pleurosigma*** W.Smith 1852; ***Donkinia*** Ralfs in Pritchard 1861; ***Plagiolemma*** Paddock 1988

Inferred genera (DNA): ***Meuniera*** P.C. Silva in Hasle & Syvertsen 1996 [Nakov et al. 2018a]; ***Carinasigma*** G. Reid 2012 [Nakov et al. 2018a]; ***Plagiotropis*** Pfitzer 1871 [Gastineau et al. 2022]

Inferred genera (morphology-G): ***Hyalosigma*** Strelnikova & Kociolek in Strelnikova et al. 2006; ***Arcuatasigma*** Reid 2012 [Reid 2012]; ***Rhoicosigma*** Grunow 1867 [Lobban & Reid 2018]

Family: Naviculaceae Kützing 1844

Genera: ***Navicula*** Bory St. Vincent 1822; ***Rhoiconeis*** Grunow 1863; ***Seminavis*** D.G.Mann in Round et al. 1990; ***Hippodonta*** Lange-Bertalot, A. Witkowski & Metzeltin 1996; ***Haslea*** Simonsen 1974

Inferred genera (DNA): ***Pseudogomphonema*** Medlin in Medlin & Round 1986 [Nakov et al. 2018a] ***Cymatoneis*** Cleve 1894 [Gastineau et al. 2022]; ***Trachyneis*** P.T. Cleve 1894 [Gastineau et al. 2022]

Inferred genus (Morphology-G): ***Gandhia*** Kulikovskiy et al. 2023 [Kulikovskiy et al. 2023]

Incertae sedis: ***Microfissurata*** Lange-Bertalot et al. 2009; ***Genkalia*** Kulikovskiy et al. 2012

Order: Diploneidales New Order

Family Diploneidaceae Mann 1990

Genus: ***Diploneis*** (Ehrenberg) Cleve 1894

Inferred genus (DNA): ***Amicula*** Witkowski, Lange-Bertalot & Metzeltin 2000 [Gastineau et al. 2022]

Order: Surirellales Mann 1990

Suborder: Neidiineae Mann 1990

Family: Neidiaceae Mereschkowsky 1903

Genera: ***Neidium*** Pfitzer 1871; ***Phaeodactylum*** Bohlin 1897; ***Biremis*** D.G.Mann & E.J.Cox in Round et al. 1990

Inferred genera (DNA): ***Scoliopleura*** Grunow 1860; ***Luticola*** D.G.Mann in Round et al. 1990 [Nakov et al. 2018a]

Inferred genera (Morphology-G): ***Muelleria*** (Frenguelli) Frenguelli 1945; ***Neidiopsis*** Lange-Bertalot & Metzeltin in Lange-Bertalot & Genkal 1999; ***Neidiomorpha*** Lange-Bertalot & Cantonati in Cantonati et al. 2010; ***Olifantiella*** Riaux-Gobin & Compère, 2009; ***Scoliotropis*** Cleve 1894; ***Scolioneis*** D.G.Mann in Round et al. 1990; ***Luticolopsis*** Levkov, Metzeltin & A.Pavlov, 2013 [Levkov et al. 2013]; ***Labellicula*** Van de Vijver & Lange-Bertalot, 2005

Suborder: Surirellineae, New Suborder

Family: Surirellaceae Kützing 1844

Genera: ***Halamphora*** (Cleve) Z. Levkov 2009; ***Thalassiophysa*** Conger 1954; ***Surirella*** Turpin 1828; ***Entomoneis*** (Ehrenberg) Ehrenberg 1845; ***Epithemia*** Brébisson ex Kützing 1844; ***Protokeelia*** Reimer & Lee 1984; ***Campylodiscus*** Ehrenberg ex Kützing 1844; ***Auricula*** Castracane 1873; ***Iconella*** Jurilj 1948; ***Coronia*** (Ehrenberg ex Grunow) Ruck & Guiry 2016

Inferred genera (DNA): ***Amphora*** Ehrenberg ex Kützing 1844 [Stepanek and Kociolek 2014]; ***Petrodictyon*** D.G.Mann in Round et al. 1990 [Nakov et al. 2018a]; ***Rhopalodia*** O.Müller 1895 [Nakov et al. 2018a]

Inferred genera (morphology-G): ***Bifibulatia*** Takano 1983; ***Hydrosilicon*** Brun 1891; ***Plagiodiscus*** Grunow & Eulenstein in Grunow 1867

Order: Sellaphorales New Order

Family: Sellaphoraceae Mereschkowsky 1902

Genera: ***Sellaphora*** Mereschkowsky 1902; ***Diprora*** Main 2003; ***Fallacia*** Stickle & D.G.Mann in Round et al. 1990

Inferred genera (DNA): ***Rossia*** Voigt 1960 [Nakov et al. 2018a]; ***Eolimna*** Lange-Bertalot & Schiller in Schiller & Lange-Bertalot 1997; ***Mayamaea*** Lange-Bertalot 1997 [Nakov et al. 2018a]; ***Pseudofallacia*** Y.Liu, Kociolek & Wang 2012 [Y. Li et al. 2022];

Inferred genera (Morphology-G): ***Okhapkinia*** Kulikovskiy, Glushchenko & Kociolek 2018 [Kulikovskiy et al. 2018]; ***Caponea*** Podzorski 1984;

Family Pinnulariaceae Mann 1990

Genera: ***Pinnularia*** Ehrenberg 1843; ***Caloneis*** Cleve 1894

Inferred genera (DNA): ***Pinnuavis*** Okuno 1975 [Nakov et al. 2018a]

Inferred genera (Morphology-G): ***Diatomella*** Greville 1855; ***Oestrupia*** Heiden ex Hustedt 1935; ***Dimidiata*** Hajos 1973; ***Spargeria*** Y.Liu, Kociolek & Fan 2024 [Liu et al. 2024]; ***Hygropetra*** Krammer & Lange-Bertalot 2000; ***Alveovallum*** Krammer & Lange-Bertalot 2000

Order Diadesmidales New Order

Family: Diadesmidiaceae Mann 1990

<u>Genus:</u> ***Diadesmis*** Kützing 1844

Order Cocconeidales Cox, New Order

Family: Achnanthidiaceae Mann 1990

<u>Genera:</u> ***Achnanthidium*** Kützing 1844; ***Planothidium*** F.E.Round & Bukhtiyarova 1996

<u>Inferred genera (DNA)</u>: ***Pauliella*** Round & P.W. Basson 1997 [Nakov et al. 2018a]; ***Lemnicola*** Round & P.W. Basson 1997 [Nakov et al. 2018a]; ***Platessa*** Lange-Bertalot 2004; ***Rossithidium*** F.E.Round & Bukhtiyarova 1996 [Kulikovskiy et al. 2016]; ***Skabitschewskia*** Kulikovskiy & Lange-Bertalot 2015 [Kulikovskiy et al. 2022]; ***Psammothidium*** Bukhtiyarova & F.E.Round 1996 [Nakov et al. 2018a]; ***Eucocconeis*** Cleve ex Meister 1912 [Nakov et al. 2018a]; ***Gliwiczia*** Kulikovskiy, Lange-Bertalot & A.Witkowski 2013; ***Gogorevia*** Kulikovskiy, Glushchenko, Maltsev & Kociolek, 2020 [Kulikovskiy et al. 2020]

<u>Inferred genera (morphology-G)</u>: ***Platebaikalia*** Kulikovskiy, Glushchenko, Genkal & Kociolek, 2020; ***Scalariella*** Riaux-Gobin in Riaux-Gobin et al. 2012; ***Crenotia*** Wojtal 2013 [Wojtal 2013]; ***Gololobovia*** Kulikovskiy et al. 2020; ***Gomphothidium*** Kociolek et al. 2021 [Kociolek et al. 2021]; ***Haloroundia*** Diaz & Maidana 2006; ***Platesiberia*** Kulikovskiy et al. 2022; ***Xenobennettella*** A.Witkowski & Riaux-Gobin 2022 [Witkowski et al. 2022]; ***Vallithidium*** Nienow & Prasad 2023 [Nienow & Prasad 2023]; ***Indoplatessa*** Tseplik et al. 2025 [Tseplik et al. 2025]

Family Cocconeidaceae Kützing 1844

<u>Genera:</u> ***Cocconeis*** Ehrenberg 1837; ***Anorthoneis*** Grunow 1868

<u>Inferred genera (Morphology-G)</u>: ***Campyloneis*** Grunow 1862; ***Cocconeiopsis*** A. Witkowski, Lange-Bertalot & Metzeltin 2000; ***Epipellis*** Holmes 1985; ***Psammococconeis*** M.Garcia 2001; ***Vikingea*** A.Witkowski, Lange-Bertalot & Metzeltin 2000; ***Australoneis*** Guerrero & Riaux-Gobin 2021 [Guerrero et al. 2021]; ***Bennettella*** Holmes 1985; ***Upsilococconeis*** Riaux-Gobin, A.Witkowski & Risjani 2022 [Riaux-Gobin et al. 2022]; ***Xenococconeis*** Riaux-Gobin 2014

Order: Cymbellales Mann 1990

Family Cymbellaceae Greville 1833

<u>Genera</u>: ***Cymbella*** C.A.Agardh 1830; ***Staurophora*** Mereschkowsky 1903

<u>Inferred genera (DNA)</u>: ***Didymosphenia*** M.Schmidt in Schmidt et al. 1899 [Nakov et al. 2018a]; ***Cymbopleura*** (K.Krammer) K.Krammer 1999 [Nakov et al. 2018a]; ***Encyonopsis*** K.Krammer 1997 [Nakov et al.

2018a]; ***Karthickia*** Kociolek, Glushchenko & Kulikovskiy 2019 [Yana et al. 2022]; ***Oricymba*** Jüttner, Krammer, Cox, Van de Vijver & Tuji 2010; ***Qinia*** Y.Liu, Kociolek & Kulikovskiy 2023 [Li et al. 2024]; ***Vladinikolaevia*** Kulikovskiy, Glushchenko, Y.Liu & Kociolek 2022;

Inferred (Morphology-G): ***Cymbellafalsa*** Lange-Bertalot & Metzeltin 2009; ***Brebissonia*** Grunow 1860; ***Gomphocymbellopsis*** K.Krammer 2003 [Krammer 2003]; ***Sichuaniella*** Y.-L.Li, Lange-Bertalot & Metzeltin 2013 [Gogoriev et al. 2015]
Celebesia Kapustin, Kulikovskiy & Kociolek 2017; ***Navicymbula*** K.Krammer 2003; ***Crucicostulifera*** J.Taylor & Lange-Bertalot 2010; ***Rexlowea*** Kociolek & Thomas 2010;

Inferred Family (DNA) Witkowskiaceae Mironov et al. 2024 [Mironov et al. 2024]

Genus: ***Geissleria*** Lange-Bertalot & Metzeltin 1996

Inferred genera (DNA): ***Placoneis*** Mereschkowsky 1903 [Nakov et al. 2018a]; ***Witkowskia*** Kulikovskiy, Mironov, Glushchenko & Kociolek 2024 [Mironov et al. 2024]; ***Paraplaconeis*** Kulukovskiy, Lange-Bertalot & Metzeltin 2012 [Mironov et al. 2024];

Family Encyonemataceae Mironov et al. 2024 [Mironov et al. 2024]

Genus: ***Enyconema*** Kützing 1833

Family Gomphonemataceae Kützing 1844

Genus: ***Gomphonema*** Ehrenberg 1832

Inferred genera (DNA): ***Gomphoneis*** Cleve 1894 [Nakov et al. 2018a]; ***Gomphonella*** Rabenhorst 1853 [Mironov et al. 2024]; ***Reimeria*** Kociolek & Stoermer 1987 [Nakov et al. 2018a];

Inferred genera (Morphology-G): ***Gomphosinica*** Kociolek, Q-M.You, Q-X.Wang & Q.Liu 2015 [Kociolek et al. 2015]; ***Afrocymbella*** K.Krammer 2003 [Kociolek & Stoermer 1988]; ***Gomphopleura*** Reichelt ex Tempère 1894 [Kociolek & Stoermer 1988];

Inferred Family (Morphology—G) Anomoeoneidaceae Mann 1990

Genera: ***Dickieia*** Berkeley ex Kützing 1844; ***Anomoeoneis*** Pfitzer 1871; ***Adlafia*** Moser, Lange-Bertalot & Metzltin 1998

Order Mastogloiales Mann 1990

Family Mastogloiaceae Mereschkowsky 1903

Genera: ***Mastogloia*** Thwaites in W. Smith 1856; ***Decussata*** (Patrick) Lange-Bertalot 2000; ***Berkeleya*** Greville 1827; ***Tetramphora*** Mereschkowsky 1903

Inferred genera (DNA) [Kezlya et al. 2024]: ***Aneumastus*** D.G.Mann & Stickle in Round et al. 1990; ***Stigmagloia*** Glushchenko, Kezlya, Kasputin & Kulikovskiy 2024

Family Stauroneidaceae Mann 1990

Genera: ***Stauroneis*** Ehrenberg 1843; ***Sternimirus*** A.Witkowski & C.Li 2016; ***Parlibellus*** E.J.Cox 1988; ***Proschkinia*** Karayeva 1978; ***Fistulifera*** Lange-Bertalot 1997; ***Craticula*** Grunow 1867; ***Schizostauron*** Grunow 1867; ***Astartiella*** A.Witkowski Lang-Bertalot & Metzeltin in Moser et al. 1998; ***Kolbesia*** Round & Bukhtiyarova ex Round, 1998

Inferred genera (DNA): ***Dorofeyukae*** Kulikovskiy et al. 2019 [Kulikovskiy et al. 2019]; ***Madinithidium*** A.Witkowski, Desrosiers & Riaux-Gobin, in Desrosiers et al. 2019 [Kulikovskiy et al. 2019]; ***Karayevia*** F.E. Round & Bukhtiyarova ex Round 1998 [Kulikovskiy et al. 2019]; ***Prestauroneis*** Bruder & Medlin 2008 [Bruder & Medlin 2008]; ***Luticola*** D.G.Mann [Nakov et al 2018a]; ***Poulinea*** Majewska, De Stefano & Van de Vijver 2015 [Ashworth et al. 2022]; ***Chelonicola*** Majewska, De Stefano & Van de Vijver 2015 [Ashworth et al. 2022]; ***Medlinella*** Frankovich, M.P.Ashworth & M.J.Sullivan 2016 [Ashworth et al. 2022]; ***Tursiocola*** R.W.Holmes, S.Nagasawa & H.Takano 1993 [Ashworth et al. 2022]

Inferred genera (morphology-G): ***Epiphalaina*** R.W.Holmes, S.Nagasawa & H.Takano 1993 [Frankovich et al. 2018]; ***Tripterion*** R.W.Holmes, S.Nagasawa & H.Takano 1993 [Majewska et al. 2015]

Inferred family (DNA) Amphipleuraceae Grunow 1862 [Nakov et al. 2018a]

Inferred genera (DNA) [Nakov et al. 2018a]: ***Climaconeis*** Grunow 1862; ***Amphipleura*** Kützing 1844; ***Frustulia*** Rabenhorst 1853

Inferred genera (Morphology-G): ***Stenoneis*** Cleve 1894; ***Cavinula*** D.G.Mann & Stickle in Round et al. 1990; ***Cosmioneis*** D.G.Mann & Stickle in Round et al. 1990; ***Frickea*** Heiden in A. Schmidt et al. 1906; ***Cistula*** Cleve 1894; ***Brachysira*** Kützing 1836; ***Pseudofrustulia*** Sawai & Nagumo 2016 [Sawai et al. 2016]

Discussion

The classification of diatoms presented here categorizes 431 genera among 10 classes, 15 subclasses, 44 orders, and 68 families. This is the first entirely natural classification of diatoms, in which names have been applied only to groups with evidence for monophyly, based principally on molecular phylogenetic analyses of taxa spanning the diatom tree of life. Previous classifications either predated the widespread application of molecular phylogenetics to diatom systematics, did not fully integrate, or in some cases, eschewed phylogenetic relationships as the guiding principle for classification. Even in the absence of formal phylogenetic analyses, however, support for monophyly of some groups is so clear based on other characters that the new classification includes many areas of overlap with past ones. For example, many of the subclasses and orders recognized by Round et al. (1990) are also present in our system, as are many families dating back to 19th and 20th century classifications. Our system also formalizes some named groups that were proposed but nomenclaturally invalid in other classifications, including the Cocconeidales and Melosirophycidae (Cox 2015).

The classification proposed here includes classic Linnaean ranks because, in our experience, most users of the diatom classification utilize the ranks for communication or other purposes. The classification presented here, which recognizes diatoms as a Division with ten named Classes, is consistent with previous systems that categorized diatoms, either implicitly or explicitly, at the level of Division (Round et al. 1990; Medlin and Kaczmarska 2004; Cox 2015; Adl et al. 2019). Although the eukaryote-wide classification of Adl et al. (2019) was technically rankless, diatoms as whole were classified into the equivalent of a Division (Diatomeae) with 8 subphyla and 5 classes. Many of these groups are also recognized in our classification scheme, with the major differences being the assigned or implied rank. This reflects limitations of the traditional Linnaean system and, as well, the element of subjectivity involved in choosing which rank the diatom clade as a whole should be assigned. Like Adl et al. (2019), the names in our classification can be applied as a rankless hierarchy without any loss of information. The classification system presented here does not fully recapitulate the diatom phylogeny. Our classification returns, for example, the equivalent of a polytomy of the 10 Classes, and within each class, a polytomy of the Orders. The relationships among them can be found in the tree presented by Alverson et al. (2025).

Another recent classification of algae is by Guiry (2024), who separated diatoms into two subphyla (“Bacillariophytina” and “Coscinodiscophytina) without reference to any specific phylogeny. This approach was remarkable for two reasons. First, there was no reference to the diatoms as a singular group. Instead, these two subphyla are classified as separate groups within the Division Heterokontophyta. This approach could be interpreted as suggesting diatoms are not monophyletic. Second, Guiry’s classification resurrects centric–pennate split of diatoms proposed back in 1896 (Karsten 1896) and not returned in any phylogenetic analysis of diatom relationships over the past 30 years. The system we propose here is based on an explicit phylogeny (Alverson et al. 2025), recognizes only monophyletic groups as indicated in that phylogeny, and attempts to use categories of taxonomic hierarchy (Classes, Orders, Families) commonly used in discussions diatom biology, taxonomy, and systematics.

Among the most obvious and arguably most important advances of the new system is the establishment of many more taxonomic classes than have been recognized previously. This increase reflects the subdivision of “centric” and “araphid pennate” diatoms into numerous classes. Despite the historical inertia and convenience associated with maintaining these groups, decades of molecular phylogenetic work have shown that both are paraphyletic grades of taxa united only by ancestral characters (Alverson and Theriot 2005, Sims et al. 2006, Theriot et al. 2010, Alverson et al. 2025). In alignment with phylogenetic relationships, our classification divides the four lineages of “radial centrics” (Coscinodiscophyceae *sensu* Medlin and Kaczmarska 2004) into four separate classes and “polar centrics” (Mediophyceae *sensu* Medlin and Kaczmarska 2004) into two classes. Araphid pennates

(Fragilariophyceae *sensu* Cox 2015) are now separated into three separate classes, with Bacillariophyceae (Cox 2015) reserved for the raphid pennate clade.

In other cases, named taxonomic groups present in our classification and previous ones differ substantially in taxonomic composition (Fig. 3). For example, genera assigned to Naviculales, Achnanthales, Biddulphiales, Fragilariales, Cymbellales and Thalassiophysales differ substantially between the new and old classifications (e.g., Round et al. 1990). Phylogenetic analyses have shown that monoraphid diatoms—previously organized into a single order—are spread across the raphid pennate clade (Kulikovskiy et al. 2016, Alverson et al. 2025). These distinct clades are now recognized and named accordingly. Similarly, taxa previously assigned to Thalassiophycidales are now found in three orders distributed across the raphid pennate clade (Stepanek and Kociolek 2019, Alverson et al. 2025). The genus *Navicula* is one of many vaguely defined diatom genera in which many species have been placed largely through a process of elimination. Although many well-defined genera have been split away from *Navicula* over the years, this work is incomplete and, in addition, the higher-level classification of the genera split away from *Navicula* has not kept pace. As a result, taxa formerly classified as Naviculales by Round et al. (1990) are now divided among seven different orders based on phylogenetic relationships (Kulikovskiy et al. 2019, 2020, Alverson et al. 2025). In the Bacillariales, it has been shown that some groups that are closely allied lack features previously thought diagnostic for the group (Mann et al. 2021), and those have been moved from Naviculales to Bacillariales in the new classification. Finally, the proposed classification highlights the need to reclassify some species into new or different genera. Although these species give the superficial impression that some of our named groups are non-monophyletic, this reflects current shortcomings of the genus-level classification (see *Achnanthes* and *Nitzschia*, for example).

Like phylogenetic relationships of many large groups, the shape of the diatom tree is highly asymmetric, i.e., in some cases there is strong imbalance in species richness between sister lineages (Alverson et al. 2025). As has been shown for several genera of marine planktonic diatoms, these patterns are a product of clade age and rates of speciation and extinction (Nakov et al. 2018b). Pre-Darwinian taxonomists often sought to balance the relative sizes of named groups with equivalent rank in their classifications (Stevens 2015), but phylogenetic classifications whose principal goal is recognizing and naming phylogenetically equivalent lineages at the same taxonomic level invariably create systems in which clades of equivalent rank differ dramatically in genus and species richness. At the class level, for example, the Corethrophyceae, Leptocylindrophyceae, and Striatellaphyceae are comparatively small in their taxonomic composition compared to Bacillariophyceae, which has experienced considerably higher rates of speciation than other diatom lineages (Nakov et al. 2018a, Alverson et al. 2025). Similar patterns exist at the order level, where lineages such as Thalassiosirales, Cymbellales, and Bacillariales contain many more genera than Striatellales Chaetocerotales, Attheyales, Licmophorales, Diploneidales, Diadesmidales, and Mastogloiales. Among the lineages with a few genera, however, some of them nevertheless contain many species (*Nitzschia*, *Mastogloia*, *Diploneis*, and *Chaetoceros*), whereas others have only a few (*Attheya* and *Diadesmis*).

Numerous studies have superimposed morphological characters onto diatom phylogenies derived from molecular data to identify putative synapomorphies (Williams 2020). Although our classification is not based on morphological data, it is predictive of certain aspects of morphological evolution. For example, the oldest diatom lineages were likely oogamous and cylindrical in shape, the raphe evolved one time, and loss of one raphe occurred several times. Our system is focused primarily on extant genera unless the fossil could be unambiguously placed, but continued morphological work will allow incorporation of additional genera—particularly fossils—into this classification system. The unique importance of fossils in shaping phylogenetic and evolutionary inferences is well documented (Gauthier et al. 1988, Donoghue et al. 1989, Mongiardino Koch et al. 2021). Building upon past successes and finding new ways to integrate the vast diversity of diatom fossils into a phylogenetic classification is an area that is ripe for future research.

Given how character-rich the diatom cell wall is, why are there no apparent morphological synapomorphies for some of the clades with strong support in molecular phylogenies? The pace of change was incredibly fast at certain points in diatom evolution, including during the near-simultaneous diversification of polar centric and pennate diatoms, and within raphid pennates (Alverson et al. 2025). Research focused principally on revealing cryptic phylogenetic diversity within what were once considered widespread ("cosmopolitan") species has revealed a lag between genomic divergence and subsequent morphological changes (Sarno et al. 2005, Lundholm et al. 2006, Alverson 2008). As a result, rapid species radiations will capture relatively few molecular synapomorphies and even fewer morphological synapomorphies. This problem is compounded by extinction, which erases the record of character states that might diagnose clades otherwise resolvable only with molecular data. As a result, although nomenclatural rules require traditional morphological descriptions of newly named taxa (Appendix 1), it was challenging to assign synapomorphies to each named lineage. Although inconvenient for a taxonomic classification, this reflects the biological reality of diatom evolutionary history. Finally, morphological synapomorphies are not restricted to frustule features. For example, a putative synapomorphy for the suborder Surillelineae, which includes *Amphora, Halamphora, Surirella, Entomoneis, Rhopalodia, Epithemia*—taxa with disparate frustule morphologies—may be related to their mode of sexual reproduction, with the number of viable gametes, number of auxospores produced, and relative position of the gamete-producing cells to the auxospores (Sato and Mann 2024; Kociolek et al. 2025b).

We developed this classification with the understanding that it reflects our current knowledge of the diatom phylogeny, which is subject to change and reinterpretation as new data become available (Williams 2020). In this sense, a classification is no different than any other hypothesis that is open to future testing and revision. A principal strength of this classification, however, is its reliance on phylogenetic trees, which impose a level of objectivity and transparency missing from other classifications. The clade-based classification will facilitate meaningful communication about all areas of diatom biology, ecology, and evolution, as named groups naturally have some degree of biological cohesion, just as named groups of equivalent rank are assured to have some degree of independence from one another. Although not a substitute for statistically based comparative biology, especially considering that equivalent ranks are not necessarily equivalent in age (Nakov et al. 2018b), the new names invite comparisons that were not previously possible. A phylogenetic classification facilitates research and discussion on a wide range of topics, including species diversification, trait evolution, species distributions across environmental gradients, and bioprospecting.

Finally, it is both timely and important to connect the advances in our knowledge about the diatom tree of life, reflected in this classification, with public outreach and education for the next generations of diatom researchers. It is no longer necessary to minimize or replace our understanding of the diatom phylogeny—with its predictive powers and explicit insights into shared ancestry and evolutionary pathways—with the conveniences of recognizing phylogenetic grades of taxa that perpetuate misunderstandings of relationships and evolutionary history.

References

Abe, K., Harwood, D.M., & Jordan, R.W. (2022). Observations on Late Cretaceous *Micrampulla* (Corethrales, Bacillariophyceae) from the Campbell Plataeu (Zealandia), southwest Pacific Ocean. *Diatom Research*, 37, 241-53.

Adl, S.M., Bass, D., Lane, C.E., Lukeš, J., Schoch, C.L., Smirnov, A., Agatha, S. et al. (2019). Revisions to the classification, nomenclature, and diversity of eukaryotes. *Journal of Eukaryotic Microbiology*, 66, 4–119.

Agardh, C.A. (1824). *Systema Algarum*. Litteris Berlingianis, Lundae.

Acs, É., Ari, E., Duleba, M., Dressler, M., Genkal, S.I., Jakó, E., Rimet, F., Ector, L. & Kiss, K.T. (2016) *Pantocsekiella*, a new centric diatom genus based on morphological and genetic studies. Fottea, 16(1): 56-78.

Alverson, A.J. & Theriot, E.C. (2005). Comments on recent progress toward reconstructing the diatom phylogeny. *Journal of Nanosciences and Nanotechnology*, 5, 57–62.

Alverson, A.J. (2008). Molecular systematics and the diatom species. *Protist*, 159, 339–53.

Alverson, A.J., Roberts, W.R., Ruck, E.C., Nakov, T., Ashworth, M.P., Bryłka, K., Downey, K.M. et al. (2025). Phylogenomics reveals the slow burning fuse of diatom evolution.

Alverson, A.J., Kang, S.-H. & Theriot, E.C. (2006). Cell wall morphology and systematic importance of *Thalassiosira ritscheri* (Hustedt) Hasle, with a description of *Shionodiscus* gen. nov. *Diatom Research* 21(2): 251-262

Ashworth, M.P., Lobban, C.S., Witkowski, A., Theriot, E.C., Sabir, M.J., Baeshen, M.N., Hajarah, N.H., Baeshen, N.A., Sabir, J.S. & Jansen, R.K. (2017). Molecular and morphological investigations of the stauros-bearing, raphid pennate diatoms (Bacillariophyceae): *Craspedostauros* E.J.Cox and *Staurotropis* T.B.B.Paddock, and their relationship to the rest of the Mastogloiales. *Protist*, 168(1), 48-70.

Ashworth, M.P., Majewska, R., Frankovich, T.A., Sullivan, M., Bosak, S., Filek, K., Van de Vijver, B., Arendt, M., Schwenter, J., Nel, R., Robinson, N.J., Gary, M.P., Theriot, E.C., Stacy, N.I., Lam, D.W., Perrault, J.R., Manire, C.K. & Manning, S.R. (2022). Cultivating epizoic diatoms provides insights into the evolution and ecology of both epibionts and hosts. *Scientific Reports*, 12, 15116.

APG. (1998). An ordinal classification for the families of flowering plants. *Annals of the Missouri Botanical Garden,* 85, 531–553.

APG II. (2003). An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. *Botanical Journal of the Linnean Society,* 141, 399–436.

APG III. (2009). An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Botanical Journal of the Linnean Society,* 161, 105–121.

Bory de Saint-Vincent, J.B.M. (1822-1831). *Dictionnaire Classique d'Histoire Naturelle*. Paris. Rey & Gravier, libraires-éditeurs; Baudouin Fréres, libraires-éditeurs. 17 volumes.

Bruder, K. & Medlin, L.K. (2008). Morphological and molecular investigations of naviculoid diatoms. II. Selected genera and families. *Diatom Research*, 23(2), 283-329.

Burliga, A.L., Kociolek, J.P., Salomoni, S.E. & D.Figueiredo. (2013). A new genus and species in the diatom family Eunotiaceae Kützing (Bacillariophyceae) from the Amazonian hydrographic region, Brazil. *Phytotaxa* 79(2): 47-57.

Cleve, P.T. (1895). Synopsis of the Naviculoid Diatoms. Synopsis of Naviculoid Diatoms. II. *KongligaSvenska-Vetenskaps Akademiens Handlingar*, 27(3), 1–219

Cox, E.J. (2015). Diatoms (Diatomeae, Bacillariophyceae s.l.). In Frey, W. [Ed.] Syllabus of Plant Families. A. Engler's Syllabus Der Pflanzenfamilien Part 2/1: Photoautotrophic Eukaryotic Algae: Glaucocystophyta, Cryptophyta, Dinophyta/Dinozoa, Haptophyta, Heterokontophyta/Ochrophyta, Chlorarachniophyta/Cercozoa, Euglenophyta/Euglenozoa, Chlorophyta, Streptophyta P.p. Borntraeger, Stuttgart, Germany, pp. 64–103.

Cox, E.J. & Van de Vijver, B. (2024). What constitutes a stigma? A review of isolated pores in raphid diatoms (Bacillariophyceae) and the value of precise terminology. *Journal of Phycology*, 60, 1498–513.

Dąbek, P., Ashworth, M.P., Górecka, E., Kkrzywda, M., Bornman, T.G., Sato, S. & Witkowski, A. (2019). Towards a multigene phylogeny of the Cymatosiraceae (Bacillariophyta, Mediophyceae) II: morphological and molecular insights into the taxonomy or the forgotten species *Campylosira africana* and of *Extubocellulus*, with a description of two new taxa. *Journal of Phycology*, 55(2), 425-441.

Dąbek, P., Sabbe, K., Witkowski, A., Archibald, C., Kurzydłowski, K. & Zgłobicka, I. (2013). *Cymatosirella* Dąbek, Witkowski & Sabbe gen. nov., a new marine benthic diatom genus (Bacillariophyta) belonging to the family Cymatosiraceae. *Phytotaxa*, 121(7), 42-56.

Danz, A., Kociolek, J.P., Van de Vijver, B., Kusber, W.-H., Guerrero, J.M., Vouilloud, A.A. & Sala, S.E. (2024). A morphology-based phylogeny of the diatoms formerly assigned to the Orthoseiraceae (Bacillariophyta): phylogenetic relationships, character analysis and classification. *European Journal of Phycology* 59(3): 290–310.

Donoghue, M.J., Doyle, J.A., Gauthier, J., Kluge, A.G. & Rowe, T. (1989). The importance of fossils in phylogeny reconstruction. *Annual Review of Ecology and Systematics*, 20, 431–60.

Downey, K.M., Julius, M.L., Theriot, E.C. & Alverson, A.J. (2021). Phylogenetic analysis places *Spicaticribra* within *Cyclotella*. *Diatom Research* 36(2): 93-99.

Frankovich, T.A., Ashworth, M.P., Sullivan, M.J., Theriot, E.C. & Stacy, N.I. (2018). Epizoic and apochlorotic *Tursiocola* species (Bacillariophyta) from the skin of Florida manatees (*Trichechus manatus latirostris*). *Protist* 169: 539-568.

Gastineau, R., Li, C., Ashworth, M.P., Witkowski, A., Turmel, M., Górecka, E., Frankovish, T.A., Wachnicka, A., Lobban, C.S., Theriot, E.C., Otis, C., Dabek, P., Binczewska, A. & Lemieux, C. (2022). A new insitught into *Amicula*, a genus of tiny marine benthic diatoms with the description of two new tropical species and the largest mitogenome known for a Stramenopile. *Frontiers in Marine Science*, 9, 941506.

Gauthier, J., Kluge, A.G. & Rowe, T. (1988). Amniote phylogeny and the importance of fossils. *Cladistics*, 4, 105–209.

Georgiev, A.A., Chudaev, D.A. Beljakova, G.A. & Gololobova, M.A. (2015). New data on the frustule morphology of rare species *Sichuaniella lacustris* (Bacillariophyceae). Novosti Sistematiki Nizshikh Rastenii 49, 5-12.

Gersonde, R. & Harwood, D.H. 1990. Barker, P. F, Kennett, J. P., et al. (1990). *Proceedings of the Ocean Drilling Program, Scientific Result*s, 113.

Gómez, F., Zhang, H., Navarrete-Carlos, T.C., Raymond, E., Tekle, Y.I., López-Osorio, Y.E., Salas, R., Alonso-Rodriguez, R. & Lin, S. (2025). Reinstatement of the genus *Coenobiodiscus* for the distinctive colonial diatom *Planktoniella muriformis* (Bacillariophyta). *Diatom Research*, 40(2), 121–132.

Gómez, F., Wang, L. & Lin, S. (2018). Molecular phylogeny suggests the affinity of the planktonic diatoms *Climacodium* and *Bellerochea* (Lithodesmiales, Mediophyceae). *Diatom Research*, 33(3), 349-54.

Gómez, F., Wang, L., Hernández-Becerril, D.U., Lisunova, Y.O., Lopes, R.M. & Lin, S. (2017). Molecular phylogeny suggests transfer of *Hemidiscus* into *Actinocyclus* (Coscinodiscales, Cosinodiscophyceae). *Diatom Research*, 32(1), 21-28.

Gregory, W. (1857a). On the Post-Tertiary Diatomaceous Sand of Glenshira. Part II. *Transactions of the Microscopical Society of London* 5:67-88.

Gregory, W. (1857b). On new forms of marine Diatomaceae found in the Firth of Clyde and in Loch Fyne, illustrated by numerous figures drawn by K.K. Greville, LL. D., F. R. S. E. *Transactions of the Royal Society of Edinburgh* 21:473-542.

Guerrero, J.M., Riaux-Gobin, C., Debandi, J.I., Zacher, K., Quartino, M.L. & Campana, G.L. (2021). Morphology of *Australoneis* gen. nov. and *A. frenguelliae* comb. nov. (Achnanthales, Bacillariophyta) from the Antarctic Peninsula. *Phytotaxa* 513(2), 81-98

Guiry, M.D. (2012). How many species of algae are there? *Journal of Phycology*, 48, 1057–63.

Guiry, M.D. (2024). How many species of algae are there? A reprise. Four kingdoms, 14 phyla, 63 classes and still growing. *Journal of Phycology* 60(2), 214-228.

Hendey, N.I. (1964). An Introductory Account of the Smaller Algae of British Coastal Waters. Part V:Bacillariophyceae (Diatoms). Her Majesty’s Stationery Office, London.

Hustedt, F. (1930a). Bacillariophyta (Diatomeae), In: A. Pascher (ed.) Die Süsswasser-Flora Mitteleuropas. Gustav Fischer, Jena. Zweite Auflage, Heft 10.

Hustedt, F. (1930b). Die Kieselalgen Deutschlands, Österreichs und der Schweiz unter Berücksichtigungder übrigen Länder Europas sowie der angrenzenden Meeresgebiete. In: L. Rabenhorst (ed.), *Kryptogamen Flora von Deutschland, Österreich und der Schweiz*. Akademische Verlagsgesell-schaft m.b.h., Leipzig, 7, 1, 4–5, 609–920.

Jordan, R.W. & Ligowski, R. (2004). New observations on *Proboscia* auxospores and validation of the family Probosciaceae fam. nov. *Vie Milieu* 54 (2-3) : 91-103.

Jovanovska, E., Hauffe, T., Stelbrink, B., Cvetkoska, A., Levkov, Z., Wagner, B., Lacey, J.H., Ognjanova-Rumenova, N., Hamilton, P.B., Brandenburg, K.M., Albrecht, C. & Wilke, T. (2022). Environmental filtering drives assembly of diatom communities over evolutionary time-scales. *Global Ecology & Biogeography* 31:954–967.

Kahlert, M., Kelly, M.G., Mann, D.G., Rimet, F., Sato, S., Bouchez, A. & Keck, F. (2019). Connecting the morphological and molecular species concepts to facilitate identification within the genus *Fragilaria* (Bacillariophyta). *Journal of Phycology*, 55(4), 948-70.

Karsten, G. (1928). Bacillariophyta (Diatomaceae), In: A. Engler and K. Prantl (eds) Die NatürlichenPflanzenfamilien, vol 2, 2nd ed. W. Englemann, Leipzig, pp. 105–303.

Kezlya, E., Glushchenko, A., Kapustin, D., Maltsev, Y., Doan-Nhu, H. & Kulikovskiy, M. (2024). *Stigmagloia lobbanii* gen. et sp. nov. (Bacillariophyceae, Mastogloiales), a new stigma-bearing diatom genus separated from *Mastogloia*. *Phytotaxa* 677 (1): 49–65.

Kociolek, J.P., Balasubramanian, K., Blanco, S., Coste, M., Ector, L., Liu, Y., Kulikovskiy, M. et al. (2025a). DiatomBase. Available at: http://www.diatombase.org/.

Kociolek, J.P., Sala, S.E., Guerrero, J., Uyua, N., Hamsher, S.E., Miller, S., Li, J. & Borsa, T. (2025b). Valve ultrastructure, systematics, and diversity of the Rhopalodiales. I. Introduction and consideration of morphological groups within the genus *Epithemia* Brébisson ex Kützing. *Nova Hedwigia,* 120, 109-185.

Kociolek, J.P., Danz, A., Amaral, M, Ikudaisi, C., Gleich, A. & Theriot, E.C. (2025c). Light and scanning electron microscopic observations on some freshwater fossil 'centric' diatoms from Szurdokpüspöki and Erdobenye, northern Hungary. *Nova Hedwigia* 121, 11–31.

Kociolek, J.P., Danz, A., Swenson, J., Thirouin, K., Williams, D.M. & Borsa, T. (2020). Taxonomy, valve ultrastructure nomenclature and a comparison of two species of Bacillariales from freshwaters of Puerto Rico. *Phytotaxa,* 468(2), 190-202.

Kociolek, J.P., You, Q., Yu, P., Li, Y, Wang, Y., Lowe, R. & Wang, Q. (2021). Description of *Gomphothidium* gen. nov., with light and scanning electron microscopy: a new freshwater monoraphid diatom genus from Asia. *Fottea* 21(1): 1-7.

Kociolek, J.P., Williams, D.M., Stepanek, J., Liu, Q., Liu, Y., You, Q., Karthick, B. et al. (2019). Rampant homoplasy and adaptive radiation in pennate diatoms. Plant Ecology and Evolution, 152, 131–41.

Kociolek, J.P., You, Q.-M, Wang, Q.-X. & Liu, Q. (2015). Consideration of some interesting freshwater gomphonemoid diatoms from North America and China, and the description of *Gomphosinica*, gen. nov. *Beihefte Nova Hedwigia* 144: 175-198,

Kociolek, J.P. & Stoermer, E.F. (1988). A preliminary investigation of the phylogenetic relationships of the freshwater, apical pore field-bearing cymbelloid and gomphonemoid diatoms (Bacillariophyceae). *Journal of Phycology*, 24, 377-85.

Kociolek, J.P. & Spaulding, S.A. (2003). Eunotioid and asymmetrical naviculoid Diatoms. In: Freshwater Algae of North America, Ecology and Classification. (Wehr, J.D. & Sheath, R.G. Eds), pp. 655-668

Komura, S. (1999). Barrel-shaped diatoms from the Miocene Nabuto Formation, central Japan. *Diatom*, 15, 51-78.

Krammer, K. (2003). *Cymbopleura*, *Delicata*, *Navicymbula*, *Gomphocymbellopsis*, *Afrocymbella*. In: Diatoms of Europe, Diatoms of the European Inland waters and comparable habitats. Vol. 4. (Lange-Bertalot, H. Eds), pp. 1-529. Rugell: A.R.G. Gantner Verlag K.G.

Kulikovskiy, M.S., Glushchenko, A.M., Genkal, S.I., Kuznetsova, I.V. & Kociolek, J.P. (2022). Revision of monoraphid diatom genus Platessa with description of Platesiberia gen. nov. from anciet Lake Baikal. *Water*, 14, 2957.

Kulikovskiy, M.S. Thacker, M. Glushchenko, A.M. Kuznetsova, I.V. Iurmanov, A.A. Karthick, B, Kociolek, J.P. (2023). *Gandhia* gen. nov.—A new diatom genus with unusual morphology split off from the genus *Navicula* Bory. *Plants* 12, 3941.

Kulikovskiy, M., Maltsev, Y., Andreeva, S., Glushchenko, A., Gusev, E., Podunay, Y., Ludwig, T.V. et al. (2019). Description of a new diatom genus *Dorofeyukea* gen. nov. with remarks on phylogeny of the family Stauroneidaceae. *Journal of Phycology*, 55, 173–85.

Kulikovskiy, M.S., Andreeva, S.A., Gusev, E.S., Kuznetsova, I.V. & Annenkova, N.V. (2016). Molecular phylogeny of monoraphid diatoms and raphe significance in evolution and taxonomy. *Biological Bulletin of the Russian Academy of Sciences,* 43, 398–407.

Kulikovskiy, M.S., Maltsev, Y.I., Glushchenko, A.M., Gusev, E.S., Kapustin, D.A., Kuznetsova, I.V., Frolova, L. et al. (2020). Preliminary molecular phylogeny of the diatom genus *Nupela* with the description of a new species and consideration of the interrelationships of taxa in the suborder Neidiineae D.G. Mann sensu E.J. Cox. *Fottea (Praha)*, 20, 192–204.

Levkov, Z., Metzeltin, D. & Pavlov, A. (2013). *Luticola* and *Luticolopsis. Diatoms of Europe* 7, 1-698.

Li, C., Ashworth, M.P., Mackiewicz, P., Dabek, P., Witkowski, J., Gorécka, E., Kryzwda, M. & Witkowski, A. (2020). Morphology, phylogeny, and molecular dating in Plagiogrammaceae family focused on *Plagiogramma-Dimeregramma* complex (Urneidophycidae, Bacillariophyceae). *Molecular Phylogenetics and Evolution*, 148, 106808.

Li, C., Witkowski, A., Ashworth, M.P., Dabek, P., Sato, S., Zglobicka, I., Witak, M., Khim, J.S. & Kwon, C-J. (2018). The morphology and molecular phylogenetics of some marine diatom taxa within the Fragilariaceae, including twenty undescribed species and their relationship to *Nanofrustulum*, *Opephora* and *Pseudostaurosira. Phytotaxa*, 355(1), 1-104.

Li, C., Ashworth, M.P., Witkowski, A., Lobban, C S., Zgłobicka, I., Kurzydłowski, K J. & Qin, S. (2016). Ultrastructural and molecular characterization of diversity among small araphid diatoms all lacking rimoportulae. I. Five new genera, eight new species. *Journal of Phycology* 52(6): 1018-1036.

Li, C.L., Ashworth, M.P., Witkowski, A., Dąbek, P., Medlin, L.K., Kooistra, W.H.C F., Sato, S., Zgłobicka, I., Kurzydłowski, K J., Theriot, E.C., Sabir, J.S.M., Khiyami, M.A., Mutwakil, M.H. Z., Sabir, M J., Alharbi, N S., Hajarah, N H., Qing, S. & Jansen, R.K. (2015). New insights into Plagiogrammaceae (Bacillariophyta) based on multigene phylogenies and morphological characteristics with the description of a new genus and three new species. *PLoS ONE* 10(10): e0139300.

Li, J., Mironov, A., Jiang, Y., Liang, J., Kociolek, J.P., Maltsev, Y., Fan, Y., Liu, Y. & Kulikovskiy, M. (2024). Molecular and morphological investigations of two new species in *Qinia* and *Cymbella* (Bacillariophyceae: Cymbellales) from China. *PLoS ONE* 19(12): e0314880.

Li, Y., Guo, X.-H., & Lundholm, N. (2020). Molecular phylogeny and taxonomy of the genus *Miniduscus* (Bacilalriophyceae) with description of *Mediolabrus* gen. nov. Journal of Phycology 56(6): 1443-1456.

Li, Y., Suzuki, H., Nagumo, T., Tanaka, J., Sun, Z. & Xu, K. (2022). Morphology, molecular phylogeny and systematics of the diatom genus *Fallacia* (Sellaphoracaeae), with descriptions of three new species. *Journal of Phycology*, 58(3), 449-464.

Li, Y., Williams, D.W., Metzeltin, D., Kociolek, J.P. & Gong, Z. (2010). *Tibetiella pulchra* gen. nov. et sp. nov., a new freshwater epilithic diatom (Bacillariophyta) from River Nujiang in Tibet, China. *Journal of Phycology* 46(2): 325-330.

Liu, Y., Kociolek, J.P., Wang, L., Lu, X., Zhu, H., Liu, G., Sui, F. & Fan, Y. (2024). A new diatom genus *Spargeria* gen. nov. (Bacillariophyceae) from Xizang, China, and the description of two new species. *Journal of Oceanography and Limnology* 42(1): 291-303

Lobban, C.S. (2023). *Disymmetrica reticulata, gen. nov., sp. nov.* (Mediophyceae: Thalassiosirales), a new

genus in Lauderiaceae emend., and transfer of *Lauderia excentrica*. *Diatom, 39*, 25-30.
Lobban, C.S & Tharngan, B.G. (2025). Benthic Marine Diatom Flora (Bacillariophyta) of Yap, Micronesia: Preliminary Annotated List, with Some New Mangrove Species. *Diversity* 17, 34
Lobban, C.S., Ashworth, M.P., Camacho, T., Lam, D.W. & Theriot, E.C. (2022). Revision of Ardissoneaceae (Bacillariophyta, Mediophyceae) from Micronesian populations, with descriptions of two new genera, *Ardissoneopsis* and *Grunowago*, and new species in *Ardissonea*, *Synedrosphenia* and *Climacosphenia*. *PhytoKeys*, 208, 103-84.
Lobban, C.S., Majewska, R., Ashworth, M.P., Bizsel, N., Bosak, S., Kooistra, W.H.C.F., Lam, D.W., Navarro, J.N., Pennesi, C., Sato, S., Van de Vijver, B. & Witkowski, A. (2021). Diatom genus *Hyalosira* (Rhabdonematales emend.) and resolution of its polyphyly in Grammatophoraceae and Rhabdonemataceae with a new genus, *Placosira*, and five new *Hyalosira* species. *Protist*, 172, 125816.
Lobban, C.S. & Navarro, J.N. (2013). *Gato hyalinus gen. et sp. nov*., an unusual tube-dwelling diatom from Western Pacific and Caribbean Islands. *Phytotaxa*, 127(1), 22-31.
Lobban. C.S. & Ashworth, M.P. (2014). *Hanicella moenia*, gen. et sp. nov., a ribbon-forming diatom (Bacillariophyta) with complex girdle bands, compared to *Microtabella interrupta* (Ehrenberg) F.E. Round and *Rhabdonema adriaticum* Kützing: implications for Striatellales, Rhabdonematales and Grammatophoraceae, fam. nov. *Journal of Phycology* 50: 860-884.
Lobban, C.S. & Reid, G. (2018). New *Arcuatasigma* species (Bacillariophyta, Pleurosigmataceae) from Guam and Belize, and the taxonomic identities of *Toxonidea challengeriensis* and its variety. *Phytotaxa*, 346(2), 169-79.
Lowe, R.L., Kociolek, P., Johansen, J.R., Van de Vijver, B., Lange-Bertalot, H. & Kopalova, K. (2014). *Humidophila gen. nov*., a new genus for a group of diatoms (Bacillariophyta) formerly within the genus *Diadesmis*: species from Hawai'i, including one new species. *Diatom Research*, 29:,351-360.
Lundholm, N., Moestrup, Ø., Kotaki, Y., Hoef-Emden, K., Scholin, C. & Miller, P. 2006. Inter- and intraspecific variation of the *Pseudo-nitzschia delicatissima* complex (Bacillariophyceae) illustrated by rRNA probes, morphological data and phylogenetic analyses. *Journal of Phycology.* 42, 464–81.
Majewska, R., Kociolek, J.P., Thomas, E.W., de Stefano, M., Santoro, M., Bolanos, F. & Van de Vijver, B. (2015). *Chelonicola* and *Poulinea*, two new gomphonemoid diatom genera (Bacillariophyta) living on marine turtles from Costa Rica. *Phytotaxa* 233(3): 236-250.
Mann, D.G., Trabajo, R., Sato, S., Li, C., Witkowski, A., Rimet, F., Ashworth, M.P., Hollands, R.M. & Theriot, E.C. (2021). Ripe for reassessment: a synthesis of available molecular data for the speciose diatom family Bacillariaceae. *Molecular Phylogenetics and Evolution,* 158, 106985.
Mann, D.G. & Vanormelingen, P. (2013). An inordinate fondness? The number, distributions, and origins of diatom species. *Journal of Eukaryotic Microbiology*, 60, 414–20.
Medlin, L.K. & Kaczmarska, I. (2004). Evolution of the diatoms: V. Morphological and cytological support for the major clades and a taxonomic revision. *Phycologia*, 43, 245–70.
Medlin, L.K., Kooistra, W.H.C.F., Gersonde, R. & Wellbrock, U. (1996). Evolution of the diatoms (Bacillariophyta). II. Nuclear-encoded small-subunit rRNA sequence comparisons confirm a paraphyletic origin for the centric diatoms. *Molecular Biology and Evolution*, 13, 67–75.
Medlin, L.K., Gersonde, R., Kooistra, W.H.C.F. & Wellbrock, U. (1996). Evolution of the diatoms (Bacillariophyta) II. Nuclear-encoded small-subunit rRNA sequence comparisons confirm a paraphyletic origin for the centric diatoms. *Molecular Biology and Evolution,* 13, 67 – 75.
Medlin, L.K., Sato, S., Mann, D.G. & Kooistra, W.H.C.F. (2008). Molecular evidence confirms sister relationship of *Ardissonea*, *Climacosphenia* and *Toxarium* within the bipolar centric diatoms (Bacillariophyta, Mediophyceae), and cladistic analyses confirm that extremely elongated shape has arisen twice in the diatoms. *Journal of Phycology,* 44(5), 1340-1348.

Medlin, L.K., Williams, D.M. & Sims, P.A. (1993). The evolution of the diatoms (Bacillariophyta). I. Origin of the group and assessment of the monophyly of its major divisions. *European Journal of Phycology*, 28, 261–75.

Mereschkowsky, C. (1902a). On the classification of diatoms. Annals Magazine of Natural History, series 7, 9, 65–68.

Mereschkowsky C. (1902b). Les types de l'endochrome chez les Diatomées. *Scripta Botanica Horti Universitatis (Imperialis)*, 21, 1–193.

Mironov, A., Maltsev, Y., Kociolek, J.P., Kezlya, E., Liu, Y. & Kulikovskiy, M. (2024). Description of Encyonemataceae fam. nov. and Witkowskiaceae fam. nov. (Bacillariophyceae, Cymbellales) based on molecular and morphological analyses. *Scientific Reports*, 14, 31045

Mongiardino Koch, N., Garwood, R.J. & Parry, L.A. 2021. Fossils improve phylogenetic analyses of morphological characters. *Proceedings of Biological Sciences*, 288, 20210044.

Nakov, T., Beaulieu, J.M. & Alverson, A.J. (2018a). Accelerated diversification is related to life history and locomotion in a hyperdiverse lineage of microbial eukaryotes (Diatoms, Bacillariophyta). *New Phytologist*, 219, 462–73.

Nakov, T., Beaulieu, J.M. & Alverson, A.J. (2018b). Insights into global planktonic diatom diversity: The importance of comparisons between phylogenetically equivalent units that account for time. *ISME Journal*, 12, 2807–10.

Nikolaev, V.A. & Harwood, D.M. (2000). Diversity and system of classification centric diatoms. In Witkowski, A & Sieminska, J [eds] The origin and early evolution of the diatoms: fossil, molecular & biogeographical approaches. W. Szafer Institute of Botany, Polish Academy of Sciences, Krakow.

Nikolaev, V.A. & Harwood, D.M. (2002). Morphology, taxonomy and system of classification of centric diatms. Nauka. St. Petersburg.

Patrick, R. and Reimer C.W. (1966). The diatoms of the United States, exclusive of Alaska and Hawaii,volume 1: Fragilariaceae, Eunotiaceae, Achnanthaceae, Naviculaceae. Academy of NaturalSciences of Philadelphia Monograph 13, Philadelphia, USA.

Petit, P. (1877). Liste des Diatomées et des Desmidiées observées dans les environs de Paris, précedée d'unessai de classification des Diatomées. Bulletin de la Société Botanique de France 23–24: 34–46.

Pfitzer, E. (1871). Untersuchungen uber Bau und Entwickelung der Bacillariaceen (Diatomaceen). Bonn,Adolf Marcus [as Heft 2 of J. Hanstein, Botanische Abhandlungen aus dem Gebiet der Morphologieund Physiologie. 1872].

Reid, G. (2012). A revision of the family Pleurosigmataceae (Bacillariophyta). pp. [1] 7-162 [163], 24 pls.. Ruggell: A.R.G. Gantner Verlag K.G.

Riaux-Gobin, C., Witkowski, A., Ruisjani, Y., Yunianta, Y., Berteaux-Lecellier, V., Kryk, A., Peszek, L. & Daniszewska-Kowalczyk, G. (2022). *Upsilococconeis dapalistriata* gen. nov & comb. nov. (Bacillariophyta) - a pantropical marine member of Cocconeidaceae. *Oceanological and Hydrobiological Studies* 51(1): 23-31.

Roberts, W.R. Ruck, E.C., Downey, K.M., Pinseel, E. & Alverson, A.J. (2023) Resolving marine-freshwater transitions by diatoms through a fog of gene tree discordance. *Systematic Biology,* 72(5): 984-997.

Round, F.E., Crawford, R.M. & Mann, D.G. (1990). *Diatoms: Biology and Morphology of the Genera.* Cambridge University Press. 747 pp.

Ruck, E.C. & Theriot, E.C. (2011). Origin and evolution of the canal raphe system in diatoms. *Protist*, 162, 723–37.

Sabir, J.S.M., Theriot, E.C., Lobban, C.S., Alhebshi, A.M., Al-Maki, A.L., Najrah, N.H., Khiyami, M.A., Obaid, A.Y., Jansen, R.K. & Ashworth, M.A. (2018). Systematics of araphid diatoms with asymmetric rimoportulae or densely packed virgae, with particular attention to *Hyalosynedra* (Ulnariaceae, Bacillariophyta). *Phytotaxa*, 347(1),1-49.

Sarno, D., Kooistra, W.H.C.F., Medlin, L.K., Percopo, I. & Zingone, A. (2005). Diversity in the genus

Skeletonema (Bacillariophyceae). II. An assessment of the taxonomy of *S. costatum*-like species with the description of four new species. *Journal of Phycology*, 41, 151–76.

Sato, S. & Mann, D.G. (2024). Morphology and life history of *Amphora commutata* (Bacillariophyta) II: Sexual reproduction and auxosporulation, with special reference to auxospore wall structures. *Phycologia*, 63:558–72.

Sato, S., Watanabe, T., Crawford, R.M., Kooistra, W.H.C.F. & Medlin, L.K. (2008). Morphology of four plagiogrammacean diatoms; *Dimeregramma minor* var. *nana*, *Neofragilaria nicobarica*, *Plagiogramma atomus* and *Psammogramma vigoensis* gen. et sp. nov., and their phylogenetic relationship inferred from partial large subunit rDNA. *Phycological Research* 56: 255–268.

Sawai, Y., Nagumo, T. & Nelson, A.R. (2016). A brackish diatom, *Pseudofrustulia lancea* gen. et sp. nov. (Bacillariophyceae), from the Pacific coast of Oregon (USA). *Phytotaxa* 267(2): 103-112

Silva, P.C. (1962). Classification of algae. In: R.A. Lewin (ed.), *Physiology and Biochemistry of Algae.* Pp. 823-837. Academic Press, New York.

Schütt, F. (1896). Bacillariales, In: A. Engler and K. Prantl (eds.) Die Natürlichen Pflanzenfamilien,vol. 1(1b). W. Englemann, Leipzig, pp. 31–153.

Simonsen, R. (1972). Ideas for a more natural system of the centric diatoms. Nova Hedwigia, Beiheft, 39, 37–54.

Simonsen, R. (1979). The diatom system: Ideas on phylogeny. *Bacillaria*, 2, 9–71.

Sims, P.A., Ashworth, M.A. Theriot, E.C. & Manning, S.R. (2023). Molecular and morphological analysis of Biddulphia sensu lato: a new diagnosis of Biddulphia, with a description of the new genera *Biddulphiella* and *Neobrighwellia*. *Marine Micropaleontology*, 178, 102186.

Sims, P.A., Mann, D.G. & Medlin, L.K. (2006). Evolution of the diatoms: Insights from fossil, biological and molecular data. *Phycologia*, 45, 361–402.

Sims, P.A., Williams, D.M. & Ashworth, M.A. (2018). Examination of type specimens for genera *Odontella* and *Zygoceros* (Bacillariophyceae) with evidence for the new family Odontellaceae and a description of three new genera. *Phytotaxa*, 382(1), 1-56.

Smith, H.L. (1872). Conspectus of the families and genera of the Diatomaceae. Lens 1: 1–19, 72–93,154–157.

Stepanek, J.G. & Kociolek, J.P. (2014). Molecular phylogeny of *Amphora sensu lato* (Bacillariophyta): An investigation into the monophyly and classification of amphoroid diatoms. Protist 165: 177-195.

Stepanek, J.G. & Kociolek, J.P. (2019). Molecular phylogeny of the diatom genera *Amphora* and *Halamphora* (Bacillariophyta) with a focus on morphological and ecological evolution. *Journal of Phycology,* 55, 442–56.

Stevens, P.F. (2015). *The Development of Biological Systematics.* Columbia University Press. 616 pp.

Sugawara, K., Kamiya, M., Osada, K. & Suzuki, H. (2024). Molecular phylogeny of the marine diatom genus *Druehlago* (Bacillariophyceae) from Japan. *Phycological Research*, 72(4), 231-37.

Theriot, E.C., Ashworth, M., Ruck, E., Nakov, T. & Jansen, R.K. (2010). A preliminary multigene phylogeny of the diatoms (Bacillariophyta): Challenges for future research. *Plant Ecology and Evolution*, 143(3), 278-96.

Thomas, E., Stepanek, J. & Kociolek, J.P. (2016). Historical and Current Perspectives on the Systematics of the 'Enigmatic' Diatom Genus *Rhoicosphenia* (Bacillariophyta), with Single and Multi-Molecular Marker and Morphological Analyses and Discussion on the Monophyly of 'Monoraphid' Diatoms. *PLoS One*, 11(4): e0152797.

Tuji, A., Mohri, Y., Ki, J-S., Jung, S.W. & Julius, M.L. (2014). Phylogeny of *Praestephanos* gen. nov. (Thalassiosirales, Bacillariophyceae) based on *Stephanodiscus suzukii*, and related freshwater thalassiosiroid diatoms. *Plankton & Benthos Research* 9(2): 132-140.

Usoltseva, M. & Titova, L. (2019). Morphological variability in *Alveolophora areolata* (Moisseeva) Moisseeva and *Alveolophora bifaria* Nevretdinova & Moisseeva. *Diatom Research* 34(1): 39-47.

Vigneshwaran, A., Liu, Y., Kociolek, J.P., & Karthick, B. (2021). A new species of *Epithemia* (Bacillariophyceae: Rhopalodiales) from the Mula River, Western Ghats, India, with comments on the phylogenetic position of the genera *Rhopalodia* and *Epithemia*. *Phytotaxa*, 489(2), 171-81.

Wetzel, C.E., Lange-Bertalot, H., Morales, E.A., Bicudo, D. De C., Hoffmann, ,L. & L. Ector. (2012). *Bicudoa amazonica* gen. nov. et sp. nov. (Bacillariophyta) a new freshwater diatom from the Amazon basin with a complete raphe loss in the Eunotioid lineage. *Phytotaxa* 75, 1-18.

Wetzel, C.E. & Kociolek, J.P. (2018). *Burliganiella* gen. nov. (Bacillariophyta, Eunotiales): another case of raphe reduction based on the type material of *Fragilaria siolii* Hustedt. *Cryptogamie Algologie* 39(2), 255-265.

Williams, D.M. (2020). Diatom classifications: What purpose do they serve? *In Modern Trends in Diatom Identification*. Springer International Publishing, Cham, pp. 11–24.

Williams, D.M. & Kociolek, J.P. (2007). Pursuit of a natural classification of diatoms: History, monophyly and the rejection of paraphyletic taxa. *European Journal of Phycology*, 42, 313–9.

Witkowski, J., Sims, P.A. & Harwood, D.M. (2011). Rutilariaceae redefined: a review of fossil bipolar diatom genera with centrally positioned linking structures, with implications for the origin of pennate diatoms. *European Journal of Phycology*, 46, 378-398.

Wojtal, A.Z. (2013). Species composition and distribution of diatom assemblages in spring waters from various geological formations in southern Poland. *Bibliotheca Diatomologica* 59, 1-436.

Xiang, Y., Kociolek, J.P., Wang, J, Xie, S. & Liu, Q. Accepted. Morphology, Phylogeny, and Chloroplast Genome of *Liparogyra sinensis* sp. nov. (Liparogyraceae), a New Species from Yunnan, China. Diatom Research.

Yana, E., Nakkaew, S., Pekkoh, J., Peerapornpisal, Y., Tuji, A., Davis, M.P., Julius, M.L. & Mayama, S. (2022). Valve and 'stigma' structure and phylogeny of an enigmatic cymbelloid diatom *Karthickia verestigmata* Glushchenko, Kulikovskiy & Kociolek, *Diatom Research* 37(3): 293-305.

Yu, P., Yang, L., You, Q., Kociolek, J.P., Wang, K., Bi, Y. & Wang, Q. (2023). *Lineaperpetua* gen. nov.: a new diatom genus in the Thalassiosirales supported by morphology and molecular data. *Journal of Oceanology and Limnology,* 42: 277-290

Appendix I. Formal Description of New Taxa with Putative morphological diagnoses of lineages

<u>Class</u>

Class: Corethrophyceae, class. nov.
Description: Frustules heterovalvate, with one valve, domed, possessing long bristles; the other valve, flat, has two types of spines. This clade is sister to all other diatoms. It was previously recognized at the rank of Subclass (Cox 2015).

Class: Leptocylindrophyceae, class. nov.
Description: Frustules elongated, narrow, tubular, with valves lacking processes. Central annulus evident. An eccentric opening located just outside the annulus. External periphery with small projections. Copulae scale-like. This clade is sister to all other diatoms except Corethrophyceae. It was previously recognized at the rank of Order (Round et al. 1990, Cox 2015).

Class: Melosirophyceae, class. nov.
Description: Valves with an elongated mantle. Forming chains, by ridges, spines or mucilage or occurring as single cells. Areolae variously formed, loculate with internal occlusions or rotae. Rimoportulae present, but usually not well developed. This clade includes *Melosira, Proboscia, Stephanopyxis, Hyalodiscus, Endictya* and *Paralia*. It is sister to all other diatoms except the Corethrophyceae and Leptocylindophyceae. The group was previously recognized at the rank of Order (Cox 2015).

Class: Thalassiosirophyceae, class. nov.
Description: Valves radial, bilateral or multipolar, with rimoportulae. Some taxa (Thalassiosirales) have special processes, fultoportulae, comprised of a central tube and smaller associated tubes around the periphery (satellite pores). Thalassiosirophyceae is sister all other diatoms except Corethrophyceae, Leptocylindrophyceae, Melosirophyceae and Coscinodiscophyceae. It was previously recognized at the rank of Subclass (Cox 2015).

Class: Biddulphiophyceae, class nov.
Description: Frustules with discoid chromatophores. Commonly form chains. Valves usually bi- to multi-angular, rarely circular. Chains produced by either mucilage exuded from pore fields or by linking spines. Rimoportulae typically present. This group is sister to all other diatoms except Corethrophyceae, Leptocylindrophyceae, Melosirophyceae, Coscinodiscophyceae, and Thalassiosirophyceae.

Class: Striatellaphyceae, class. nov.
Description: Valves symmetrical to apical and transapical axes. Striae with slit-like areolae oriented perpendicular to the narrow central sternum, each stria having areolae that are slightly offset from the adjoining striae. The sternum terminates at each end in a rimoportulae that is oriented to the apical axis. On the mantle at both poles is a defined pore field sunken slightly off the valve surface. Internally, the sternum is elevated and rimportulae are distinct but sessile, aligned about the apical axis. Numerous open copulae possess septa at their closed apex. Class Striatellaphyceae is the sister group to the clade of pennate diatoms that includes Plagiogrammophyceae, Fragilariophyceae, and Bacillariophyceae. This group was previously recognized at the rank of Order (Cox 2015).

Class: Plagiogrammaphyceae, class. nov.
Description: Frustules forming chains. Valves elongate-elliptical, with pore fields at both apices. Areolae extend across the face of the valve and have occlusions externally. Internally, costae may be present at central area and each apex bordering the pore field. Valves bordered by small spines. Rimoportulae near the valve apices, if present. Class Plagiogrammaphyceae is the sister group to the clade that includes Fragilariophyceae and Bacillariophyceae. This Class was previously recognized at the rank of Family

(Round et al. 1990, but within the Tricertiales), and Cox (2015) created a nomen nudum for the group at the rank of Order in the Fragilariophyceae.

Subclass

Subclass: Leptocylindrophycidae, subclass nov.
Description: Possesses all the characters of the Class Leptocylindrophyceae: frustules elongated, narrow, tubular, with valves lacking processes. Central annulus evident. An eccentric opening located just outside the annulus. External periphery with small projections. Copulae scale-like.

Subclass: Proboscidiphycidae, subclass nov.
Description: Elongated cells with areolate valves extended into a tapered funnel-like terminus, the proboscis. Rimoportula, if present, within proboscis.

Subclass: Melosirophycidae Cox, subclass nov.
Description: Elongated cells with convex or flat valves, rows of areolae often continuous from valve face to deep mantle. Cells form chains connected by linking spines.

Subclass: Ardissoniophycidae, subclass nov.
Description: Cells of diverse shape, including subcircular, bipolar, multipolar, and highly elongated. Cells with circular or elongated annulus.

Subclass: Eupodiscaphycidae, subclass nov.
Description: Cells mostly bi to multipolar in outline, possessing discoid chromatophores. Apical pore fields surrounded by hyaline border—ocellus or ocellulus—and rimoportulae present. Cingula many. Planktonic or attached.

Subclass: Attheyaphycidae, subclass nov.
Description: Frustules usually observed in girdle view. Valve face a shallow dome, with the face having a densely packed poroids, the margins with lightly silicified extensions. A single rimportula is positioned off-center on the valve face. Two short, apical extensions or horns occur one at each end of the valve. Cingulum with many copulae, open, each has many rows of poroids, each row with several poroids.
At present, this Subclass includes a single genus, *Attheya*.

Subclass: Tabellariaphycidae, subclass nov.
Description: Frustules solitary, or forming chains joined by mucilage at alternating apical pore fields on the valve. Valves elongate with distinct pore fields at one or both apices. Areolae extend across the face of the valve, interrupted by a thin transverse sternum and occluded externally. Internal costa present in many taxa. Rimoportulae associated with valve apices when present. Conspicuous septa typically present on porose copulae.

Subclass: Staurosiraphycidae, subclass nov.
Description: Frustules forming chains joined by mucilage at apical pore fields and by spines on the valve margin. Valves elongate-elliptical, with distinct pore fields at one or both apices on the valve mantle. Areolae extend across the face of the valve interrupted by thin-to-thick transverse sternum and occluded externally. When present, spines on the margin of valves associated with vimenes. Rimoportulae absent. This clade includes the order Staurosirales and is sister to the Thalassionematophycidae and Tabellariaphycidae.

<u>Order</u>

Order: Proboscidiales, ord. nov.

Description: Elongated cells with areolate valves that extend into a tapered funnel-like terminus, the proboscis. It is sister to a clade that includes Melosirales, Paraliales, and Stephanopyxales.

Typus: *Proboscia* Sundström 1986

Order: Trigoniumales, ord. nov.

Description: Frustules rectangular in girdle view, usually found in chains with discoid chromatophores. Valves rounded or prism-shaped. Valve face finely rugose, with sharp demarcation to the steep mantle. Areolae radiate from the center where the annulus and rimoportulae are present. When valve apices present, areolae of decreased size at the corners.

Typus: *Trigonium* Cleve

Order: Eucampiales, ord. nov.

Description: Frustules in chains formed by interlocking apical elevations of the valve face, forming a spiral configuration in many taxa. Chromatophores many, discoid. Valves elliptical to linear in shape, with a central annulus bearing a single rimoportula. Areolae radiate with complex cribra. At each end of the valves are perforated elevations that are poroids within series separated by ridges. The extensions are flattened at the terminus with a ring of short spines.

Typus: *Eucampia* Ehrenberg 1839

Order: Acanthoceratales, ord. nov.

Description: Frustules nearly always seen in girdle view. Valves with a tubular extension on each end of an elongate frustule, with a narrow isthmus between them. Simple areolae extend from the isthmus and up the cap until near the end of the tubular extensions which are solid spines. Girdle bands numerous, open, imbricating around the frustules. Planktonic in freshwater ecosystems.

Typus: *Acanthoceras* Honigmann 1909

Inferred Order: Hydroseratales, ord. nov.

Description: Frustules with numerous, small discoid chromatophores. Valves triangular to triundulate, forming chains of varying length by mucilage pads at the corners. Pseudocelli present at the corners or ends of the valves. Areolae loculate. Strong demarcation between the flat (but sometime rugose) face and the steep mantle. Rimoportulae with undulate internal opening prominent. Pseudosepta or internal ribs partition the valves.

Typus: *Hydrosera* Wallich 1858

Order: Attheyales, ord. nov.

Description: As for the Subclass.

Typus: *Attheya* T. West 1860

Order: Plagiogrammiales Cox, ord. nov.
Description: Frustules forming chains. Valve shape elliptical to elongate with distinct groups of pores apices, sometimes with transverse internal pseudosepta or ribs oriented transversely across the valve. Striae uniseriate. Areolae with external cribra, rimoportulae absent. Valvocopulae open and without pores. all other copulae open bands with single row of poroids.

Typus: *Plagiogramma* Greville 1859.

Order: Staurosirales, ord. nov.
Description: As for the Subclass.

Typus: *Staurosira* Ehrenberg 1843

Order: Amblyamphorales, ord. nov.
Description: Frustules rectangular in girdle view, with numerous cingulum elements, expressing amphoroid symmetry, i.e. the frustules are segment-like. Striae comprised of fine, round areolae in transverse rows. A raphe ledge is lacking. Axial area is distinct. Raphe is angled, from higher on the valve face at the apices and lower on the valve face towards the central nodule. Distal raphe ends may be bent towards either the dorsal or ventral margin.

Typus: *Amblyamphora* (Cleve) gen. nov.

Order: Diploneidales, ord. nov.
Description: Cells occurring singly, never in colonies, with 2 plate-like chloroplasts. Frustules planar, and valves symmetrical about the apical and transapical axes. A canal runs on either side of the raphe internally. Areolar structure variable, either elongated openings or small openings variable in shape externally, occluded by hymens internally. External proximal raphe ends usually dilated, distal ends deflected onto the valve mantle. This lineage is sister to the clade that includes Pinnulariales, Diadesmidales, Cocconeidales, Cymbellales, and Mastogloiales. This Order, currently represented by a single genus, was previously recognized as Diploneidineae D.G.Mann by Round et al. (1990) at the rank of Suborder.

Typus: *Diploneis* (Ehrenberg) Cleve 1894

Order: Sellaphorales, ord. nov.
Description: See the description of Sellaphorineae (Round et al. 1990, p. 657). This lineage of morphologically heterogenous taxa includes diatoms with unique protoplast features, shared by some members of the lineage, as well as morphological features that are shared by most taxa (e.g. a raphe system). Features of the girdle and areolae are highly variable among members of the group. It is recognized as the clade that is sister to the clades that include Diadesmidales, Cocconeidales, Cymbellales and Mastogloiales. This group was previous recognized at the level of suborder (Sellaphorineae D.G.Mann in Round et al.), but described based on the type genus, but not the others.

Typus: *Sellaphora* Mereschkowsky 1902

Order Diadesmidales, ord. nov.

Description: Small, individual cells or connected to each other by the valve faces to create chains. A single chromatophore is present. Symmertical about the apical and transapical axes. Valve shape linear, lanceolate, or elliptical. Striae uniseriate. Areolae circular or elongated transapically enclosed by hymens. Filiform raphe system with external proximal and distal ends often similar to each other, straight, sometimes in depressions.

Typus: *Diadesmis* Kützing 1844

Comments: This group contains a single genus and is sister to a clade that includes Cocconeidales and Cymbellales. *Diadesmis* previously included *Luticola*, and specimens of *Humidophila* Lowe et al. (2014 were also illustrated for *Diadesmis*. *Luticola* is now within the Stauroneidaceae, and the systematic position of *Humidophila* is unknown at present.

Order Cocconeidales Cox, ord. nov.
Description: Hetervalvate frustules; one valve bearing a raphe the other valve rapheless. Valves nearly circular to elliptical to linear in shape. Raphe simple or filiform, positioned in the middle of the valve or off to one side, straight or sigmoid. Areolae with internal hymenate occlusions. Cingulae non-porous.

Typus: *Cocconeis* Ehrenberg 1837

Comments: This group comprises species formerly identified as the "Monoplacatae" as described by Mereschkowsky [(1902b see Thomas et al. (2016)].

<u>Suborder</u>
Suborder: Surirellineae, subord. nov.
Description: Lineage with members forming 2 gametes per parent and having 2 auxospores oriented perpendicular to the parental cells. Most members have a canal raphe system, with the raphe elevated onto a keel. The canal can run around the circumference of the cells or along the main axis. Canal and keel absent in *Amphora* and *Halamphora*.

Comments: Members of this suborder were placed in 4 different orders in past classification systems (e.g. Round et al. 1990; Cox 2015), and the features shared by all members are related to features and outcomes of the sexual reproduction process, not the valve structures.

<u>Family</u>
Family: Lampriscaceae, fam. nov.
Description: Cells with deep mantles, multi-angular in shape due to presence of three or more large marginal pseudocelli for connection of adjacent cells into chains. A single genus, *Lampriscus*, is currently assigned to this family.

Typus: *Lampriscus* A. Schmidt 1882

Family: Hydroserataceae, fam. nov.
Description: Per the description for the Order.

Typus: *Hydrosera* Wallich 1858.

Family Amblyamphoraceae, fam. nov.
Description: Frustules rectangular in girdle view, with numerous cingulum elements, expressing amphoroid symmetry. Fine, round areolae in transverse rows. Raphe ledge is lacking. Axial area distinct. Raphe angled, from higher on the valve face at the apices and lower on the valve face towards the central nodule. Distal raphe ends may be bent towards either margin.

Typus: *Amblyamphora* (Cleve) gen. nov.

Comments: This family includes the former *Amphora laevissima* Gregory (1857a) and *Amphora obtusa* Gregory, two species that were shown by Stepanek & Kociolek (2014) to be sister taxa and comprising a lineage far removed from *Amphora* and *Halamphora* in the raphid diatom tree of life. Cleve (1895) and Stepanek & Kociolek (2014) indicated these two taxa (*A. laevissima* represented in Cleve as a variety of *A. laevis* Gregory, 1857) have different chloroplast morphologies and structure of the raphe.

Genus

Genus *Amblyamphora* (Cleve) gen. nov.
Description: As for the family.
Generitype: *Amblyamphora obtusa* (Gregory) comb. nov.
Basionym: *Amphora obtusa* Gregory 1857, p. 72, figure 34
Gregory, W. 1857. On the Post-Tertiary Diatomaceous Sand of Glenshira. Part II. Transactions of the Microscopical Society of London 5:67-88.

Amblyamphora laevissima (Gregory) comb. nov.
Basionym: *Amphora laevissima* Gregory 1857, p. 513, plate 12, fig. 72
Gregory, W. 1857. On new forms of marine Diatomaceae found in the Firth of Clyde and in Loch Fyne, illustrated by numerous figures drawn by K.K. Greville, LL. D., F. R. S. E. Transactions of the Royal Society of Edinburgh 21:473-542, pls. 9-14.

Comments: This name was originally established for a subgenus within *Amphora* by Cleve (1895). Stepanek and Kociolek (2014) showed this group was distinct from other taxa previously included in the genus *Amphora*.

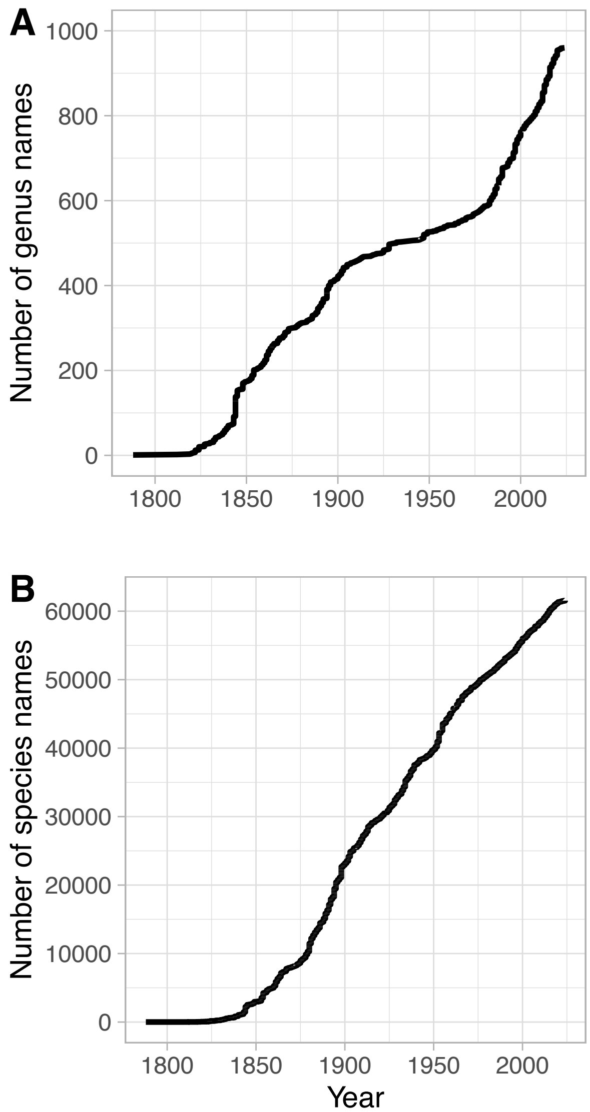

Figure 1. Publication of diatom genus (1A) and species (1B) names over time, based on data from Kociolek et al. (2025a).

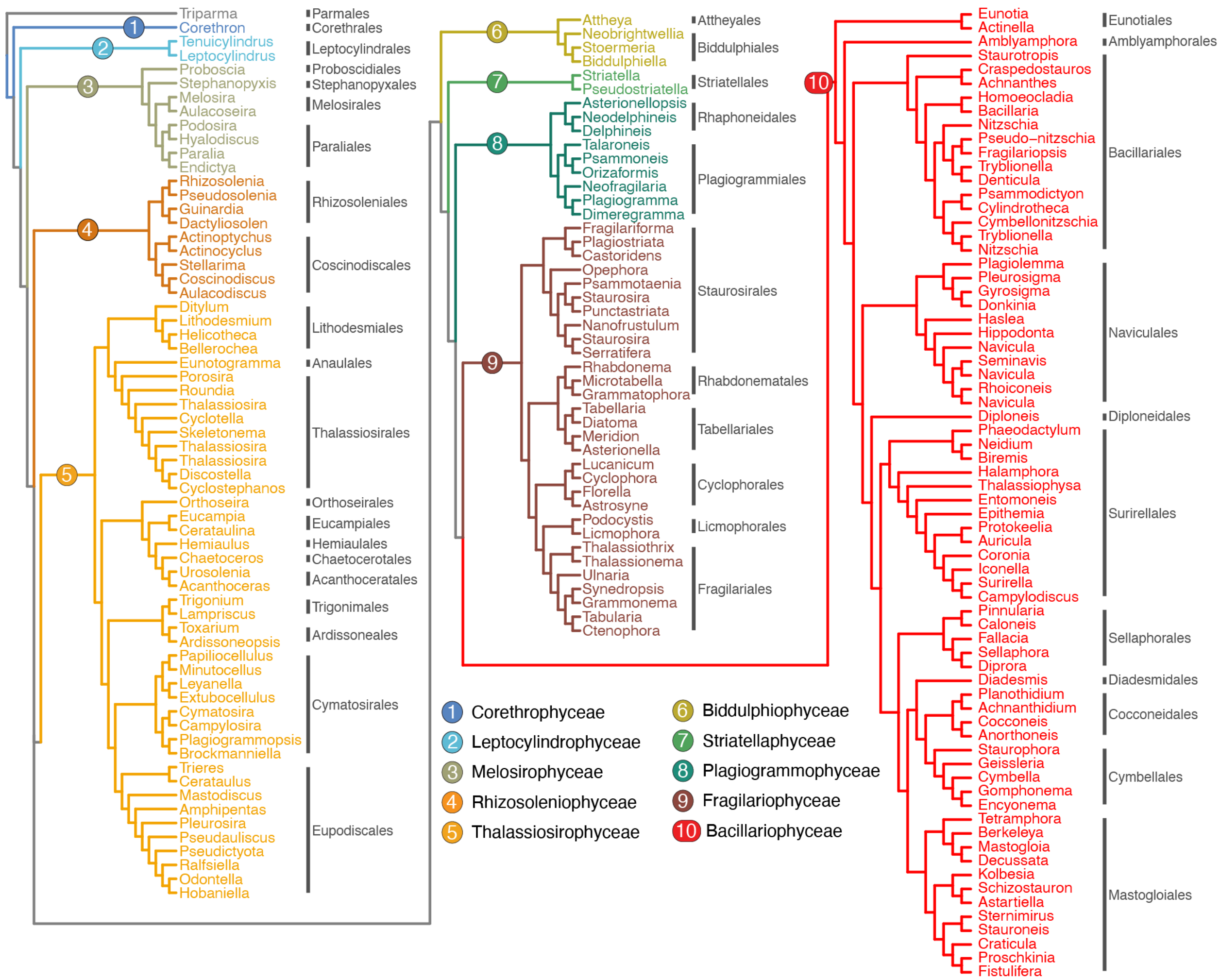

Figure 2. Genus-level phylogeny of diatoms based on Alverson et al. (2025). Phylogenetic positions of ten newly described taxonomic classes and 44 taxonomic orders present in the dataset of Alverson et al. dataset are shown. Some taxonomic orders are described herein based on other data and are not included in this tree.

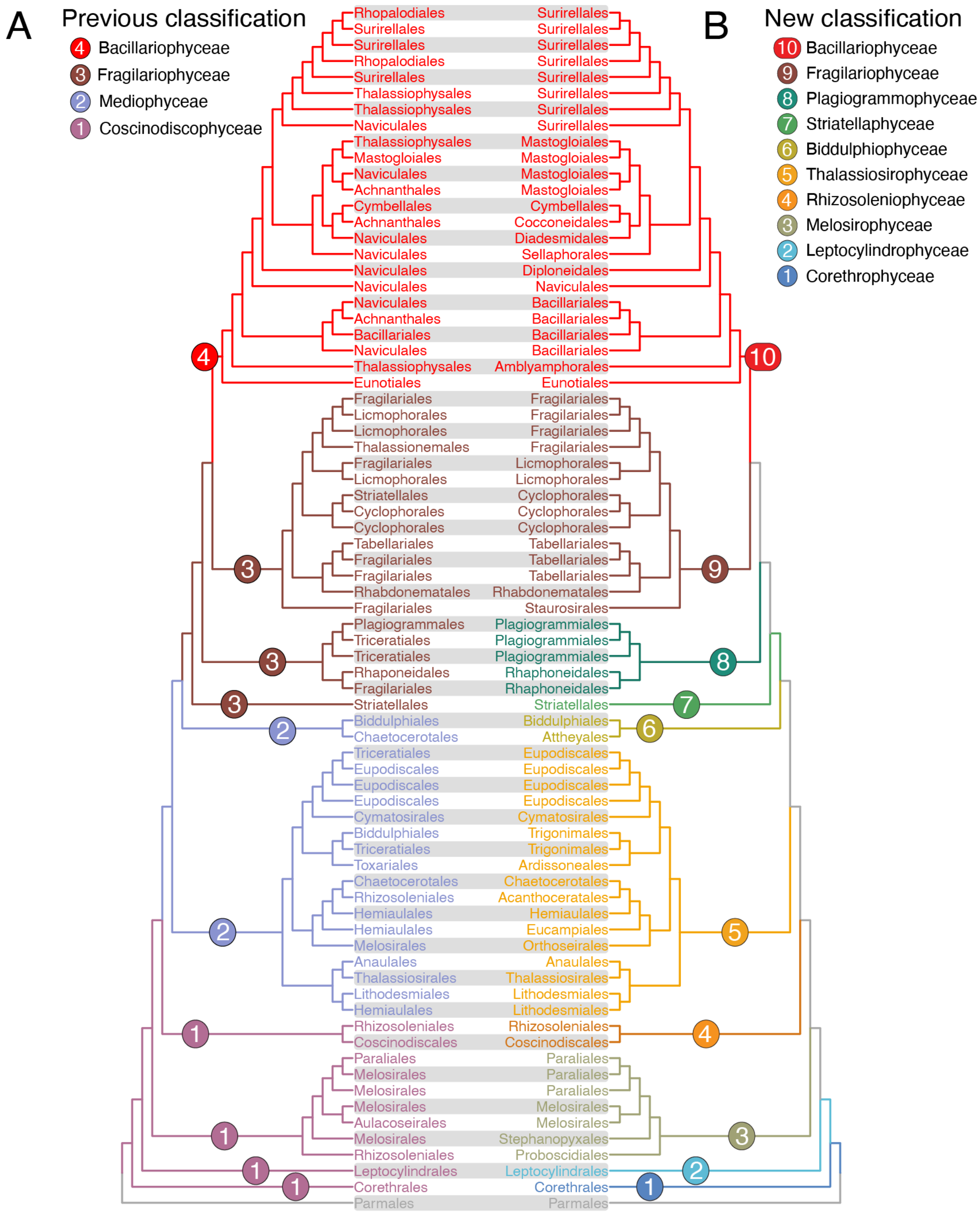

Figure 3. Comparison of the old (Cox 2015) and new classification systems, demonstrating the number of non-monophyletic groups in the older system (A) versus only monophyletic groups in the new classification (B). The phylogeny is based on Alverson et al. (2025).