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EDITED BY

Jin Sun,
Ocean University of China, China

REVIEWED BY

Daniele De Luca,
Anton Dohrn Zoological Station Naples, Italy
Romain Yves Olivier Gastineau,
University of Szczecin, Poland
Sang Deuk Lee,
Nakdonggang National Institute of Biological
Resources, Republic of Korea

*CORRESPONDENCE

JunMo Lee

✉ junmolee@knu.ac.kr

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Comparative analysis of organelle genomes provides conflicting evidence between morphological similarity and phylogenetic relationship in diatoms

YuJin Jeong¹ and JunMo Lee^{1,2*}

¹Department of Oceanography, Kyungpook National University, Daegu, Republic of Korea,

²Kyungpook Institute of Oceanography, Kyungpook National University, Daegu, Republic of Korea

Diatoms (Bacillariophyta) are abundant phytoplankton groups in marine environments, which contribute approximately 20% of global carbon fixation through photosynthesis. Moreover, diatoms exhibit the highest species diversity (approximately 18,000 diatom species) among marine photosynthetic eukaryotes, which were identified by morphological characteristics. Molecular phylogenetic analyses could shed new insights into the evolutionary relationships of diverse diatom species. Nevertheless, a comprehensive understanding of the phylogenetic relationships of diatom species still remains unclear because the available molecular data are insufficient compared with their high species diversity. Furthermore, several novel diatom species were reported from field samples with no molecular evidence. In particular, the phylogenies of diatom species constructed using organelle genomes revealed that several diatom genera are paraphyletic with high supporting values. We constructed high-resolution phylogenetic trees of diatom species using organelle genomes (plastids and mitochondria) and compared the morphologies in several paraphyletic diatom genera. Especially, the clades *Nitzschia* and *Thalassiosira* include several different diatom genera with high phylogenetic supports. Our study demonstrated that some morphological characteristics (e.g., genus characters) of several diatom genera could not represent current genus boundaries. Based on the results, we highlight the necessity for taxonomic reinvestigation. To reestablish this in diatoms, it will be essential to incorporate more genome data from a broader range of taxon samples, along with a comparison of morphological characteristics.

KEYWORDS

diatom, *Nitzschia*, organelle genome, multigene phylogeny, genus boundary

1 Introduction

Diatoms (Bacillariophyta) are unicellular photosynthetic eukaryotes widely distributed in marine environments (Mann et al., 2017). A total of 18,374 diatom species have been reported based on morphological characteristics (Hasle and Syvertsen, 1997; Finkel and Kotrc, 2010), which indicates the highest species diversity among photosynthetic algae (e.g., red algae: 7,538, green algae: 7,766, and brown algae: 2,120; Algaebase; Guiry and Guiry, 2023). Nonetheless, a comprehensive understanding for molecular phylogenies of diatom species still remains unaddressed because available molecular data (e.g., molecular markers and organelle genomes) is insufficient to construct a high-resolute phylogenetic tree of diatom species despite their high species diversity (Visco et al., 2015; Wang et al., 2022a). Furthermore, several novel diatom species were reported with no molecular evidence because they were observed from field samples (Kryk et al., 2021; Kulikovskiy et al., 2021). Mann et al. (2021) mentioned about controversial molecular data from morphologically unverified diatom species, which are available in the public databases (e.g., NCBI). Therefore, to establish their phylogenetic relationships, sufficient molecular data are required from morphologically verified diatom species.

Genomic studies are increasingly in diverse taxa due to the significantly reduced costs of genome sequencing approaches (e.g., next-generation sequencing technologies). As a result, huge amounts of genomic information are currently available. The phylogenetic analysis using single or several nuclear marker genes generally show insufficient phylogenetic resolution with low support values (Winchell et al., 2004; Bruder and Medlin, 2007; Dong et al., 2010). In addition, nuclear genetic variation could result from hybridization and introgression through sexual reproduction (Baack and Rieseberg, 2007; Colbeck et al., 2011; Harrison and Larson, 2016). In contrast, the organelle genomes are maternally inherited, and as a result, they generally have conserved gene contents, which are useful for phylogenetic studies (Timmis et al., 2004; Lee et al., 2016; Liu et al., 2021). In addition, the organelle genomes are relatively easier to handle in the generation and analysis of sequencing data compared to complete nuclear genome data (Cunha et al., 2009; Song et al., 2016). Consequently, the organelle genomes have much more available data than complete nuclear genomes. In diatoms, for example, 141 plastid and 81 mitochondrial genomes were reported in the NCBI database, while complete nuclear genomes were reported from only seven species (November 2023; NCBI database). Phylogenetic analyses using concatenated genes from organelle genomes could provide high-resolution phylogenetic relationship in diverse taxa (Lemieux et al., 2007; Lee et al., 2016; Jeong and Lee, 2021; Liu et al., 2021). Through these phylogenetic approaches, traditionally established taxonomic relationships were revised in several taxonomic groups (Wang et al., 2022b; Park et al., 2023). To study phylogenetic relationships in diatom species, therefore, current studies have been frequently conducted using organelle genome (Jeong and Lee, 2021; Wang et al., 2022a). Interestingly, the phylogeny analysis using organelle genomes shows that several diatom genera exhibit paraphyletic relationships with high

phylogenetic support values (Liu et al., 2021; Wang et al., 2022a). For instance, the genus *Nitzschia* are paraphyletic with respect to the genera *Cylindrotheca*, *Pseudo-nitzschia*, and *Fragilariopsis* (Wang et al., 2022a). In particular, the genus *Nitzschia* exhibits a high species diversity among diatom genera (878 *Nitzschia* species are reported; Algaebase; Guiry and Guiry, 2023). To better understand the phylogenetic relationships in diatoms, more organelle genome data are required in diverse diatom taxa. However, the number of available organelle genomes is still insufficient to cover their high species diversity, estimated at about 100,000 species (Mann et al., 2017). In addition, further discussion is required to address the conflict between phylogenetic relationships and morphology-based genus boundaries.

In this study, we newly report the complete organelle genomes (plastids and mitochondria) from *Entomoneis umbratica*, *Navicula avium*, *Pleurosigma inscriptura*, *Nitzschia dissipatoides*, *Nit. anomalus* sp. nov., and *Nit. reversa* var. *latus* var. nov. We constructed multigene phylogenies using available organelle genomes of diatom species, and discussed about the morphological similarity in several diatom genera, which exhibit paraphyletic with high phylogenetic supports. We suggest a potential for taxonomic revisions of the diatom taxa (or genera).

2 Materials and methods

2.1 Collection and observation of diatom species

Target diatoms were collected from field samples in Korean coastal waters. *Entomoneis umbratica* (MEG002), *Navicula avium* (MEG004), *Pleurosigma inscriptura* (MEG005), and *Nitzschia reversa* var. *latus* (MEG012) were isolated from Gijang (Busan, Korea; 35°21'82.93"N, 129°22'97.99"E) on June 12, 2020. *Nit. anomalus* (MEG011) and *Nit. dissipatoides* (MEG028) were isolated from Homigot (Pohang, Korea; 36°02'19.1"N 129°34'49.4"E; May 17, 2020) and Shinan-gun (Jeollanam-do, Korea; 34°83'20.36"N, 126°36'64.67"E; December 5, 2020), respectively (Figure 1). Single-cell isolation method was performed using customized Pasteur pipettes (glass) under light microscopic observation. The isolated strains were cultured in L1 medium at 20°C (Marine Ecological Genomics Lab. at Kyungpook National University).

The morphological characteristics of the target diatoms were observed using a light microscope (LM; Nikon ECLIPSE Ni-U, Nikon, Tokyo, Japan), scanning electron microscope (SEM; Hitachi SU8220; Hitachi Ltd., Tokyo, Japan), and transmission electron microscope (TEM; Hitachi HT7700, Hitachi Ltd., Tokyo, Japan). The diatom cultures were fixed with 2.5% glutaraldehyde, and the organic matters of diatom cells were removed using sodium hypochlorite (NaClO; Vilhena et al., 2021). The type specimens (permanent slides) of diatom cells (*Nit. anomalus* sp. nov. MABIK DI00043462 and *Nit. reversa* var. *latus* var. nov. MABIK DI00043463) prepared in this study were deposited to the National Marine Biodiversity Institute of Korea (MABIK; <http://www.mabik.re.kr>).

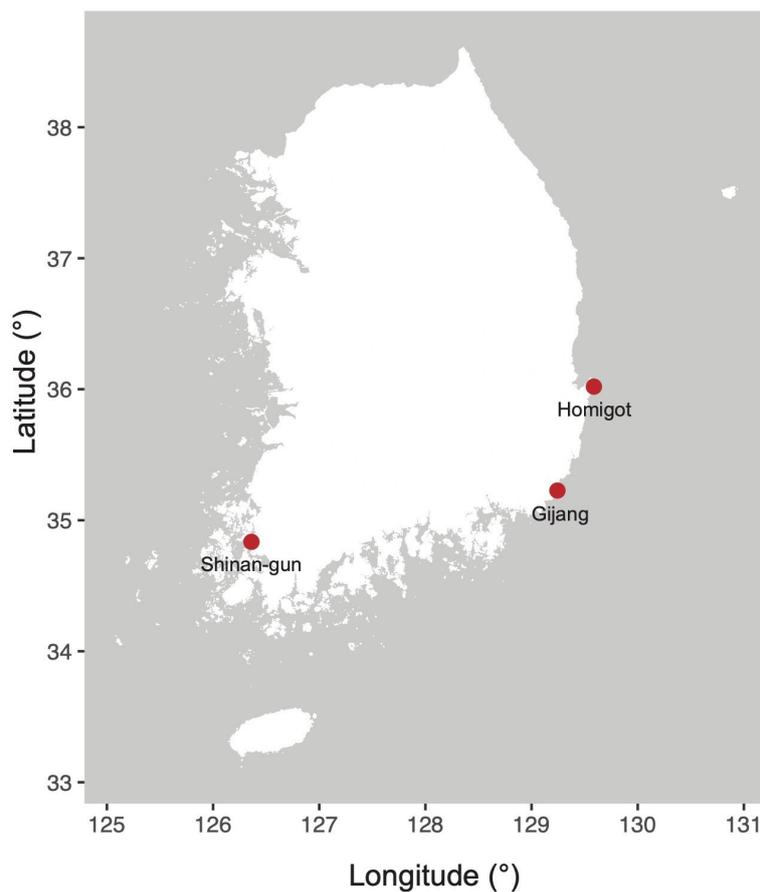


FIGURE 1
Sampling locations (South Korea) in this study.

2.2 DNA sequencing, genome assembly, and organelle genome analysis

Genomic DNA was extracted using the DNeasy Plant Mini kit (Qiagen, Hilden, Germany) according to the manufacturer's protocol. Genome sequencing was performed using Illumina Novaseq 6000 (Illumina, San Diego, CA; 150 bp paired-end library), and the sequencing raw reads were assembled using SPAdes assembler (v3.14.2; Bankevich et al., 2012). To predict 18S rDNA regions from the assembled genomes, local BLASTn searches (e -value cutoff = $1.e-05$) were performed with 18S rDNA sequences of *Phaeodactylum tricornutum* (JF489968.1).

Organelle (plastid and mitochondrion) contigs were selected by local BLASTn search (e -value cutoff = $1.e-05$) using their comparable organelle genomes (MF997419.1, NC056793.1, MT383639.1, NC038001.1, NC056794.1, and MW971520.1), and reassembled as circular organelle genomes using Geneious Prime (v2023.0.4). Protein-coding regions in the organelle genomes were manually predicted by BLASTx search (NCBI nr database; e -value cutoff = $1.e-05$) with codon table 11 (plastid) and 4 (mitochondria), and annotated using Geneious Prime (v2023.0.4). Transfer RNAs (tRNAs) and ribosomal RNAs (rRNAs) were analyzed using tRNA scan-SE 2.0 (Lowe and Chan, 2016; Chan and Lowe, 2019) and barnap 0.9 (<https://github.com/tseemann/barnap>), respectively.

2.3 Phylogenetic analysis

The 18S rDNA phylogenies were constructed using the BLASTn top 1,000 hits (e -value cutoff = $1.e-05$; NT database in NCBI) of 18S rDNA sequences from the target diatoms, excluding unclassified strains (Supplementary Figures S1–S4).

A total of 147 plastid and 86 mitochondrial genomes were used in this study (Supplementary Tables S1, S2). Homologous groups of organelle genes were identified by local BLASTp search (e -value cutoff = $1.e-05$). Each homologous gene set was aligned using MAFFT (v7.313; Katoh and Toh, 2008) with the default options. Concatenated alignments were constructed using 123 plastid and 34 mitochondrial genes, respectively. Maximum-likelihood (ML) trees constructed using each concatenated alignment were analyzed using the IQ-tree program (v1.6.12; Nguyen et al., 2015) with the following options: gene partition information (-q), model test (-m TEST), and ultrafast bootstrapping with 1,000 replications (-bb 1,000).

2.4 Comparisons of morphological characteristics of diverse diatom genera

To clearly distinguish morphological features, we compared six target diatoms with their morphologically similar counterparts as

follows: *E. umbratica* MEG002 was compared with *E. umbratica*, *E. infula*, *E. adriatica*, *E. punctulate*, *E. tenera*, *E. gracilis*, *E. pusilla*, and *E. vilicicii* (Osada and Kobayasi, 1990; Mejdandžić et al., 2017; Mejdandžić et al., 2018). *Navicula avium* MEG004 was compared with *N. avium*, *N. babeiensis*, *N. pseudokuseliana*, *N. coraliana*, *N. nielsfogedii*, *N. bergstromiana*, *N. kuseliana*, *N. serotina*, and *N. zanonii* (Hustedt, 1949; Metzeltin and Lange-Bertalot, 1998; Rumrich et al., 2000; Kulikovskiy et al., 2012; Taylor et al., 2016; Li et al., 2017a; Sabbe et al., 2019; Chudaev et al., 2020; Kulikovskiy et al., 2021). *P. inscriptura* MEG005 was compared with *P. inscriptura*, *P. obtusum*, *P. strigosum*, *P. rigidum*, and *P. williamsii* (Sterrenburg, 2001; Reid, 2002; Stidolph, 2002; Sterrenburg, 2003; Harper et al., 2009). *Nit. reversa* var. *latus* MEG012 was compared with *Nit. reversa*, *Nit. droebakensis*, *Nit. gobbii*, *Nit. acicularis*, *Nit. decipiens*, *Nit. draveillensis*, *Nit. kavirondoensis*, *Nit. longissima*, and *Nit. ventricosa* (Cleve and Grunow, 1880; Smith, 1853; Hasle, 1964; Coste and Ricard, 1980; Hasle and Syvertsen, 1997; Sitoki et al., 2013; Giulietti et al., 2021). *Nit. dissipatoides* MEG028 was compared with *Nit. dissipatoides*, *Nit. erosa*, *Nit. thienemanni*, *Nit. fragilariiformis*, *Nit. hybridaeformis*, *Nit. pseudoamphioxys*, *Nit. serrata*, *Nit. yunchengensis*, and *Nit. albicostalis* (Hustedt, 1938; Hustedt, 1942; Bourrelly and Manguin, 1952; Hustedt, 1955; Giffen, 1966; Archibald, 1982; Compère, 1986; Li and Volcani, 1987; Shu-qi and Ting, 1994). *Nit. anomalus* MEG011 was compared with *Nit. nanodissipata*, *Nit. volvendirostrata*, *Nit. aestatis* (Giffen, 1973; Witkowski et al., 2016).

To visualize and compare the morphological characteristics of paraphyletic diatom genera, we redrew the illustrations of several representative diatom species based on their previously reported morphological descriptions and images as follows: *Pseudo-nitzschia simulans* (Li et al., 2017b; Ajani et al., 2020), *Pseudo-nitzschia micropora* (Priisholm et al., 2002; Rivera-Vilarelle et al., 2013), *Pseudo-nitzschia multiseriata* (Hasle, 1995; Evans et al., 2004), *Pseudo-nitzschia pungens* (Lim et al., 2012; Kim et al., 2015), *Pseudo-nitzschia americana* (Lundholm et al., 2002a; Rivera-Vilarelle et al., 2013), *Fragilariopsis cylindrus* (Von Quillfeldt, 2001; Cefarelli et al., 2010), *Nitzschia inconspicua* (Sonneman et al., 2000; Trobajo et al., 2013), *Nitzschia alba* (Lewin and Lewin, 1967), *Nitzschia palea* (Crowell et al., 2019; Wang et al., 2020), *Cylindrotheca closterium* (Reimann and Lewin, 1964; Ryabushko et al., 2019), *Tryblionella apiculata* (Gregory, 1857; Yamamoto et al., 2017), *Psammodictyon constrictum* (Yamamoto et al., 2017), *Nitzschia traheaformis* (Witkowski et al., 2016), *Nitzschia dissipatoides* (Archibald, 1982; this study), *Bacillaria paxillifer* (*B. paxillifera*; Jahn and Schmid, 2007), *Skeletonema marinoi* (Jung et al., 2009), *Thalassiosira nordenskiöldii* (Cleve, 1873; Shevchenko et al., 2020), *Discostella pseudostelligera* (Houk and Klee, 2004; Guerrero and Echenique, 2006), *Minidiscus spiculatus* (Li et al., 2020), *Cyclotella tecta* (Prasad and Nienow, 2006), *Thalassiosira pseudonana* (Horvát et al., 2021), and *Conticribra weissflogii* (Cavalcante et al., 2013).

3 Results and discussion

We classified and described the morphological characteristics of six diatom species (*E. umbratica*, *N. avium*, *P. inscriptura*, *Nit.*

reversa var. *latus*, *Nit. dissipatoides*, and *Nit. anomalus*), which are observed using LM, SEM, and TEM (See Methods). We also conducted phylogenetic analyses of 18S rDNA sequences from the target diatoms to discuss the molecular taxonomy of the target species.

3.1 Morphological descriptions of six diatom species

3.1.1 *Entomoneis umbratica* Mejdandžić & Bosak 2018

One multilobed plate plastid was observed in the central region of living cells (Figure 2A). Frustules are panduriform, with a markedly constricted bilobate keel in the middle part of the valve (Figure 2B). Cells are torsional around the apical axis and have numerous girdle bands (Figure 2C). The valve shape is linear-lanceolate, with a length (apical axis) of 18–32 μm (avg. 24 μm , $n = 100$) and a width (transapical axis) of 8–15 μm (avg. 11 μm , $n = 100$; Figure 2C). Striae density in the valve and keel was observed 45 in 10 μm (Figure 2D). Striae are closed by hymens with parallel-located roundish-to-elliptical perforations (Figure 2E). The copula and valve copula have similar ultrastructure, showing 47 striae in 10 μm (Figure 2F; Mejdandžić et al., 2018).

Entomoneis umbratica (MEG002) demonstrated similar valve outlines with those of *E. infula* and *E. adriatica*, but its cell length (apical axis) and valve width (transapical axis) were larger than those of others (Supplementary Table S3). Moreover, the striae in *E. infula* and *E. adriatica* were denser than those *E. umbratica* (Supplementary Table S3). The BLASTn search of *E. umbratica* (MEG002; OR398973) revealed 99.88% identity with the 18S rDNA sequences of *E. umbratica* (MF000604.1), and their phylogenetic analysis with homologous sequences (top 500 matches of BLASTn search, e -value cutoff = $1.e-05$) revealed a monophyletic clade of *Entomoneis* species (Supplementary Figure S1).

3.1.2 *Navicula avium* (M.A.Tiffany, Herwig & Sterrenburg) Yuhang Li & Kuidong Xu 2017

The valve shape is narrowly lanceolate with acute apices, and the valve has a straight raphe (Figures 3A–C). Cells are 20–27 μm (avg. 24 μm , $n = 100$) in length and 7–11 μm (avg. 11 μm , $n = 100$) in width (Figures 3C, D). The external valve face exhibits continuous longitudinal strips and two pore-like extensions at the external central raphe endings (Figures 3D, E). In the internal valve view, the accessory rib is parallel to the raphe slit (Figure 3F). Small helictoglossae are found at the tip of the terminal raphe slits, and the region around helictoglossa is thickened with three pores (Figure 3G). The transverse striae are arranged parallel or radiate, and their density is 12 in 10 μm with apically elongated linear areola (Sterrenburg et al., 2015; Li et al., 2017a).

Navicula avium (MEG004) displays a smaller cell size (20–27 μm) than previously reported *N. avium* (Li et al., 2017a; 32.4–62.5 μm), but their 18S rDNA sequences are identical (Supplementary Table S4); hence, the difference is considered cell size variation in *N. avium*. The valve outlines of *N. avium* and *N. babeiensis* are similar (narrowly lanceolate with broadly rounded), but the shape of the valve apices in

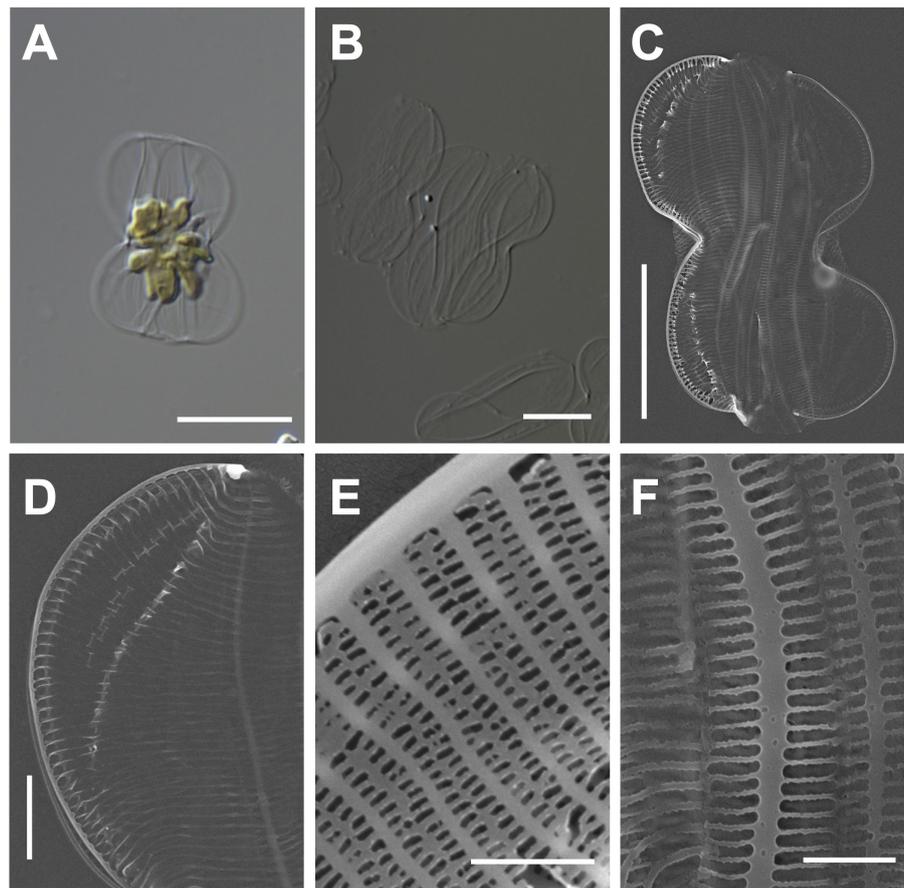


FIGURE 2

Light and electron microscopic images of *Entomoneis umbratica* (MEG002). (A) Panduriform frustule containing one multilobed plate plastid. (B) Cleaned frustules. (C) Numerous girdle bands in the external valve view. (D) Keel structures. (E) Striae with parallel-located roundish-to-elliptical perforations (F) Valvocopula structures. Scale bars: (A, B) = 5 μm , (C) = 10 μm , (D) = 2 μm , and (E) = 0.5 μm .

N. babeiensis is slightly subrostrate (Supplementary Table S4). Moreover, the striae density in 10 μm of *N. avium* (7–11) was lower than that of *N. babeiensis* (17–19; Supplementary Table S4). The phylogenetic analysis conducted using the 18S rDNA sequences of *N. avium* (MEG004; OR398987) with homologous sequences (top 500 matches of BLASTn search, e -value cutoff = $1.e-05$) revealed a monophyletic clade of *N. avium* (Supplementary Figure S2).

3.1.3 *Pleurosigma inscriptura* M.A.Harper 2009

Cells have lanceolate valves with rounded apices and sigmoid raphe with a 3.6° raphe angle (Figures 4A–C). Cells measure 104–115 μm (avg. 111 μm , $n = 100$) in length and 15–25 μm (avg. 4 μm , $n = 100$) in width. Each cell has a small oval central nodule with no hyaline (Figure 4D). Transverse striae are 20 in 10 μm . The internal polar raphe ends appear as small triangles (Figure 4E; Harper et al., 2009; Jeong and Lee, 2021).

Pleurosigma inscriptura (MEG005) shows a similar size as that of *P. obtusum*, but *P. obtusum* exhibits a rhombic valve shape (Supplementary Table S5). The BLASTn search of 18S rDNA sequences of *P. inscriptura* (MEG005; OR398989) revealed 97.90% identity with the 18S rDNA sequences of *Pleurosigma* sp. (KX981840.1), and their phylogenetic analysis with homologous

sequences (top 500 matches of BLASTn search, e -value cutoff = $1.e-05$) revealed a monophyletic clade of *P. intermedium* (Supplementary Figure S3).

3.1.4 *Nitzschia reversa* var. *latus* Jeong & Lee var. nov.

Cells are 38–50 μm (avg. 46 μm , $n = 100$) in length and 2–5 μm (avg. 4 μm , $n = 100$) in width (Figures 5A, B). The valve outline is lanceolate-fusiform with a slightly sigmoid and subrostrate shape (Figures 5C, D). The raphe ends are slightly curved at the poles, and the raphe canal is eccentric (Figures 5C, D). The striae of cells are 54 in 10 μm , and square poroids with rounded corners are 7 in 1 μm with finely perforated areolae (Figures 5D–F). Fibulae are randomly arranged as 9–15 in 10 μm , and the interval in the middle part is particularly wide (Figure 5G). Helictoglossae were observed at the tip of the terminal raphe slits (Figure 5H). The central nodule is visualized in the internal view (Figure 5I).

Etymology: The name refers to a distinctly wider interval between fibulae than that in *Nitzschia reversa*.

Comparison with similar species: The morphology with a lanceolate central portion and fine protrusions is commonly found in the genus *Nitzschia* (Hasle, 1964; Giuliotti et al., 2021).

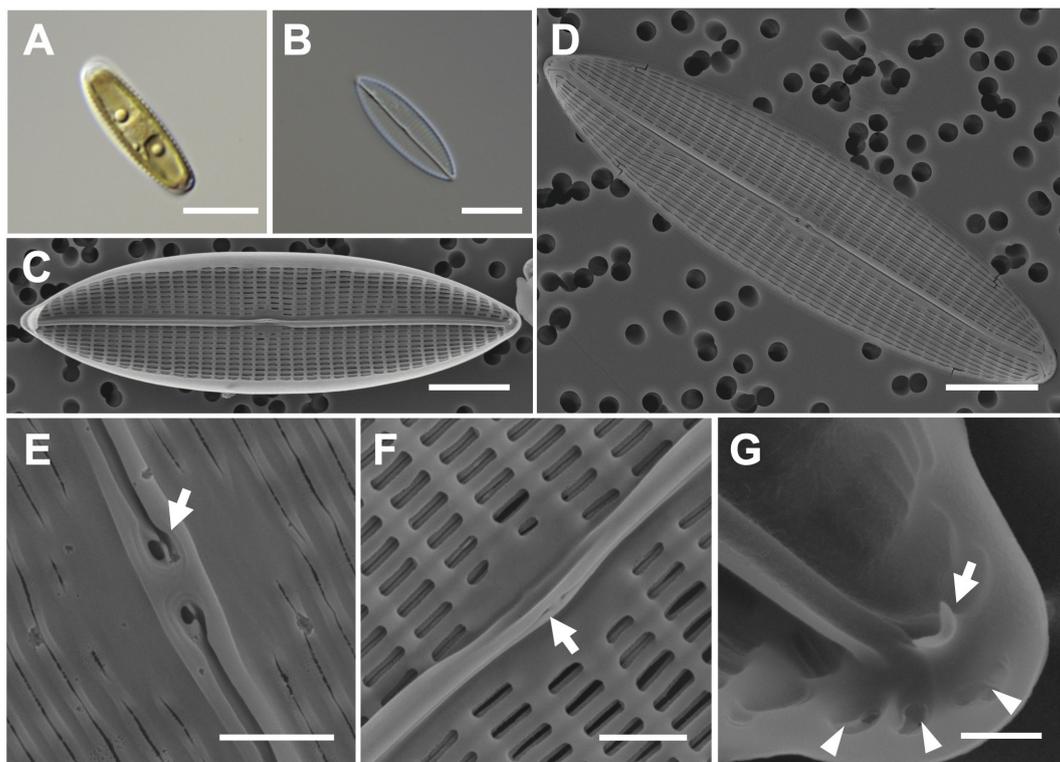


FIGURE 3

Light and electron microscopic images of *Navicula avium* (MEG004). (A) Narrowly lanceolate cell containing two plastids. (B) Cleaned frustule. (C) Straight raphe in the internal valve view. (D) Acute apex in the external valve view. (E) External central raphe endings with two pore-like extensions (arrow). (F) Accessory rib (arrow) in the internal valve view. (G) Internal terminal raphe slits with helictoglossa (arrow) around three pores (arrowhead). Scale bars: (A–D) = 5 μm , (E, F) = 1 μm , and (G) = 0.5 μm .

Nitzschia reversa var. *latus* (MEG012) displays similar morphological characteristics as those of *Nit. reversa* such as the cell size, raphe canal, and central nodule (Supplementary Table S6; Smith, 1853). However, the fibulae density of *Nitzschia reversa* var. *latus* (MEG012) is larger than that of *Nit. reversa*; thus, this species (MEG012) is considered a variety of *Nit. reversa* (Supplementary Table S6). Most morphological characteristics of *Nit. reversa* var. *latus* were also similar to those of *Nit. droebakensis* without fibulae density (Supplementary Table S6; Hasle, 1964; Giulietti et al., 2021). Nonetheless, all the described morphological characteristics (cell size, valve outline, raphe canal, central nodule, and fibulae density) of *Nit. droebakensis* were almost identical to those of *Nit. reversa* (Supplementary Table S6). Therefore, *Nit. droebakensis* Hasle (1964) is considered a synonym of *Nit. reversa* Smith (1853) because of priority in nomenclature. *Nit. reversa* var. *latus* displays a sigmoid valve outline, whereas other comparable *Nitzschia* species exhibit a linear valve outline (e.g., *Nit. gobbii*; Supplementary Table S6). Furthermore, the valve length of *Nit. reversa* var. *latus* (38–50 μm) is smaller than that of *Nit. draveillensis* (55–110 μm), *Nit. longissima* (ca. 200 μm), and *Nit. ventricose* (100–650 μm ; Supplementary Table S6).

3.1.5 *Nitzschia dissipatoides* Archibald 1983

Cells are 20–30 μm (avg. 25 μm , $n = 100$) in length and 3–6 μm (avg. 4 μm , $n = 100$) in width (Figures 6A, B) and have numerous

girdle bands (Figure 6C). The valve shape is lanceolate constricted in the middle part of the keel (Figure 6D). The rostrate apices are slightly curved (Figure 6D). The raphe canal is eccentric (Figure 6D). Fibulae are 10 in 10 μm but are irregularly arranged in interval (Figure 6E). A central nodule was observed in the internal valve view (Figure 6F). Striae density is 35 in 10 μm on the elevated virgae (Figure 6G).

Nitzschia dissipatoides (MEG028) exhibited similar morphological characteristics as those of the previously reported *Nit. dissipatoides* (Archibald, 1982; Supplementary Table S7). The valve outline of *Nit. dissipatoides* (lanceolate) is different from those (linear) of *Nit. erosa*, *Nit. fragilariiformis*, *Nit. hybridaeformis*, *Nit. pseudoamphioxys*, and *Nit. yunchengensis* (Supplementary Table S7). The valve length of *Nit. dissipatoides* (21.21–30.35 μm) is smaller than that of *Nit. thienemanni* (47–90 μm) and *Nit. hybridaeformis* (60–93 μm ; Supplementary Table S7). The striae density of *Nit. dissipatoides* (35 in 10 μm) is larger than that of *Nit. serrata* (25 in 10 μm) and *Nit. pseudoamphioxys* (24 in 10 μm) but smaller than that of *Nit. yunchengensis* (60 in 10 μm ; Supplementary Table S7).

3.1.6 *Nitzschia anomalus* Jeong & Lee sp. nov.

The valve is lanceolate with a slightly rounded apices (Figures 7A, B). Numerous girdle bands are present (Figures 7C, D). Cells are 18–33 μm (avg. 26 μm , $n = 100$) in length and 4–7 μm (avg. 11 μm , $n = 100$) in width (Figure 7D). The external valve has a

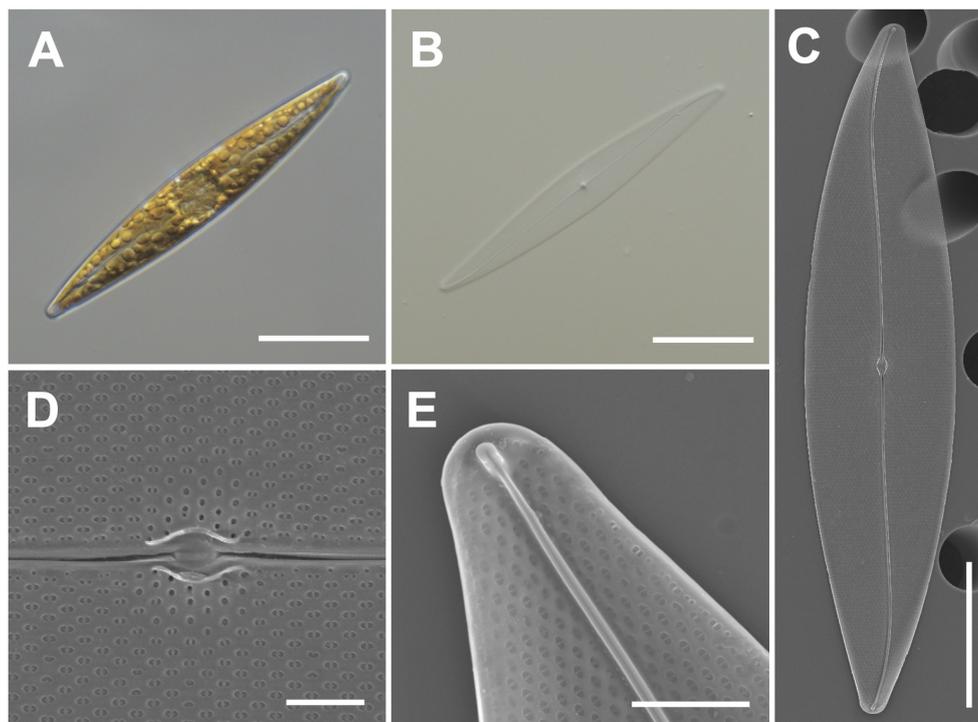


FIGURE 4
Light and electron microscopic images of *Pleurosigma inscriptura* (MEG005). (A) Lanceolate cell. (B) Cleaned frustule. (C) Sigmoid raphe in the external valve view. (D) Small oval central nodule in the external valve view. (E) Internal polar raphe ends with small triangles. Scale bars: (A–C) = 20 μm , (E) = 3 μm , and (D) = 2 μm .

slightly curved central raphe canal (Figure 7E). The internal valve reveals a central raphe canal (slightly curved) with 8 fibulae in 10 μm (Figures 7F, G). The striae density is 37 in 10 μm , and they are arranged on elevated virgae parallel to the transapical axis (Figure 7H). Helictoglossae were detected in the internal terminal raphe slits (Figure 7I). The areolae with silicified rings are randomly arranged on the striae (Figure 7J). The central nodule is absent (Figure 7K).

Etymology: The name refers to randomly distributed areolae on the striae.

Comparison with similar species: *Nitzschia anomalus* (MEG011) displays a similar lanceolate valve outline to that of *Nit. nanodissipata* (Witkowski et al., 2016), but their valve apices, cell size, and striae density are different (Supplementary Table S8). *Nit. anomalus* exhibits a larger valve in length (17.69–32.97 μm) than *Nit. volvendirostrata* (7–11.5 μm). Furthermore, the striae density of *Nit. volvendirostrata* (80–90 in 10 μm) is larger than that of *Nit. anomalus* (37 in 10 μm ; Supplementary Table S8). *Nit. anomalus* exhibits a lanceolate valve outline and a central raphe canal, while *Nit. aestatis* displays a rectangular-linear valve outline and an eccentric raphe canal. Moreover, *Nit. anomalus* shows a smaller valve in length (18–33 μm) than *Nit. aestatis* (44–50 μm ; Supplementary Table S8).

The phylogenetic analysis of 18S rDNA sequences from the *Nitzschia* species (OR418054, OR418055, and OR418056) with their homologous sequences (top 500 matches of BLASTn search, *e*-value cutoff = $1.e-05$) revealed a monophyletic relationship with other *Nitzschia* species (Supplementary Figure S4). However, the

phylogenetic clade includes other diatom genera (e.g., *Cylindrotheca*, *Tryblionella*, and *Bacillaria*) with morphologically unverified diatom species; hence, further studies without controversial molecular data are required (Mann et al., 2021).

3.2 Phylogenetic analysis using 18S rDNA sequences

The 18S rDNA phylogeny reveals that *Enotomoneis* species exhibit a paraphyletic relationship with respect to the genera *Amphiprora*, *Auricula*, and *Epithemia* (Supplementary Figure 1). In the phylogenetic analysis using 18S rDNA sequences, the genus *Navicula* shows a paraphyletic relationship with respect to the genera *Haslea*, *Minutocellus*, and *Seminavis* (Supplementary Figure 2). The genus *Pleurosigma* shows a monophyletic clade based on the 18S rDNA phylogeny (Supplementary Figure 3). The genus *Nitzschia* shows paraphyletic relationship with respect to the genera *Phaeodactylum*, *Pseudo-nitzschia*, *Fragilariopsis*, *Cymbella*, *Conticribra*, *Durinskia*, *Peridinium*, *Amphora*, *Hantzschia*, *Achnantheidium*, *Achnanthes*, *Bacillaria*, *Navicula*, *Tryblionella*, and *Cylindrotheca* in the 18S rDNA phylogeny (Supplementary Figure 4).

We postulate that several types of nuclear genetic variation (Baack and Rieseberg, 2007; Colbeck et al., 2011; Harrison and Larson, 2016) could introduce confusion in phylogenetic signals. Consequently, the paraphyletic relationships in several diatom genera may be attributed to use of single or several nuclear

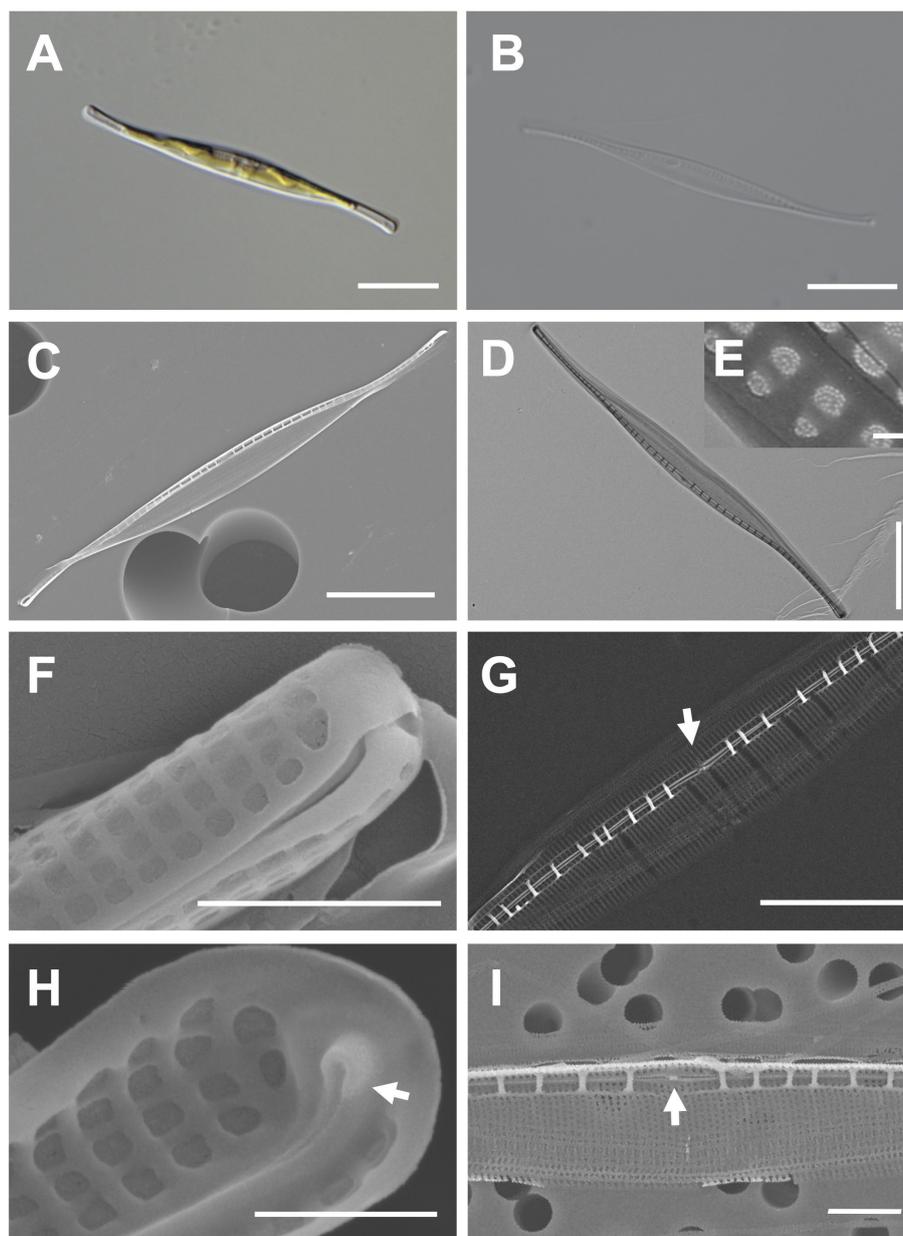


FIGURE 5

Light and electron microscopic images of *Nitzschia reversa* var. *latus* Jeong & Lee var. nov. (MEG012). (A) Lanceolate-fusiform cell. (B) Cleaned frustule. (C) Eccentric raphe canal in the external valve view. (D) Frustule (TEM). (E) Perforate hymenate areolae (TEM). (F) Round to square poroids in the external valve view. (G) Randomly arranged fibulae in the internal valve view, and particularly wide interval of fibulae (arrow) in the central area. (H) Internal terminal raphe slits with helictoglossae (arrow). (I) Central nodule (arrow) in the internal valve view. Scale bars: (A–D) = 10 μm , (G) = 5 μm , (I) = 2 μm , (F) = 1 μm , (H) = 500 nm, and (E) = 100 nm.

marker genes (e.g., 18S rDNA). Another potential cause of the paraphyletic relationships could arise from misidentified or morphologically unverified species (Kooistra et al., 2008; Nguyen et al., 2011; Cimarelli et al., 2015; Mann et al., 2021). Although more taxon samples from morphologically verified species with their complete nuclear genome data can help resolve this issue, available nuclear genomes in diatoms are still insufficient. Therefore, we attempted to address this using diatom organelle genomes in this study.

3.3 Multigene phylogenies using conserved plastid and mitochondrial genes of diatom species

We completely constructed the circular organelle (plastid and mitochondrial) genomes of the six diatom species (Supplementary Table S9). The plastid genomes of these diatoms range from 121 to 177 kbp in length and contain 127 to 140 protein-coding sequences (CDS), 30 to 31 tRNAs, and 6 ribosomal RNAs (rRNAs). The

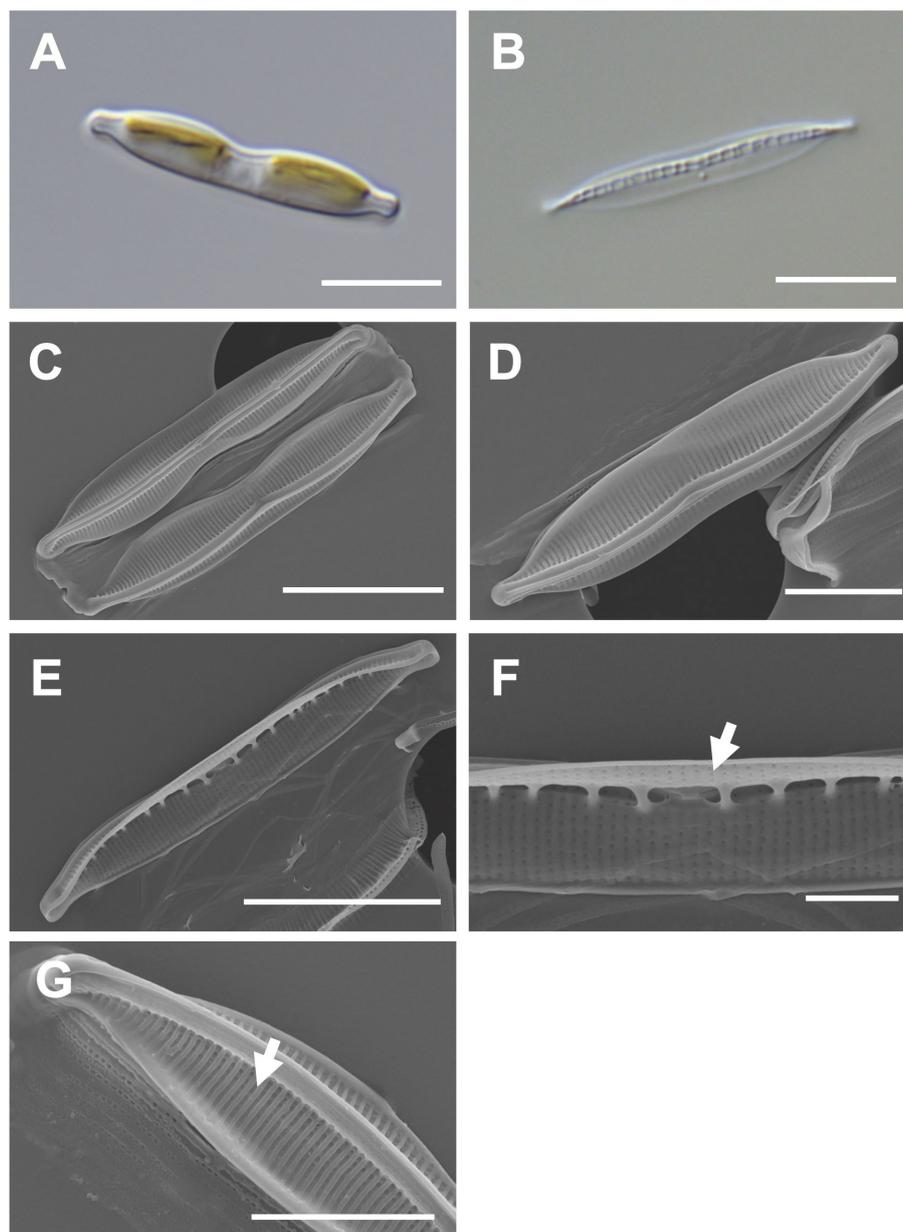


FIGURE 6

Light and electron microscopic images of *Nitzschia dissipatoides* (MEG028). (A) Lanceolate cell. (B) Cleaned frustule. (C) Lanceolate valve constricted in the middle part of the keel (external valve view). (D) Rostrate apices in the external valve view. (E) Fibulae structures in the internal valve view. (F) Central nodule (arrow) in the internal valve view. (G) Elevated virgae (arrow) in external valve view. Scale bars: (A, B, D), and (F) = 5 μm , (C, E) = 10 μm , and (G) = 2 μm .

mitochondria genomes of six diatoms range from 36 to 61 kbp in length and contain 33 to 36 CDS, 19 to 25 tRNAs, and 2 rRNAs (Supplementary Table S9).

Several diatom genera showed paraphyletic relationships in the plastid phylogeny with high bootstrap support values (BS). For example, the genus *Navicula* showed a paraphyletic relationship with respect to *Seminavis robusta* (MH356727), and this clade showed a 100% BS (Figure 8). The genus *Seminavis* has two plate-like plastids that typically lie along each side of the girdle, with valves exhibiting a strong dorsiventral orientation, distinguishing it from the genus *Navicula* (Bruder and Medlin, 2008; Li et al., 2022). *Seminavis*

robusta also possesses distinct morphological characteristics compared with those of the closely related *Navicula* species (e.g., *N. veneta* and *N. arenaria*) in the phylogenetic clade (Figure 8; Donkin, 1858; Kützing, 1844; Danielidis and Mann, 2002; Chudaev et al., 2022). However, to clarify the phylogenetic and taxonomic position of the genus *Seminavis*, more taxon samples from this genus are required. In the plastid phylogeny, *Pleurosigma inscriptura* (MEG005) and *Entomoneis umbratica* (MEG002) are clustered with their sister species, respectively (BS: 100%; Figure 8). Interestingly, the *Nitzschia* species (yellow blocks in Figure 8) exhibit a paraphyletic relationship with respect to the genera

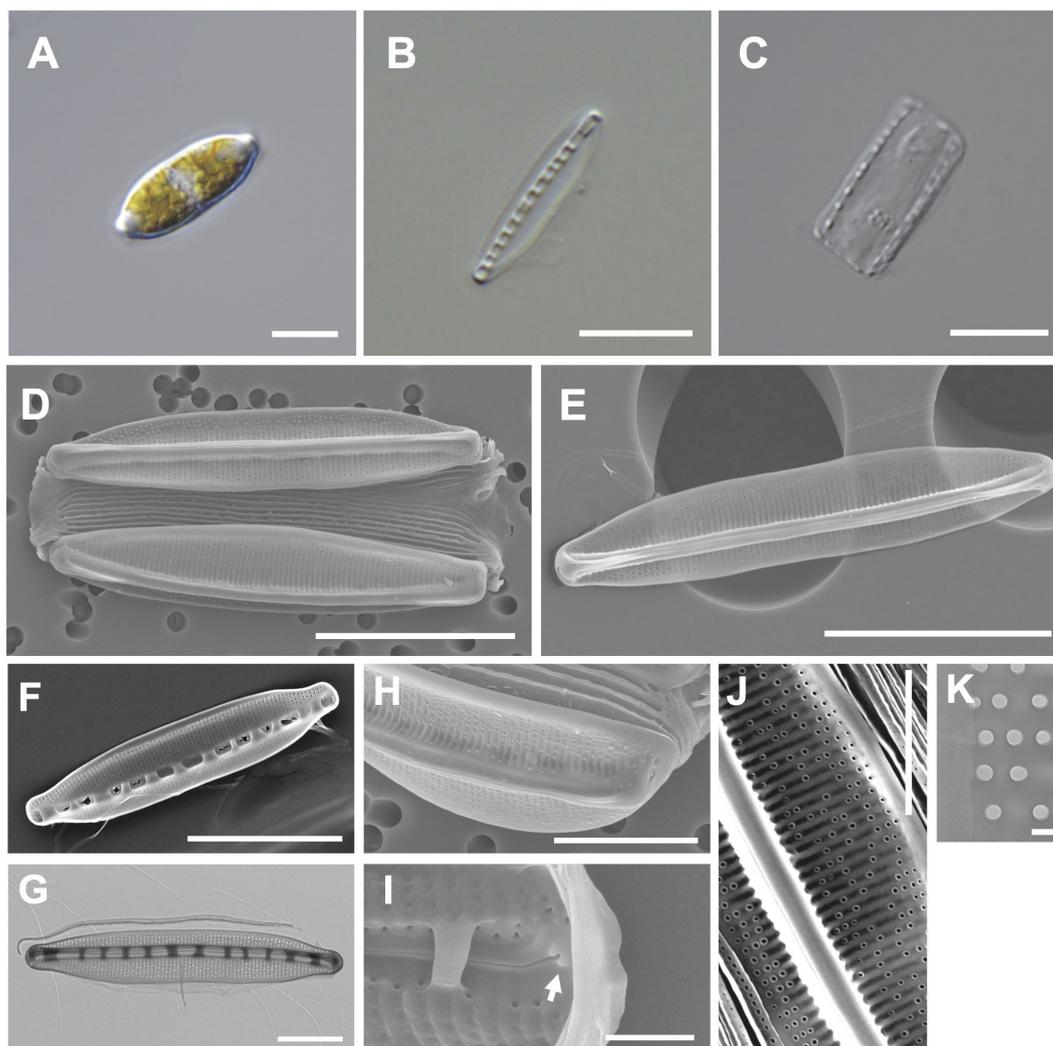


FIGURE 7

Light and electron microscopic images of *Nitzschia anomalus* Jeong & Lee sp. nov. (MEG011). (A) Lanceolate cell. (B) Cleaned frustule. (C) Numerous girdle bands in cleaned frustule. (D) Slightly rounded apices in the external valve view. (E) Slightly curved central raphe canal in the external valve view. (F) Fibulae structures in the internal valve view. (G) Frustule (TEM). (H) Randomly arranged areolae in the external valve view. (I) Internal terminal raphe slits with helictoglossae (arrow). (J) Elevated virgae in the external valve view. (K) Valve areolae (TEM). Scale bars: (A–C, G, H) = 5 μm , (D–F) = 10 μm , (J) = 3 μm , (I) = 1 μm , and (K) = 200 nm.

Pseudo-nitzschia, *Fragilariopsis*, *Cylindrotheca*, *Tryblionella*, *Psammodictyon*, and *Bacillaria* (BS: 95%; Figure 8), even though taxon samples to compare inter-genera relationship are adequate only from the genera *Nitzschia* and *Pseudo-nitzschia*. In particular, *Nit. anomalus* (MEG011) and *Bacillaria paxillifer* (NC_061049) present an early diverged subclade within the *Nitzschia* clade (Figure 8). Although the mitochondrial phylogeny constructed using diatom species is slightly different in the topologies of *Nitzschia* species compared with the plastid phylogeny, the *Nitzschia* clade (BS: 100%) exhibits paraphyletic relationship with respect to the genera *Tryblionella*, *Cylindrotheca*, and *Pseudo-nitzschia* (Figure 9). Diatom species in the *Nitzschia* clade have relatively conserved gene contents in plastid and mitochondrial genomes (Supplementary Tables S10, S11). However, several plastid genes such as *psaE*, *psaI*, *serC*, *syfB*, and *ycf35* were not found in most *Pseudo-nitzschia* species (Supplementary Table S10). In addition,

only *Nitzschia palea* (MH113811) and *Tryblionella apiculata* (NC_056791) possessed *ycf91* and *tyrC*, respectively (Supplementary Table S10). The non-photosynthetic diatom *Nitzschia alba* has lost most plastid genes (Supplementary Table S10). Therefore, the molecular and evolutionary histories of several different diatom genera are closely related to each other despite the distinctly different morphological characteristics, such as genus boundaries. The development of morphological features could be influenced by various types of interactive nuclear-encoded genes. For example, in plants, the transcription factor MADS-box genes are involved in flower morphogenesis (Coen and Meyerowitz, 1991; Saedler et al., 2001). Therefore, morphological characteristics and their related genes in diatoms may not accurately represent their phylogenetic and evolutionary relationships.

In the plastid phylogeny, *Thalassiosira* species (blue blocks in Figure 8) are also clustered with other genera such as *Discostella*,

Plastid



FIGURE 8
Multigene phylogeny constructed using a concatenated alignment of 123 plastid genes from diatom species (only ≥ 50 bootstrap supporting values are shown).

Minidiscus, *Skeletonema*, and *Cyclotella* (BS: 100%; Figure 8). The mitochondrial phylogeny also revealed that *Thalassiosira* species shows paraphyletic relationship with respect to *Skeletonema* species (BS: 100%; Figure 9). These diatom species in the *Thalassiosira* clade exhibit conserved gene contents in plastid and mitochondrial genomes (Supplementary Tables S12, S13). Based on our results, we postulate that the morphological characteristics of several different diatom genera, which are currently established, were independently diverged within the genetically close diatom groups.

The family Thalassiosiraceae exhibits paraphyletic relationship with respect to the families Stephanodiscaceae and Skeletonemataceae in the plastid phylogeny (Supplementary Figure S5). The family Chaetoceroaceae exhibits paraphyletic relationship with respect to the family Hemiaulaceae in the plastid phylogeny (Supplementary Figure S5). In the mitochondrial phylogeny, these families (Thalassiosiraceae-Skeletonemataceae and Chaetoceroaceae-Hemiaulaceae) are also paraphyletic (Supplementary Figure S5). The order Naviculales

Mitochondria

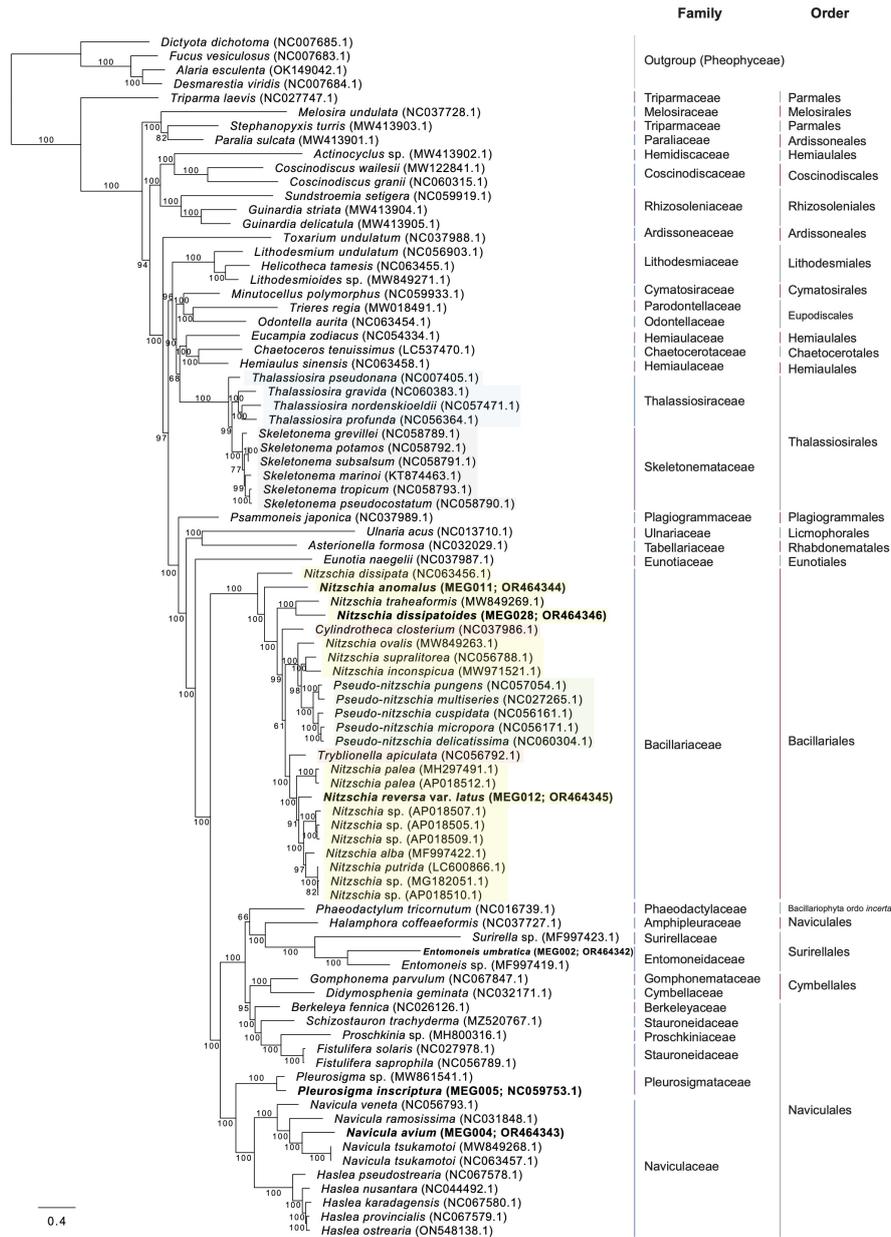


FIGURE 9

Multigene phylogeny constructed using a concatenated alignment of 34 mitochondrial genes from diatom species (only ≥ 50 bootstrap supporting values are shown).

exhibits paraphyletic relationship with respect to the orders Surirellales and Cymbellales in both plastid and mitochondrial phylogenies (Supplementary Figure S6). The order Thalassiosirales exhibits paraphyletic relationship with respect to the order Stephanodiscace in the plastid phylogeny (Supplementary Figure S6). The order Chaetocerotales displays a paraphyletic relationship with respect to the order Hemiaulales in both plastid and mitochondrial phylogenies (Supplementary Figure S6). Paraphyletic relationships at the family- and order-level in diatoms are completely supported by both plastid and mitochondrial phylogenies (BS 100% as red dots in Supplementary Figures S5, S6).

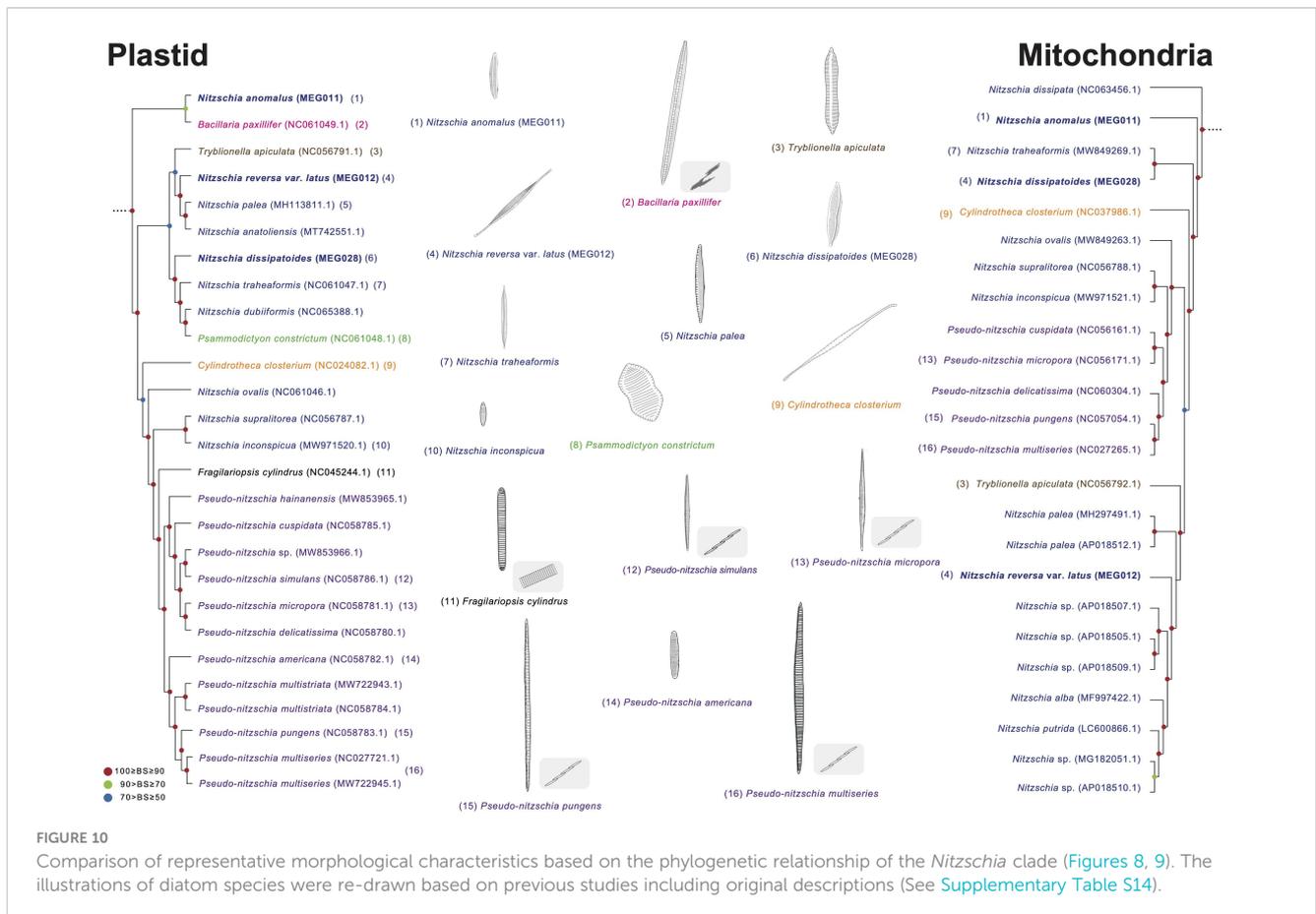
3.4 Phylogenetic relationships of morphologically similar diatom genera

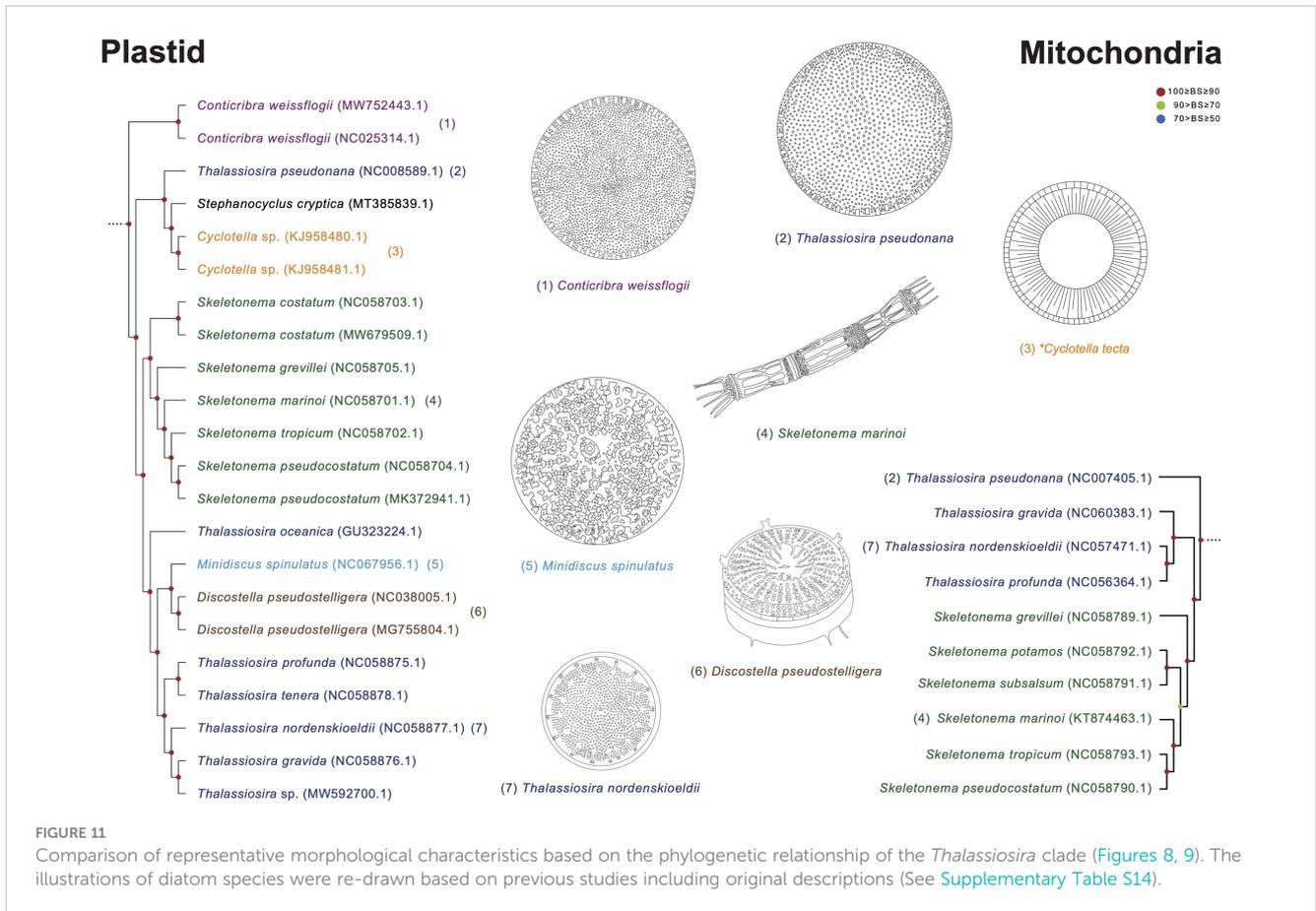
Approximately 800 *Nitzschia* species are currently reported (Guiry and Guiry, 2023) based on their morphological characteristics as follows: symmetric nitzschoid cell shape, position of the raphe, transverse extension of the fibula, and the number of striae and aleolae (Mann, 1981; Morales et al., 2020). Interestingly, several species from the genera *Pseudo-nitzschia*, *Fragilariopsis*, *Cylindrotheca*, *Tryblionella*, and *Bacillaria* had been reported as *Nitzschia* species, but these were reclassified by morphological characteristics such as colony formations and raphe structures

(Reimann and Lewin, 1964; Hasle, 1994; Li et al., 2007; Schmid, 2007; Cefarelli et al., 2010; Cavalcante et al., 2013). These diatom genera were also clustered as the *Nitzschia* clade in this study (Figures 8, 9). Moreover, as one of the early diverged taxa in the *Nitzschia* clade of the plastid phylogeny, *Nit. anomalus* displays typical morphological characteristics of the genus *Nitzschia*, but this is clustered with *Bacillaria paxillifer* (Figure 10). Individual cells of *B. paxillifer* exhibit similar morphological features as those of *Nitzschia* species, but *B. paxillifer* colonies exhibit a gliding motion (Schmid, 2007; image no. 1 and 2 in Figure 10). Moreover, in the mitochondrial phylogeny, *Nit. dissipata* (NC_063456) is an earlier diverged taxon (this study) than *Nit. anomalus* in the *Nitzschia* clade (Figure 10). Therefore, we postulate that the typical genus characters of *Nitzschia* species could be considered phylogenetically early diverged features. *Psammodictyon constrictum* and *Tryblionella apiculata* are similar to the *Nitzschia* species in possessing symmetry of the raphe on a frustule, wide valves, and eccentric raphe (Round et al., 1990; Yang et al., 2020). However, the genera *Psammodictyon* and *Tryblionella* are distinguished from *Nitzschia* by the differences in valve shape and plastid position (Round et al., 1990; Yang et al., 2020). Moreover, these genera exhibit different characteristics in valve outline and arrangement and structure of areolae (e.g., *Psammodictyon*: panduriform valve with distinctively centrally constricted; *Tryblionella*: linear-lanceolate or elliptic in shape, with only slightly centrally constricted; Round et al., 1990; Yang et al., 2020). Although the morphological characteristics of *Cylindrotheca closterium*, such as valve shape, are similar to those of

sigmoid *Nitzschia* species (e.g., *Nitzschia longissima* and *Nitzschia reversa* var. *latus*) under light microscopic observation, *Cylindrotheca closterium* has twisted frustules in the apical axis and slightly silicified raphe in the valves, which are different from those of *Nitzschia* species (Reimann and Lewin, 1964; Li et al., 2007). *Pseudo-nitzschia* and *Fragilariopsis* species exhibit a paraphyletic relationship with respect to the *Nitzschia* species (BS 100%; Figure 10). The genera *Pseudo-nitzschia* and *Fragilariopsis* demonstrate morphological differences in colony formation (*Pseudo-nitzschia* species: stepped colonies; *Fragilariopsis* species: ribbon-shape colonies; Hasle, 1994; Lundholm et al., 2002b) compared with *Nitzschia*. However, *Pseudo-nitzschia americana* exhibits a unicellular formation (Figure 10; Lundholm et al., 2002a).

Thalassiosira species display paraphyletic relationship with respect to the genera *Cyclotella*, *Minidiscus*, *Discostella*, and *Skeletonema* (Figure 11). In the *Thalassiosira* clade, the early diverged taxa are *T. pseudonana* and *Cyclotella* species. Although *T. pseudonana* was previously reported as *Cyclotella nana*, these two genera present morphological differences in the central area of the valve surface (Figure 11; Lowe and Busch, 1975). *T. nordenskioldii* is the type (i.e., representative) species of the genus *Thalassiosira*, which clustered with *Thalassiosira* sp., *T. gravida*, *T. profunda*, and *T. tenera*, but their sister clade includes *Discostella pseudostelligera* and *Minidiscus spinulatus*, which exhibit different morphological characteristics in marginal fulcportulae, location of rimoportula, and central area (Figure 11; Houk and Klee, 2004). Nevertheless, several





morphological features (e.g., cell size and marginal fultoportulae) to distinguish genus boundaries are still controversial (Park et al., 2017). Furthermore, the *Thalassiosira* and *Skeletonema* species exhibit completely different morphological characteristics. For instances, *Skeletonema* has cylindrical cells with a ring of long processes emerging from the edge of the valve face, and the colony is linked by elongate tubular processes (Jung et al., 2009; Spaulding et al., 2021). However, *Thalassiosira* has disk-shaped valves, and the colony is linked by chitin fibrils (Johansen and Fryxell, 1985).

Paraphyletic relationships are recognized in diverse taxonomic levels of diatoms based on the highly supported organelle phylogenies (Figures 8, 9). As a result, we believe that taxonomic reinvestigation in diatoms is required. However, almost all genome data have no morphological descriptions and images of the target diatoms, which is a critical limitation for further discussion.

4 Conclusion

We isolated six diatom species from field samples, and each extracted DNA sample was sequenced and assembled to make organelle (plastid and mitochondrial) genomes. Based on the highly supported plastid and mitochondrial phylogenies, we demonstrate that several morphologically similar diatom genera show paraphyletic relationships, thus suggesting that the morphology-based genus boundaries and phylogeny relationships

frequently conflict in diatoms. To reestablish the conflict relationship in diatoms, there is a need for more organelle and nuclear genomes from broader taxon samples of diatom species with a comparison of morphological characteristics. In particular, photographic materials (especially SEM images) of target diatoms are necessary, along with morphological descriptions, when new genomic references are generated. This ensures that many researchers can avoid the confusion caused by several pieces of genome information generated from misidentified or morphologically unverified species. Finally, highly supported phylogenetic trees (e.g., organelle phylogenies) and their accompanying photographic materials in diatoms can lead to active discussion for taxonomic reinvestigation.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repository and accession number(s) can be found in the article/Supplementary Material.

Author contributions

YJ: Data curation, Formal analysis, Investigation, Methodology, Software, Validation, Visualization, Writing – original draft, Writing –

review & editing. JL: Conceptualization, Funding acquisition, Project administration, Resources, Supervision, Validation, Writing – original draft, Writing – review & editing.

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The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2023.1283893/full#supplementary-material>

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