Placoneis modaomensis sp. nov. (Bacillariophyta; Cymbellaceae), a new species from Guangdong Province, China

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Abstract – One new species, *Placoneis modaomensis*, found in a freshwater environment from a tributary of the Pearl River, which lies in Modaomen Channel, Zhuhai County, Guangdong Province, China, is described based on light and scanning electron microscope observations. *P. modaomensis* sp. nov. has the morphological features that are typical for the genus, including external terminal raphe fissures curved to the opposite sides and areolae with internal volate occlusions. The new species is similar to *P. amphibola* (Cleve) E.J. Cox, *P. amphiboliformis* (Metzeltin, Lange-Bertalot & Soninkhishig) Vishnyakov, *P. parvapolonica* Lange-Bertalot & Wojtal, *P. clementispronina* Lange-Bertalot & Wojtal and *P. nanoclementis* Lange-Bertalot & Wojtal in the shape of the valves and in having coarse striae but it can be easily distinguished by the two main morphological characteristics: external central raphe endings bent in the opposite directions, and areolae covered by volate occlusions externally. The latter feature appears to be new for taxa assigned to the genus *Placoneis*. Data on the associated diatom flora and its ecology are also given. These findings increase our understanding about the morphology of *Placoneis* in general and the distribution of the genus in China.

Keywords: diatoms, morphology, new species, Placoneis, taxonomy

Introduction

The genus Placoneis Mereschkowsky was erected by Mereschkowsky in 1903 for a group of species showing a single chloroplast with a central bridge and lateral lobes (Mereschkowsky 1903). With the shift to an emphasis on using frustular features to diagnose taxa (e.g., Hustedt 1930), species assigned to Placoneis were considered part of the large genus Navicula Bory (1822). Due to its structure of the chloroplast, Cox (1987) resurrected the genus Placoneis with P. gastrum (Ehrenberg) Mereschkowsky (Basionym: Pinnularia gastrum Ehrenberg) as the type species. Phylogenetic analysis of Placoneis based on morphological and molecular data showed that the genus was part of the Cymbellales, a group with valves that are asymmetrical to the apical and/or transapical axes, despite having symmetrical valves. Support for this phylogenetic placement includes the straight and expanded central raphe endings and more or

less hooked distal ones, striae composed of rounded areolae which are internally closed by volae (tectulum), and a single chloroplast with a central bridge and lateral lobes extending under the valves (Cox 1987, 2003, 2004, Mann and Stickle 1995, Bruder and Medlin 2007). To date, more than 136 species are recognized to be part of this genus (Guiry and Guiry 2022).

The genus *Placoneis* has a relatively wide distribution range, including Europe (Cox 1987, Bruder and Medlin 2007, Levkov and Williams 2011, Kulikovskiy et al. 2016, Vishnyakov 2020), Asia (Mayama and Kawashima 1998, Metzeltin et al. 2009, Kulikovskiy et al. 2012, Pomazkina et al. 2019, Kezlya et al. 2020), North America (Johansen et al. 2004, Kociolek and Thomas 2010, Kociolek et al. 2014), South America (Metzeltin and Lange-Bertalot 1998, Metzeltin and Lange-Bertalot 2007, Straube et al. 2013, Maidana et al.

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2017), West Africa (Fofana et al. 2014) and Antarctica (Zidarova et al. 2009). In China, research on Placoneis has focused on the discovery of newly recorded species for the country, such as P. prespanensis Levkov, Krstic & Nakov (Li et al. 2010), P. explanata (Hustedt) S. Mamaya (Liu et al. 2012), P. interglacialis (Hustedt) E.J. Cox (Liu et al. 2012), P. opportuna (Hustedt) Chudaev & Gololobova (Lin et al. 2018), P. anglophila var. signata (Hustedt) Lange-Bertalot (Liu et al. 2020). New Placoneis species have been proposed from China by Gong et al. (2013) but otherwise only few new species of this genus have been reported. In Guangdong Province the diversity of diatoms is relatively rich (Qiu et al. 2016, Lin et al. 2018), but previous studies have mainly focused on Navicula Bory, Nitzschia Hassall, Cymbella C. Agardh and Gomphonema Ehrenberg (Wang et al. 2018, 2021). Our understanding of Placoneis from Guangdong Province is very limited (Wang et al. 2021).

The purposes of our study are: (i) to describe a *Placoneis* species new to science from the tributary of the Pearl River: Modaomen Channel, Zhuhai County, Guangdong Province, China based on detailed morphological observation using both light and scanning electron microscopy, (ii) to discuss its characteristics compared to related species, and (iii) to provide ecological information on this new species.

Materials and methods

Modaomen is located in Zhuhai County, Guangdong Province, China, one of the eight major gates at the mouth of the Pearl River. The length of the Modaomen Channel is about 45 km, and the water depth varies from 5 to 13 m. The Channel is relatively straight and about 2200 m wide (Chen et al. 2014, Tong et al. 2018).

In 2021, samples containing *Placoneis* were collected from the Modaomen Channel (22°24'20"N, 113°36'25"E). Channel water pH and specific conductance were measured using a YSI 650 multi-parameter display system (650 MDS, YSI Incorporated 1700/1725 Brannum Lane, Yellow Springs, OH 45387 USA) with a 600XL probe. The diatom samples were further processed as described by Battarbee (1986). After several rinses in distilled water, the partially cleaned diatom material was air-dried onto cover slips and mounted onto slides using Naphrax. The sample and slides were deposited in the Herbarium of the Institute for Ecological Research and Pollution Control of Plateau Lakes, Yunnan University, Kunming, P.R. China (YUK). The isotype slides were stored in the Key Laboratory of Biodiversity of Aquatic Organisms, Harbin Normal University.

Morphological observations of specimens were made under oil immersion at 1000× magnification with light microscopy (LM) using an OLYMPUS BX51-DIC research microscope and a C5060 Olympus digital camera. At least 500 valves were identified and counted in each surface sediment sample. Cleaned material for scanning electron microscope (SEM) analysis was air-dried onto cover glasses, mounted onto stubs, and coated with 20 nm of Au (EMSCOP SC 500 sputter coater). Resulting stubs were examined in the LEO 1530 scanning electron microscope (SEM). Description of the new species follows the terminology provided by Round et al. (1990), Cox (2003), Metzeltin et al. (2009) and Lange-Bertalot and Wojtal (2014).

Results

Taxonomy

- Division Bacillariophyta Haeckel 1878: 95
- Class Bacillariophyceae Haeckel 1878 emend D.G. Mann in Round et al. 1990: 651
- Subclass Bacillariophycidae D.G. Mann in Round et al. 1990: 125
- Order Cymbellales D.G Mann in Round et al. 1990: 653
- Family Cymbellaceae Greville 1833: 263, 409
- Genus Placoneis Mereschkowsky 1903: 3
- *Placoneis modaomenensis* Y.-L. Li sp. nov. Fig. 1A–H; Fig. 1C is the holotype

LM (Fig. 1): Valves elliptical to broadly elliptical, nearly symmetrical about the apical axis, with rostrate or rostrate-rounded apices. Length 25.0–32.5 μ m, width 14.0–16.5 μ m, length/width ratio 1.62–2.16, median 1.89 (n = 30). Raphe filiform, almost straight with slightly expanded, but not clearly deflected to any side. External central raphe ends slightly straight, no significant expansion or bending. External terminal raphe fissures hooked to opposite sides. Axial area narrow, linear. Central area transverse, irregular to bow-tie-shaped, rarely asymmetrical, occupying nearly 1/2 of the valve width. Isolated pore is absent from the central area. Striae radiate throughout, 12–14 in 10 μ m.



Fig. 1. Placoneis modaomensis, Light Microscopy (LM), Differential Interference Contrast (DIC). A–H – valve views, showing size range and variability of the holotype population. Scale bar = $10 \mu m$.



Fig. 2. *Placoneis modaomensis*, Scanning Electron Microscope (SEM), external views. A, B – external view of an entire valve. C, D, E, F – valve apices, striae with elliptic/rounded areolae and hook-shaped terminal raphe fissures bent onto the valve margin. G, H, I – external view of valve center, the central raphe endings hooked in the opposite directions from each other, note volate occlusions. Scale bar = 2 µm

In SEM (Fig. 2 and Fig. 3): External raphe narrow, central raphe endings hooked opposite to each other (Fig. 2A, B, G, H, I). The terminal fissures curved, deflected in the opposite

directions, extend onto the valve margin (Fig. 2C, D, E, F). Striae uniseriate, composed of round or elliptical areolae, extending to valve margin (Fig. 2A–F). Areolae covered by



Fig. 3. *Placoneis modaomensis*, Scanning Electron Microscope (SEM), internal views. A, B, C – internal view of entire valve. D, E, F – internal view of valve apex with terminal raphe ends offset and bent slightly towards the margin. G, H – internal detail of central area showing raised central part and areolae covered by volate occlusions. Scale bar = 2 μm

volate occlusions (Fig. 2G, H, I). Each areola has almost 1–4 siliceous protrusions internally, forming a variety of different shapes (Fig. 2A–I). Internal striae uniseriate, formed by elliptical areolae, separated by robust silica ribs (Fig. 3A–H). The raphe sternum clearly raised above the valve plane and expanded in the central area. Internal raphe straight, discontinuous with intermissio, lying in a prominent and raised raphe sternum. Central raphe endings straight, not expanded. Terminal raphe ends terminate as helictoglossae, offset from the raphe branch, bent slightly towards the valve margin (Fig. 3D, E, F). Striae are uniseriate, distinctly radiate, formed by round to elliptical shaped areolae (11–14 in 10 µm) and covered by dentate occlusions (Fig. 3G, H).

Type: – CHINA. Guangdong Province: Zhuhai County, Modaomen Channel, GD1, 22°24'20" N, 113°36'25" E, elevation 0 m a.s.l., samples collected by Dr. Hong-Qu Tang, 26th July 2021. Holotype MDM202172601 in Coll. Yan-Ling Li, Yunnan University, Kunming, China. Fig. 1C is of the holotype; Isotype YUNGL20220218, Harbin Normal University, Harbin, China)

Etymology: – *modaomensis*, referring to the type locality from which the new species was obtained.

Associated diatom flora: *Placoneis modaomensis* is known from the Channel, situated at 0 m a.s.l. This species was associated with *Amphora linearis* F. Meister (1935: 97), *Seminavis strigosa* (Hustedt) Danielidis & Economou-Amilli (2003: 30), *Aulacoseira granulata* (Ehrenberg) Simonsen (1979: 58), *Gomphonema parvulum* (Kützing) Kützing (1849: 65), *Navicula schroeteri* F. Meister (1932: 38), *Navicula viridula* var. *rostellata* (Kützing) Cleve (1895: 15), *Nitzschia clausii* Hantzsch (1860: 40) and *Nitzschia frustulum* (Kützing) Grunow (1880: 98).

Ecology: The Modaomen Channel showed slightly alkaline conditions (pH 7.81), 29.8 °C of water temperature, 262 μ S cm⁻¹ of conductivity and 7.46 mg L⁻¹ of dissolved oxygen (DO).

Discussion

Because Placoneis modaomenensis has symmetrical valve and radiate striae, it could easily be placed in one of four other genera: Paraplaconeis Kulikovskiy, Lange-Bertalot & Metzeltin (2012), Geissleria Lange-Bertalot & Metzeltin (1996), Rexlowea Kociolek & E.W.Thomas (2010) or Navicula Bory (1822). First, our new species resembles Paraplaconeis by symmetry of valve, but differs by the specific morphology of internal and external areolae patterns (Cox 1987, Cox 2003, Lange-Bertalot and Wojtal 2014). Second, P. modaomenensis is similar to the genus Geissleria on the basis of features observed with LM. These two genera are similar in terms of valve outline, but differ by the presence of the subpolar elongated areolae in the latter (Novais et al. 2013, Kulikovskiy et al. 2014). Third, P. modaomenensis is morphologically close to Rexlowea due to the valve outline, but these two genera are very distinct from one another by the arrangement, radiation and density of the striae (Kociolek and Thomas 2010). Fourth, *P. modaomenensis* can be confused with *Navicula* based on the valve symmetry. However, the former has exterior areolae covered by volate occlusions and internal areolae covered by dentate occlusions; while the latter areolae are all individually covered on the inside by a weakly convex hymen (Lange-Bertalot 2001, Li and Qi 2018). The characters found in *Placoneis modaomensis* are compared with those of morphologically most similar genera in Tab. 1.

While Placoneis seems easily placed as a member of Cymbellales, by virtue of its cytoplasmic features, its position in this lineage has been quite variable. Placoneis has been reported as outside the group of asymmetrical genera (Kociolek and Stoermer 1988, Nakov et al. 2014), deep within the cymbelloid lineage with some other genera naviculoid symmetry (Thomas et al. 2016, Kezlya et al. 2021) or in both positions depending upon the gene(s) used in the analysis (Bruder and Medlin 2007). Groupings within Placoneis are also enigmatic. Cox (1987) identified two groups within Placoneis, one with isolated pores, external terminal raphe fissures deflected in directions opposite one another and straight internal central raphe endings, while the other group has features of isolated pores absent, external terminal raphe fissures deflected in the same direction and recurved internal central raphe endings. Kociolek and Thomas (2010) noted some species from Colorado, USA, that did not conform to this organization of the genus. For example, P. fourtanierii Kociolek & Thomas (2010: 204) has external terminal raphe fissures that are deflected in opposite directions, but lack isolated pores and deflected internal raphe ends. P. coloradoensis Kociolek & Thomas (2010: 205) has external terminal raphe fissures that are deflected towards the same side, internal central raphe endings that are straight, but this species has isolated pores. In the case of *P. modaomenensis*, it has external terminal raphe fissures that curve in opposite sides, but has internal central raphe endings that are straight and no isolated pores. In addition, P. modaomenensis has areolae with volate occlusions positioned on the valve exterior which appears to be unique within Placoneis. Presence of central raphe endings turned opposite to one another in P. modaomenensis is shared with P. uruguayensis Metzeltin et al., a species without many features in common with other Placoneis species. The statement of Levkov et al. that "the full range of variation of morphology with the genus has been underestimated" (2007, p. 116) seems even more true now than when it was offered more than 15 years ago.

In terms of general valve shape and striae, *P. modaomenensis* shows some resemblance to *P. amphibola* (Cleve) E.J. Cox, *P. amphiboliformis* (Metzeltin, Lange-Bertalot and Soninkhishig) Vishnyakov, *P. parvapolonica* Lange-Bertalot & Wojtal, *P. clementispronina* Lange-Bertalot & Wojtal and *P. nanoclementis* Lange-Bertalot & Wojtal. However, *P. modaomenensis* differs strikingly from these species that are morphologically similar with respect to two features by the following: 1) external central raphe endings are bent in the

Tab. 1. Morpho	Tab. 1. Morphological comparison of <i>Placoneis</i> to the most similar genera.	to the most similar genera.				
	Placoneis modaomensis sp. nov.	Placoneis	Paraplaconeis	Geissleria	Rexlowea	Navicula
Reference	This study	Cox 1987, Cox 2003, Lange-Bertalot and Wojtal 2014	Kulikovskiy et al. 2012, Lange-Bertalot and Wojtal 2014	Novais et al. 2013, Kulikovskiy et al. 2014	Kociolek and Thomas 2010	Lange-Bertalot 2001, Li and Qi 2018
Areolae	Being covered by volate occlusions externally, being covered by dentate occlusions internally	Being closed internally by volae	Open internally and occluded externally	Straight slit-like pores openings without hymens, presence of the subpolar elongated areolae	Large and more coarsely arranged puncta on the marginal valve	Being all individually covered on the inside by a weakly convex hymen
Striae	Uniseriate, radiate through- out, extending to valve margin	Usually uniseriate but sometimes biseriate, radiate near the centre of the valve, more parallel or convergent, at the apices	Uniseriate only on the valve mantle, consistently biseriate on the valve face	Radiate throughout, the proximal three ones wider spaced than the others	Radiate, with the 1st and or 2nd striae at the apices parallel or, rarely, conver- gent	Uniseriate, rarely biseriate, parallel, radiate or conver- gent
Chloroplast	1	Single, asymmetrical chloroplast, central portion more or less along the apical axis of the cell, from which lobes extend under the valves	1	Single, large plastid is divided into two plates lying one against each valve, connected by a broad column	1	Two plastids, located on each side of the apical axis, and each plastid contains an elongated, slender protein nucleus
Raphe system	The external central raphe ends slightly straight, the terminal fissures deflected in the opposite directions; the internal central raphe endings straight, terminal raphe ends terminate as helictoglossae	The external central raphe endings are straight and slightly expanded; the internal endings usually deflected towards the secondary side, occasionally hooked in opposite directions	The external raphe slit together with terminal fissures often curving primarily to opposite sides but finally to the same side	The external raphe is almost straight; the internal raphe is not deflected between the central nodule and helictoglossa, internal rib has never been observed	The external proximal ends swollen, external distal ends hooked	The external terminal fissures are deflected to the secondary side; the internal central raphe ends are not deflected

	P. modaomensis sp. nov.	P. parvapolonica	P. amphibola	P. amphiboliformis	P. clementispronina	P. nanoclementis
Reference	This study	Lange-Bertalot and Wojtal 2014	Cox 2003	Metzeltin et al. 2009	Lange-Bertalot and Wojtal 2014	Lange-Bertalot and Wojtal 2014
Valve shape	Elliptical to broadly elliptical and the valve mar- gin more convex	Broadly elliptical	Linear-elliptic to linear- lanceolate	Elliptical	Elliptical-lanceolate	Elliptical-lanceolate to elliptical
Central area	Bow-tie, transverse	Extended transapically	Bow-tie, transverse	Not given	Variable in size	Extended transapically, variable in shape
Isolated pores	Absent	Two	Not given	Not given	Two	Two
Valve length (μm)	25.0-32.5	16-20	37–75	34-63	20-40	14-23
Valve width (µm)	14.0-16.5	8.0-9.5	22–27	18-24	10-14	8.0-8.6
Number of striae in 10 µm	12–14	14-15	7-8	7–8	11-14	12–13
Number of areolae in 10 µm	11–14	40-44	Not given	10-12	38-41	40-44
External terminal raphe fissures	Undulate, deflected in the opposite directions, extend to valve margin	Turning first to opposite sides, finally turning to the same side as at the opposite pole	Deflected towards one side	Not given	Weakly sinuous subapically and deflected to opposite sides, at one of the poles curving back weakly to the same side	Shortly curved to appar- ently opposite sides
External central raphe end-ings	Hooked in the opposite directions from each other	Distinctly expanded central pores, not clearly deflected to any side	Expanded	Not given	Expanded but hardly deflected central pores	Distinctly expanded central pores, not clearly deflected to any side
Areolae	Uniseriate, exterior areolae covered by volate occlu- sions and formed a variety of different shapes, internal areolae are mostly round to elliptical covered by dentate occlusions	Uniseriate, circular to slightly elongate apically	Not given	Regularly elongated transapically	Small, circular to weakly elongated apically	Slightly elongated apically

Tab. 2. Morphological comparison of the currently described species in *Placoneis*.

opposite directions, and 2) both internal and external areolae are covered by volate occlusions. The characters found in *P. modaomenensis* are compared with other closely-related species of the genus in Tab. 2.

Based on valve outline, the new species is similar to P. amphibola, P. amphiboliformis, P. parvapolonica, P. clementispronina and P. nanoclementis, and P. modaomenensis sp. nov. most resembles P. parvapolonica based on its more convex valve margin and the structure of raphe and areola. However, they can be easily separated from one another. For example, in terms of the central raphe endings, the central raphe endings of the new species hooked in the opposite directions from each other while they do not clearly deflect to any side in *P. parvapolonica*. Comparing the shape of the areolae, the exterior areolae come in a variety of shapes and internal areolae are mostly round to elliptical in the new species, but P. parvapolonica differs in having areolae whose exterior and internal openings are nearly circular to slightly elongated in shape. Taking into consideration the occlusion of the areolae, the exterior and internal areolae are covered by volate and dentate occlusions respectively in the P. modaomenensis sp. nov., while there is an absence of occlusions in exterior and internal areolae in *P. parvapolonica*. Besides, the size range of P. modaomensis is larger than *P. parvapolonica* (16–20 \times 8.0–9.5 µm). Finally, the stria and areola density are much lower compared to P. parvapolonica (stria: 14-15 µm, areola: 40-44 in 10 µm). In summary, these differences are sufficient to justify the description of P. modaomensis as an independent species.

Placoneis species are prevalent in freshwater bodies, including alkaline waters, mesotrophic and oligotrophic conditions (Cox 1987, Fujita and Ohtsuka 2005, Bruder and Medlin 2007, Kezlya et al. 2021). Of the five species similar to our new species, P. amphibola has a nordic-alpine distribution in Europe, and also occurs in freshwater fossil deposits (Cox 2003). Except for P. amphibola, the relevant information of nutrition, pH, and conductivity are not recorded, but other species have certain similarities or differences with our species. In terms of pH, P. parvapolonica, P. clementispronina and P. nanoclementis were found in alkaline waters, but P. amphiboliformis was known from acidic rivers (Metzeltin et al. 2009, Lange-Bertalot and Wojtal 2014). From the nutritional level, P. clementispronina and P. nanoclementis were distributed in eutrophic waters, and P. parvapolonica was found in mesotrophic waters (Metzeltin et al. 2009, Lange-Bertalot and Wojtal 2014). As for the conductivity, P. parvapolonica and P. nanoclementis are found predominantly in waters with moderate to high conductivity, whereas P. amphiboliformis was discovered rivers with low conductivity (Metzeltin et al. 2009, Lange-Bertalot and Wojtal 2014). Here, the new species of Placoneis was collected from alkaline waters with moderately high conductivity, which is the most similar to *P. parvapolonica* and *P.* nanoclementis.

In short, the discovery of this new species promotes the understanding of morphological features and ecological distribution about the genus *Placoneis*, and contributes to our understanding of diatom diversity, especially in Guangdong Province.

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References

- Battarbee, R. W., 1986: Diatom analysis. In: Berglund, B. E. (ed.), Handbook of holocene palaeoecology & palaeohydrology, 527–570. John Wiley and Sons Ltd., Chichester, UK.
- Bory de Saint-Vincent, J. B. G. M., 1822: Bacillariées. Dictionnaire Classique d'Histoire naturelle 2, 127–129.
- Bruder, K., Medlin, L. K., 2007: Molecular assessment of phylogenetic relationships in selected species/genera in the naviculoid diatoms (Bacillariophyta). I. The genus *Placoneis*. Nova Hedwigia 85(3–4), 331–352. https://doi.org/10.1127/0029– 5035/2007/0085–0331
- Chen, W. H., Zou H. Z., Dong Y. J., 2014: Hydrodynamic of saltwater intrusion in the Modaomen waterway. Advances in Water Science 25(5), 713–723. [In Chinese with English abstract] https://doi.org/10.14042/j.cnki.32.1309.2014.05.003
- Cox, E. J., 1987: *Placoneis* Mereschkowsky: the re-evaluation of a diatom genus originally characterized by its chloroplast type. Diatom Research 2(2), 145–157. https://doi.org/10.108 0/0269249X.1987.9704994
- Cox, E. J., 2003: *Placoneis* Mereschkowsky (Bacillariophyta) revisited: resolution of several typification and nomenclatural problems, including the generitype. Botanical Journal of the Linnean Society 141(1), 53–83. https://doi.org/10.1046/j.1095-8339.2003.00115.x
- Cox, E. J., 2004: Pore occlusions in raphid diatoms a reassessment of their structure and terminology, with particular reference to members of the Cymbellales. Diatom: the Japanese journal of diatomology, 20, 33–46. https://doi.org/10.11464/ diatom1985.20.0_33
- Fofana, C. A. K., Sow, E. H., Taylor, J., Ector, L., Van de Vijver, B., 2014: *Placoneis cocquytiae* a new raphid diatom (Bacillariophyceae) from the Senegal River (Senegal, West Africa). Phytotaxa 161(2), 139–147. https://doi.org/10.11646/phytotaxa.161.2.5
- Fujita, Y., Ohtsuka, T., 2005: Diatoms from paddy fields in northern Laos. Diatom 21, 71–89. https://doi.org/10.11464/diatom1985.21.0_71
- Gong, Z. J., Li, Y. L., Metzeltin, D., Lange-Bertalot, H., 2013: New species of *Cymbella* and *Placoneis* (Bacillariophyta) from late Pleistocene fossil, China. Phytotaxa 150(1), 29–40. https:// doi.org/10.11646/phytotaxa.150.1.2
- Guiry, M. D., Guiry, G. M., 2022: AlgaeBase. World-wide electronic publication, National University of Ireland, Galway. Retrieved on May 5, 2022 from https://www.algaebase.org.
- Hantzsch, C. A., 1860: Neue Bacillarien: *Nitzschia vivax* var. *elongata, Cymatopleura nobilis.* Hedwigia 2, 1–40.
- Hustedt, F., 1930: Bacillariophyta (Diatomeae). In: Pascher, A., (ed.), Die Süsswasser-Flora Mitteleuropas, 10 (2 Auflage). Gustav Fischer, Jena.
- Johansen J. R., Lowe, R., Gómez, S. R., Kociolek, J. P., Makosky, S. A., 2004: New algal species records for the Great Smoky Mountains National Park, U.S.A., with an annotated checklist of all reported algal species for the park. Algological Studies 111(1): 17–44. https://doi.org/10.1127/1864– 1318/2004/0111–0017
- Kezlya, E., Glushchenko, A., Maltsev, Y., Gusev, S., Kuznetsov, A., Kociolek, J. P., Kulikovskiy, M., 2020: *Placoneis cattiensis*

sp. nov. — a new, diatom (Bacillariophyceae: Cymbellales) soil species from Cát Tiên National Park (Vietnam). Phytotaxa 460(4), 237–248. https://doi.org/10.11646/phytotaxa.460.4.1

- Kezlya, E. M., Glushchenko, A. M., Maltsev, Y. I., Gusev, E. S., Genkal, S., Kociolek, J. P., Kulikovskiy, M. S., 2021: Three new species of *Placoneis* Mereschkowsky (Bacillariophyceae: Cymbellales) with comments on cryptic diversity in the *P. elginensis*-Group. Water 13(22): 3276. https://doi.org/10.3390/ w13223276
- 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(3), 377–385. https://doi.org/10.1111/j.1529-8817.1988.tb04480.x
- Kociolek, J. P., Thomas, E. W., 2010: Taxonomy and ultrastructure of five naviculoid diatoms (class Bacillariophyceae) from the Rocky Mountains of Colorado (USA), with the description of a new genus and four new species. Nova Hedwigia 90(1–2), 195–214. https://doi.org/10.1127/0029– 5035/2010/0090–0195
- Kociolek, J. P., Laslandes, B., Bennett, D., Thomas, E., Brady, M., Graeff, C., 2014: Diatoms of the United States, 1. Taxonomy, ultrastructure and descriptions of new species and other rarely reported taxa from lake sediments in the western U.S.A. Cambridge University Press, Cambridge.
- Kulikovskiy, M. S., Lange-Bertalot, H., Metzeltin, D., Witkowski, A., 2012: Lake Baikal: Hotspot of endemic diatoms I. Iconographia Diatomologica 23, 1–607.
- Kulikovskiy, M., Gusev, E., Andreeva, S., Annenkova, N., 2014: Phylogenetic position of the diatom genus *Geissleria* Lange-Bertalot & Metzeltin and description of two new species from Siberian mountain lakes. Phytotaxa 177(5), 249–260. https://doi.org/10.11646/phytotaxa.177.5.1
- Kulikovskiy, M., Glushchenko, A., Genkal, S. I., Kuznetsova, I., 2016: Identification book of diatoms from Russia. Filigran, Yaroslavl [in Russian].
- Kützing, F. T., 1849: Species algarum. Friedrich Arnold Brockhaus, Leipzig.
- Lange-Bertalot, H., 2001: *Navicula* sensu stricto, 10 genera separated from *Navicula* sensu lato, Frustulia. Diatoms of Europe 2, 1–526.
- Lange-Bertalot, H., Wojtal, A. Z., 2014: Diversity in species complexes of *Placoneis clementis* (Grunow) Cox and *Paraplaconeis placentula* (Ehrenberg) Kulikovskiy, Lange-Bertalot & Metzeltin. Beihefte zur Nova Hedwigia 143, 403–420. https:// doi.org/10.1127/1438–9134/2014/021
- Levkov, Z., Williams, D. M., 2011: Fifteen new diatom (Bacillariophyta) species from Lake Ohrid, Macedonia. Phytotaxa 30, 1–41. https://doi.org/10.11646/phytotaxa.30.1.1
- Li, J. Y., Qi, Y. Z., 2018: Bacillariophyta, Naviaulaceae (III). In: Flora Algarum Sinicarum Aquae Dulcis. Science Press, Tomus, XXIII. [In Chinese with English abstract]
- Li, Y. L., Gong, Z. J., Wang, C.C., Shen, J., 2010: New species and new records of diatoms from Lake Fuxian, China. Journal of Systematics and Evolution 48(1), 65–72. https://doi. org/10.1111/j.1759–6831.2009.00059.x
- Lin, X. R., Rioual, P., Bai, Z. J., Peng, W., Sun, M. J., Huang, X. Z., 2018: The recent diatom flora in Lake Kanas, Xinjiang: unusual species and new records in China. Acta Hydrobiologica Sinica 42(3), 641–654. [In Chinese with English abstract] https://doi.org/10.7541/2018.080
- Liu, Y., Fan, Y. W., Wang, Q. X., 2012: Newly recorded species in Cymbellaceae and Gomphonemataceae from Great Xing'an

Mountains, China. Acta Hydrobiologica Sinica 36, 496–508. [In Chinese with English abstract]

- Liu, Z. X., Liu, B., Quan, S. J., Long, J. Y., Mo, W. H., 2020: Two biraphid diatom species reported from China for the first time-*Prestauroneis tumida* and *Placoneis anglophila* var. *signata*. Acta Botanica Boreali-Occidentalia Sinica 40, 1784– 1791. [In Chinese with English abstract]
- Maidana, N. I., Aponte, G. A., Fey, M., Schäbitz, F., Morales, E. A., 2017: Cyclostepanos salsae and Placoneis patagonica, two new diatoms (Bacillariophyta) from Laguna Cháltel in southern Patagonia, Argentina. Nova Hedwigia Beiheft 146, 89–102. https://doi.org/10.1127/1438–9134/2017/089
- Mann, D. G., Stickle, A. J., 1995: Sexual reproduction and systematics of *Placoneis* (Bacillariophyta). Phycologia 34(1), 74– 86. https://doi.org/10.2216/i0031-8884-34-1-74.1
- Mayama, S., Kawashima, A., 1998: New combinations for some taxa of *Navicula* and *Stauroneis*, and an avowed substitute for a taxon of *Eunotia*. Diatom 14, 69–71. https://doi.org/10.11464/diatom1985.14.0_69
- Meister, F., 1932: Kieselalgen aus Asien. Gebrüder Borntraeger Verlag, Berlin.
- Meister, F., 1935: Seltene und neue Kieselalgen I. Bericht der Schweizerischen Botanischen Gesellschaft 44, 88–108.
- Mereschkowsky, C., 1903: Über *Placoneis*, ein neues Diatomeen-Genus. Beihefte zum Botanischen Centralblatt 15, 1–30.
- Metzeltin, D., Lange-Bertalot, H., 1998: Tropical diatoms of South America I: About 700 predominantly rarely known or new taxa representative of the neotropical flora. Iconographia Diatomologica 5, 3–695.
- Metzeltin, D., Lange-Bertalot, H., 2007: Tropical Diatoms of South America II. Special remarks on biogeography disjunction. Iconographia Diatomologica 18, 1–877.
- Metzeltin D., Lange-Bertalot, H., Soninkhishig, N., 2009: Diatoms in Mongolia. Iconographia Diatomologica 20, 3–686.
- Nakov, T., Ruck, E. C., Galachyants, Y., Spaulding, S. A., Theriot, E. C., 2014: Molecular phylogeny of the Cymbellales (Bacillariophyceae, Heterokontophyta) with a comparison of models for accommodating rate variation across sites. Phycologia 53(4), 359–373. https://doi.org/10.2216/14-002.1
- Novais, M. H., Wetzel, C. E., Van de Vijver, B., Morais, M. M., Hoffmann, L., Ector, L., 2013: New species and combinations in the genus *Geissleria* (Bacillariophyceae). Cryptogamie Algologie 34(2), 117–148. https://doi.org/10.7872/crya.v34. iss2.2013.117
- Pomazkina, G. V., Rodionova, E. V., Sherbakova, T. A., 2019: Validation of 123 names of new diatom taxa from Lake Baikal. Limnology and Freshwater Biology 1: 181–198. https:// doi.org/10.31951/2658–3518–2019–A–1–181
- Qiu, L. C., Wei, G. F., Li, X. J., Shi, L. S., Lin, S. Z., Han, B. P., 2016: Species diversity and temporal-spatial distribution of benthic diatoms in Jianjiang River, Guangdong Province. Journal of Tropical and Subtropical Botany 24: 197–207. [In Chinese with English abstract] https://doi.org/10.11926/j. issn.1005-3395.2016.02.011
- Round, F. E., Crawford, R. M., Mann, D. G., 1990: The diatoms. biology and morphology of the genera. Cambridge University Press, Cambridge.
- Simonsen, R., 1979: The diatom system: ideas on phylogeny. Bacillaria 2, 9–71.
- Straube, A., Tremarin, P. I., de Castro-Pires, E. C., Marquardt, G. C., Veiga Ludwig, T. A., 2013: Morphology, ultrastructure and distribution of *Placoneis itamoemae* sp. nov. (Cymbel-

laceae) from Brazil. Phytotaxa 76(3): 55–62. https://doi. org/10.11646/phytotaxa.76.3.13

- Thomas, E. W., Stepanek, J. G., 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. https://doi. org/10.1371/journal.pone.0152797
- Tong, C. F., Li, L., Meng, Y. Q., Wang, B., 2018: Analysis of stratification-mixing mechanism during spring tide of dry season in the Modaomen waterway. Hydro-Science and Engineering, 48–57. [In Chinese with English abstract] https:// doi.org/10.16198/j.cnki.1009-640X.2018.01.008
- Vishnyakov, V. S., 2020: Description of *Placoneis mologaensis*, a new diatom from the Rybinsk reservoir on the Volga river,

European Russia. Phytotaxa 464(3): 217–226. https://doi. org/10.11646/phytotaxa.464.3.3

- Wang, H. P., Li, D. D., Sun, S. J., Wang, H. J., 2018: The investigation of diatom species composition and database of diatom scanning electron microscope in the Pearl River of Guangdong province. Chinese Journal of Forensic Medicine 33: 154–161. [In Chinese with English abstract] https://doi. org/10.13618/j.issn.1001-5728.2018.02.010
- Wang, X. T., Huang, Y. Y., Huang, S. F., Li, S. J., Lei, Y. D., 2021: Atlas of common diatoms and benthic animals in the Pearl River Basin. China Water & Power Press, Beijing.
- Zidarova, R., Van De Vijver, B., Mataloni, G., Kopalova, K., Nedbalova, L., 2009: Four new freshwater diatom species (Bacillariophyceae) from Antarctica. Cryptogamie, Algologie 30(4): 295–310.