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A new species of *Amphorotia* (Bacillariophyta) from a freshwater section of the Pearl River with comments on associated species and biogeography of the genus

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Abstract: Based on a review of material previously studied, and new water samples, species of the genus *Amphorotia* were investigated with respect to their morphology and geographical distribution, especially in subtropical Asian coastal areas. Six *Amphorotia* species from China are investigated. They all possess amphoroid frustule symmetry, presence of spines and, when detected, a single plastid. These features as well as other details of the frustules were documented with light and scanning electron microscopy. Five of the taxa, *A. reimerii*, *A. mokonensis*, *A. baicalensis*, *A. zhujiangensis*, and *A. curvata* are newly recorded as fossil specimens in the Jianghan Plain. Further comments on the taxonomy and morphological variation of several known species are given. One taxon, *A. liangyanlingii* sp. nov. was discovered from freshwater samples in the Pearl River. This new species is most similar to *A. zhujiangensis* Wu, Williams et Flower when observed in LM, but can be distinguished by ultrastructural details when viewed with the scanning electron microscope (SEM). Taxonomical studies of species in the genus *Amphorotia* are considered together with their biogeography and ecology.

Key words: Diatom, *Amphorotia*, new species, Asia, distribution

Introduction

The genus *Amphorotia* Williams et Reid 2006 was established based on *A. clevei* (basionym: *Eunotia clevei* Grunow in Cleve 1891) as the generitype to accommodate a group of diatoms formerly assigned to *Eunotia* Ehrenberg. Main characters of the genus are distinctly different from other eunotioid genera in the Eunotiaceae, including the amphoroid shape of the frustule, relatively large cell size, thick silica cell walls, coarsely punctate striae, as well as presence of spines, a single plastid, large terminal nodules, orientation of the raphe mostly on the valve mantle and rimoportulae. After Williams & Reid (2006) reviewed 19 *Amphorotia* species, two additional new taxa have been described (Wu & Flower 2016; Wu et al. 2019), bringing the total number of taxa in this genus to 21. Previous work described the diversity of *Amphorotia*, mostly from the Pacific region of South China and Southeastern Asia (Wu & Flower 2016), and especially in the Pearl River (Chen et al. 2014; Wu & Flower 2016; Wu et al. 2019) and Jianghan Plain (Shi 1991, 1997).

This study examines *Amphorotia* spp. from different sites/regions in China. In terms of the Pearl River, previous work by Lan (2007) and Wang et al. (2021) demonstrated that diatoms are rich in the Xijiang River (a tributary of the Pear River; see Fig. 1), and a total of 168 species and varieties belonging to 48 genera were reported. Earlier studies focused on *Amphorotia* in sediments of the lower Pearl River, Guangdong Province (Chen et al. 2014; Wu & Flower 2016; Wu et al. 2019). Moreover, Wu & Flower (2016) suggest that *A. curvata* Williams et Reid seems now to be extinct in the Pearl River delta. Therefore, it is not known if the genus *Amphorotia* can survive in the current freshwater environment of the Pearl River. Our recent work in Guangxi Province on the Xijiang River showed that this region is also interesting for diatom diversity, and two new taxa were described including *Cymbella hechiensis* Y.–L. Li et W. Zhang (Li et al. 2019) and *Delicatophycus liuweii*

Y.–L. Li (LIU et al. 2021).

For the Jianghan Plain, it has been well documented that diatoms are rich in the No.47 borehole collected in this area (Fig. 1); 148 taxa belonging to 26 genera, including one variety of *Amphorotia*, were recognized (SHI 1991, 1997). In addition, our recent work also shows that the Jianghan Plain is excellent for exploring diatom diversity, resulting in the description of 9 new species from the genera *Cymbella* C.A. Agardh, *Cymbopleura* (K. Krammer) K. Krammer in Lange–Bertalot et Genkal, *Geissleria* H. Lange–Bertalot et D. Metzeltin, *Gomphonema* C.A. Agardh, and *Placoneis* C. Mereschkowsky (LI et al. 2005, 2007; GONG et al. 2013); 24 newly recorded species from the genera *Cymbella*, *Cymbopleura, Encyonopsis* K. Krammer, *Geissleria, Gomphonema, Gomphosphenia* H. Lange–Bertalot, *Navicula* J.B.M. Bory de Saint–Vincent, *Pinnularia* C.G. Ehrenberg, *Sellaphora* C. Mereschkowsky (LI et al. 2005, 2007; HU et al. 2013); and 6 newly recorded genera from this region, including *Aneumastus* D.G. Mann et A.J. Stickle in F.E. Round, R.M. Crawford et D.G. Mann, *Cymbopleura, Delicata* K. Krammer, *Encyonopsis, Geissleria,* and *Gomphosphenia* (LI et al. 2005, 2007) have been noted. Nevertheless, our understanding of *Amphorotia* from the two regions is very limited.

To further document regional diatom biodiversity, we investigated the occurrence and distribution of *Amphorotia* species in China derived from freshwater and borehole samples collected from the Pearl River and the Jianghan Plain, respectively. The aims of this paper are: 1) to report the geographical distribution of *Amphorotia* in freshwater and sediments in China in order to a better understanding of this genus, and 2) to provide information about light (LM) and scanning electron microscopical (SEM) observations of a new species.

MATERIAL AND METHODS

Study area. The Pearl River (located between 21.31°–26.49° N and 102.14°–115.53° E, Fig. 1) is the second largest river in southern China with a total watershed of 4.5×10^5 km^2 and a length of 2240 km. It has tributaries comprised of the Xijiang, Beijiang, and Dongjiang rivers (LU et al. 2009; ZHEN et al. 2016). The discovery of one new species is based on freshwater records of the Guijiang River part of the Xijiang River and located in the Pearl River watershed. The Guijiang River (24°15'23.89478" N, 110°46'2.05771" E, 97.495 m a.s.l, Fig. 1), which is one of the major tributaries of the Xijiang River, originates from Maoershan Mountain at an elevation of 2142 m. The river has an area of 18790 km^2 with 438 km long, and it is characterized by the East Asian Monsoon climate with an annual average temperature of about 20 °C in the its catchment from south to north, and significant spatial differences (ZHANG et al. 2019).

The Jianghan Plain (29°26'–31°12' N, 111°45'–114°16' E, Fig. 1), is one of the lowest plains in China, located in the central and southern part of Hubei Province, and formed by the alluvium of the Yangtze River and its tributary, the Han River (XU 2020). This region has an area about 40,000 km^2 with an average altitude of 27 m above sea level (a.s.l), and it is characterized by subtropical monsoon climate with annual mean precipitation of ca. 1100–1300 mm (XU 2020). Our review of five known *Amphorotia* species is based on sedimentary records of No.47 borehole located in the Jianghan Plain. The No.47 borehole (30°11'18" N, 112°35'33" E, Fig. 1) is located in Jiangling County on the Jianghan Plain, Hubei Province, China (SHI 1997). SHI (1997) also deduced that the paleoclimate of this area during the period of luxuriant growth of diatoms was somewhat colder than the present time based on pollen analysis and mineral analysis with diatoms.

Table 1. Physical and chemical parameters in Guijiang River.

Latitude (°N)	24°15'23.89478"
Longitude (°E)	110°46'2.05771"
Altitude (m)	97.495
Water temperature (°C)	37.1
pH	8.35
DO (mg.l^{-1})	7.94
Conductivity (μS.cm^{-1})	181.5

Sampling and testing. A water sample containing species of *Amphorotia* studied herein was taken from the Guijiang River (Table 1) in July 2021. This water sample was collected from 50 cm under the water surface. Physical and chemical features of the river were analyzed according to a variety of methods. pH and specific conductance of river water were measured in the field 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 sediment samples containing species of *Amphorotia* were taken from the No.47 borehole, which is the same as studied by SHI (1991, 1997). The material was collected from the No. 10 stratigraphic sequence in the No.47 borehole (SHI 1997), but previous studies did not provide a precise geological age for this sequence. This material is thought to be of Late Pleistocene age (GONG et al. 2013), laid down under cooler environmental conditions (SHI 1997). Abundant diatoms were found in the upper section of the borehole (46.6–2.2 m) (SHI 1991).

Diatom preparation, identification, and counting. In the field, water samples from the Guijiang River containing *Amphorotia* were fixed in 4 % formaldehyde. Diatom samples were kept under 4 °C in a refrigerator before further laboratory treatments. In the laboratory, carbonates and organic matter of sub–samples were removed using HCl and H_2O_2 in accordance with the method of BATTARBEE (1986). After several rinses in distilled water, a portion of the cleaned diatom material was air–dried onto cover slips and mounted onto slides using Naphrax.

Morphological observations of specimens were performed with light microscopy (LM) (OLYMPUS, BX51, DIC, ×1500, oil immersion lens) and images captured with a C5060 Olympus digital camera. At least 500 valves were identified and counted in each 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). Stubs containing the cleaned material were examined using an LEO 1530 scanning electron microscope at an acceleration voltage of 5–10 kV. Image analysis and plate arrangement were processed with the

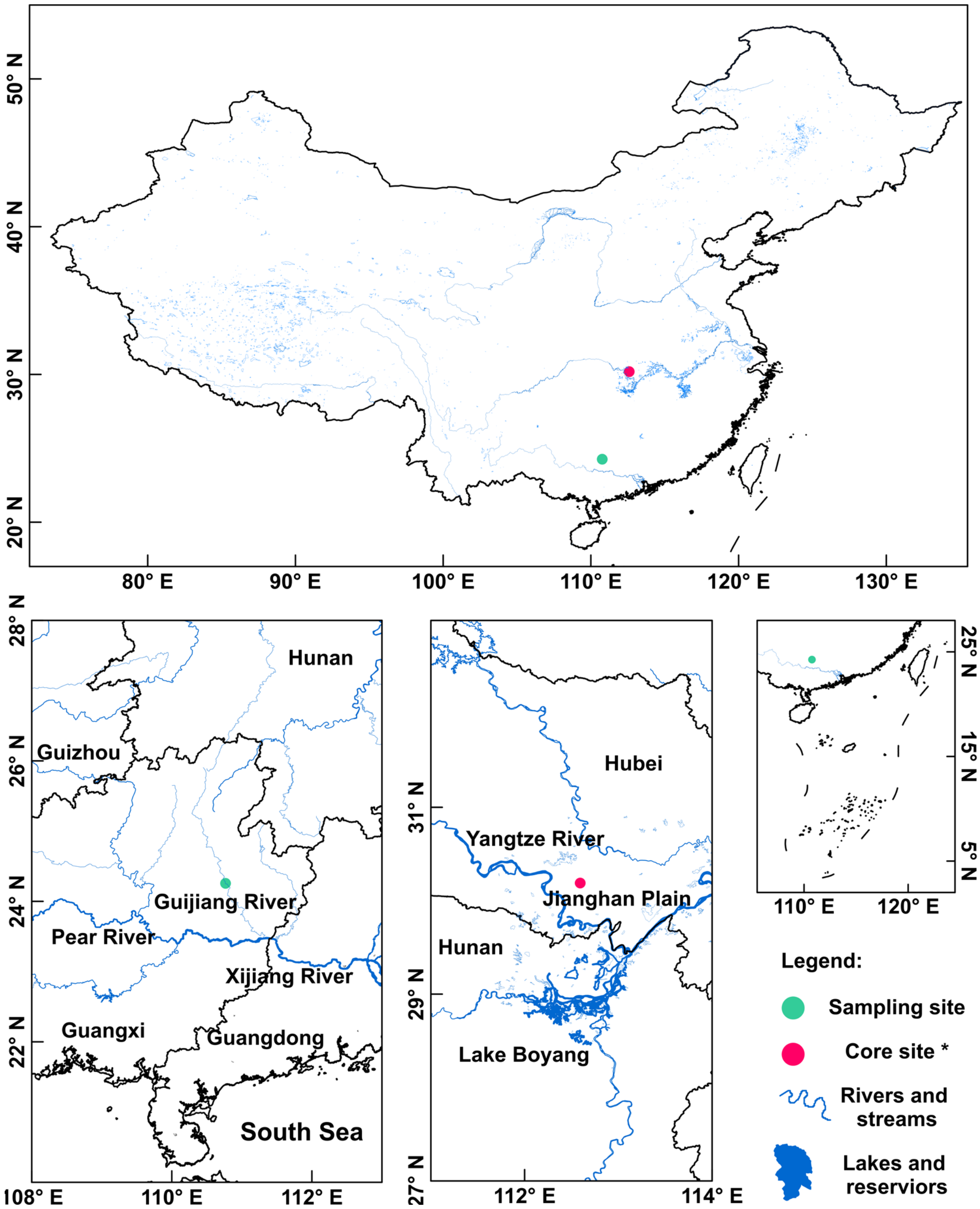


Fig. 1. Study areas and the sampling sites. Sampling site (●: Samples of living species were collected from Guijiang River; ●*: Fossil diatoms were observed in the No.47 core samples located in Jianghan Plain of previous research (Shi 1997)).

program Adobe Photoshop (CS5) (V. 12.1, Adobe Systems, San Jose, CA, USA). The description of the new species follows mainly the terminology provided by Williams & Reid (2006).

Results

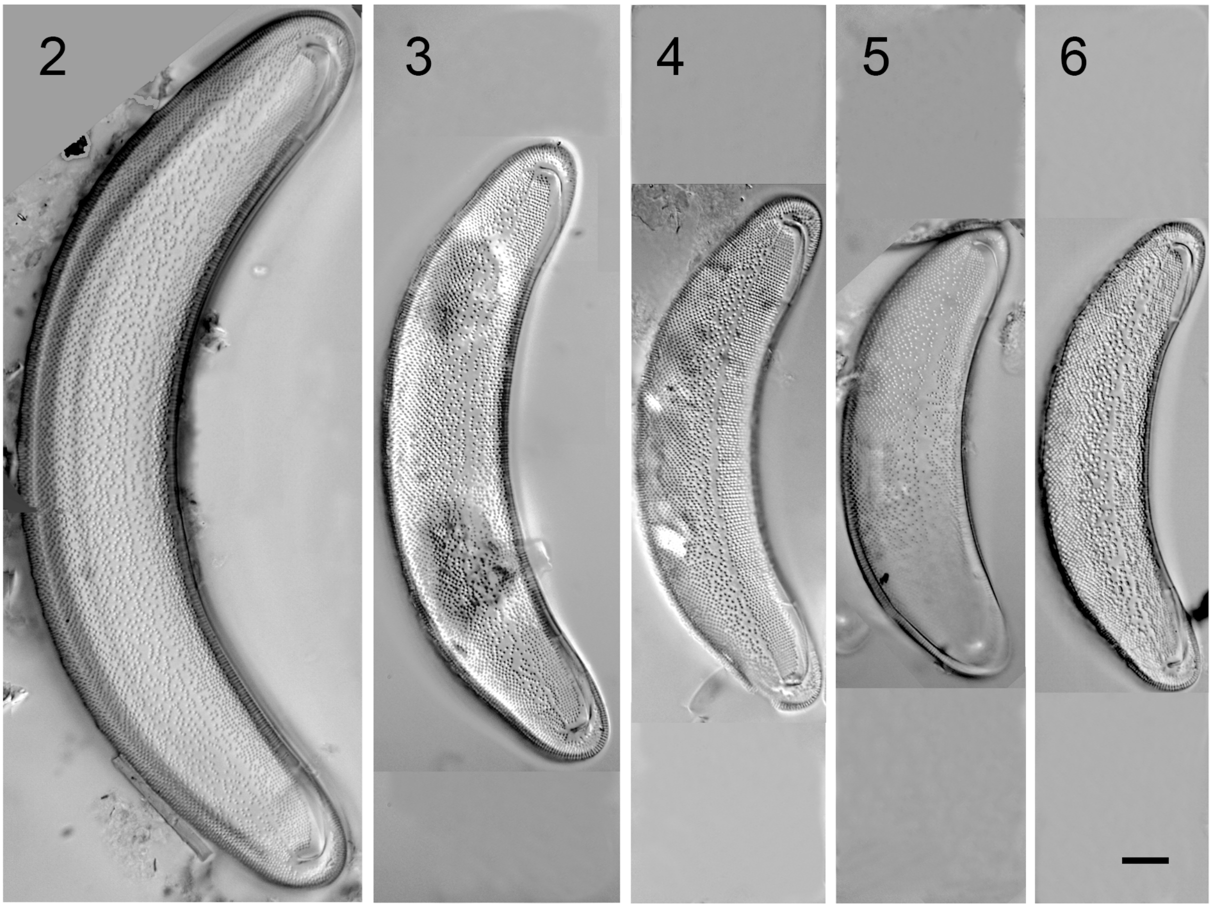
Diatom species morphology

The results of the morphological analyses showed five of the taxa encountered corresponded to known species, including *Amphorotia reimerii*, *A. mekonensis*, *A. baicalensis*, *A. zhujiangensis*, and *A. curvata*. We provide new observations that extend the known variation of these taxa. One additional taxon is described as a new species, *A. liangyanlingii* sp. nov.

Amphorotia reimerii **(Williams et Reid) Williams et Reid 2006 (Figs 2–6)**

Description

Light microscopy (Figs 2–6): Valves large, broadly arcuate to lunate with gently tapering towards two poles; 109–216 µm in length, 24–34 µm in width. Transapical striae regular and evenly spaced towards the valve margin, irregular and scattered at sternum and most of the valve, 9–16 in 10 µm. No oblique striae present.



Figs 2–6. *Amphorotia reimerii*, LM, DIC. Valve views, showing variability of the holotype population. Scale bar 10 µm.

Samples: (in this article) the No.47 borehole in the Jianghan Plain.
Comments: Based on observations previously presented by Williams and Reid (2006), combined with our observations presented herein, the valve size range of this species should be 109–216 µm in length, 20–35 µm in width. The range of transapical striae should be 8–16 in 10 µm.

Amphorotia mekonensis **Williams et Reid 2006 (Figs 7–12)**
Description
Light microscopy (Figs 7–12): Valves broadly arcuate to lunate with gently tapering poles; 120–193 µm in length, 19–30 µm in width. Transapical striae regular, evenly spaced, 9–15 in 10 µm, uniseriate, becoming irregular around the sternum. Rimoportula is adjacent to end of raphe slit, clearly seen at each valve apex. Sternum not well defined, appearing diffuse towards valve centre, terminating and meeting helictoglossa.
Samples: (in this article) the No.47 borehole in the Jianghan Plain.
Comments: Based on observations previously presented by Williams & Reid (2006), combined with our observations presented herein, the valve size range of this species should be 120–193 µm in length, 19–32 µm in width. The range of transapical striae should be 9–15 in 10 µm.

Amphorotia baicalensis **(Skvortzov) D.M. Williams et G. Reid 2006 (Fig. 13)**
Description
Light microscopy (Fig. 13): Valve arcuate with slightly tapering poles; 174 µm in length, 31 µm width. Transapical striae regular towards dorsal margin, uneven and scattered between sternum and ventral mantle edge; 10–17 in 10 µm. No oblique striae present.
Samples: (in this article) the No.47 borehole in the Jianghan Plain.
Comments: Based on observations previously presented by Skvortzov (1929) and Williams and Reid (2006), combined with our observations presented herein, the valve size range of this species should be 100–240 µm in length, 18–31 µm in width. The range of transapical striae should be 10–17 in 10 µm.

Amphorotia zhujiangensis **Wu, Williams et Flower 2019 (Figs 14–15)**
Description
Light microscopy (Figs 14–15): Valves arcuate to lunate, gently tapering at poles, occasionally tapering abruptly; 169–176 µm in length, 28–30 µm width. Transapical striae regularly arranged on most of the

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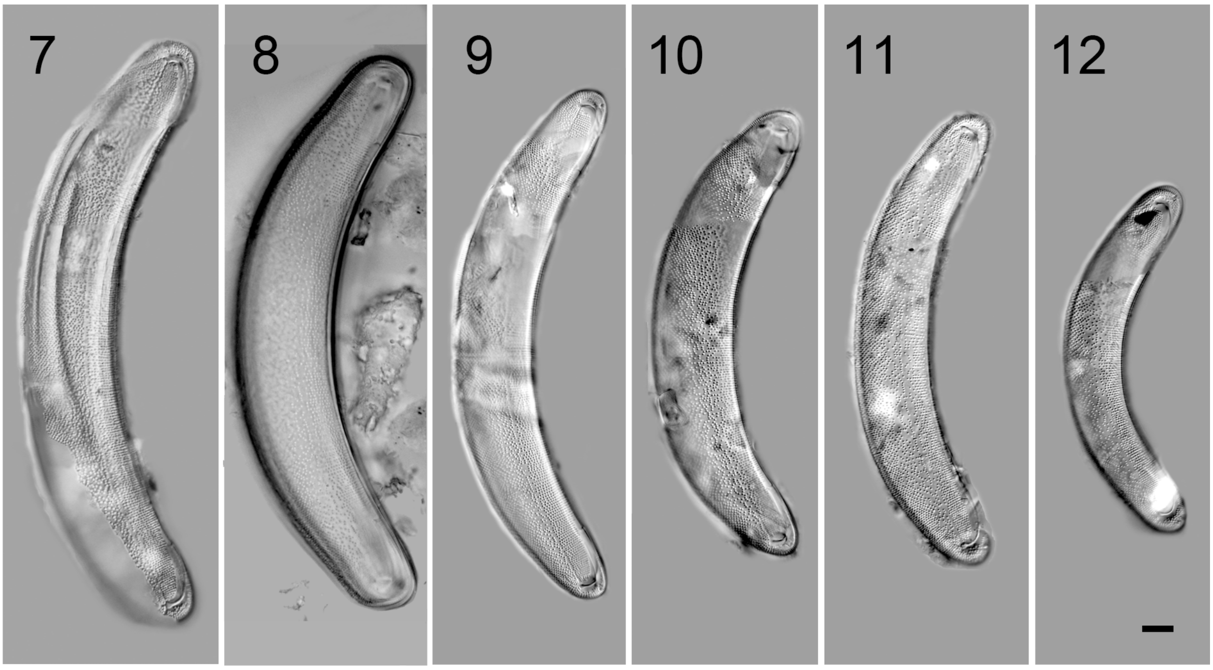


Figs 7–12. *Amphorotia mekonensis*, LM, DIC. Valve views, showing variability of the holotype population. Scale bar 10 µm.

ventral margin, rather irregular on the dorsal side, striae becoming abruptly denser towards valve middle on the dorsal margin, 11–16 in 10 µm. Oblique striae present only on the dorsal margin, 10–13 in 10 µm.
Samples: (in this article) the No.47 borehole in the Jianghan Plain.
Comments: Based on observations previously presented by Wu et al. (2019), combined with our observations presented herein, the valve size range of this species should be 75–176 µm in length, 20–30 µm in width. The range of transapical striae should be 8–16 in 10 µm, and the range of oblique striae should be 10–15 in 10 µm.

***Amphorotia curvata* Williams et Reid 2006 (Figs 16–20)**
Description
Light microscopy (Figs 16–20): Valves arcuate, almost lunate, with abruptly rounded apices, almost parallel margins; 128–222 µm length, 27–34 µm width. Transapical striae from 11–16 in 10 µm. Oblique striae interrupted longitudinally with sternum that terminates at each large apical helictoglossa, 11–15 in 10 µm.
Samples: (in this article) the No.47 borehole in the Jianghan Plain.
Comments: Based on observations previously presented by Williams & Reid (2006), combined with our observations presented herein, the range of valve size of this species should be 72–222 µm in length, 16–34 µm in width. The range of transapical striae should be 11–18 in 10 µm, while the range of oblique striae should be 11–16 in 10 µm.

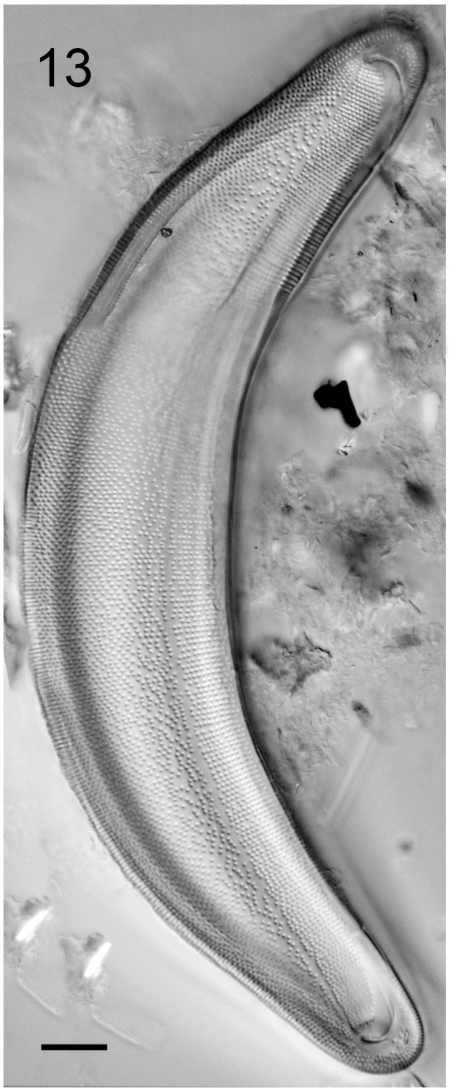


Fig. 13. *Amphorotia baicalensis*, LM, DIC. Valve views, showing variability of the holotype population. Scale bar 10 µm.

Figs 14–15. *Amphorotia zhujiangensis*, LM, DIC. Valve views, showing variability of the holotype population. Scale bar 10 µm.

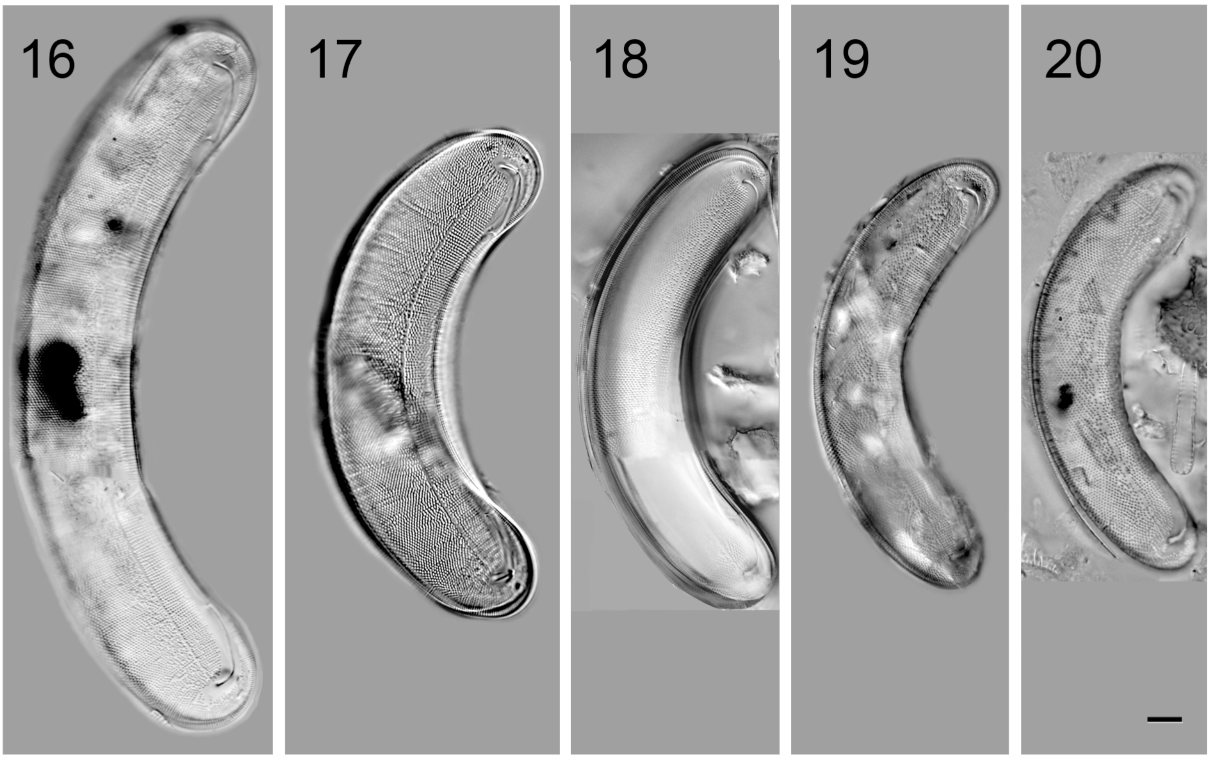
***Amphorotia liangyanlingii* Y.–L. Li sp. nov. (Figs 21–38)**
Description
Light microscopy: Frustules (Figs 21–24): Distinctively 'wedge–shape' in girdle view with truncate ends. Each cell with convex dorsal margin and subtly concave ventral margin, slightly flattened in the center. Frustule symmetry similar to species of *Epithemia* Kützing and *Amphora* Kützing.
Valve (Figs 25–31): Valves arcuate to lunate, dorsal and ventral margins similarly arched or dorsal margin more inflated, ends gently tapering or occasionally tapering abruptly, poles bluntly rounded. Length 92–149 µm, width 21–29 µm, length/width ratio 4.4–5.6, median 5.3 (n = 7). Raphe short, appearing as a clear hyaline area at both poles. External central raphe ends deflected gently towards the ventral side. External terminal raphe fissures slightly dilated, curved towards dorsal margin. Transapical striae regularly arranged on most of the ventral side, rather irregular on the dorsal side, striae becoming considerably denser close to dorsal margin, 9–18 in 10 µm. Oblique striae present only on the dorsal margin and extended to the valve mantle, 9–15 in 10 µm. Areolae not distinctly discernible on the valve face.
Scanning electron microscopy: Valve exterior (Figs 32–35): Small spines situated on both valve margins, irregularly spaced (Figs 32–34). Raphe short with central raphe ends deflected ventrally and extending from valve face towards mantle edge, turning inwards (Figs 32, 33, 35), terminal fissures slightly hooked, deflected towards the dorsal side, terminating in clear hyaline areas; there is a small pore near sternum terminus (Figs 32, 33, 35). Striae uniseriate, characters observed similar to those in LM (Figs 32–35). Areolae dot–like, 9–20 in 10 µm (Figs 33–35).
Valve interior (Figs 36–38): Striae formed by crescent to rounded, uniseriate areolae (Figs 36–38). Internal terminal raphe slit terminates within a large helictoglossa at each valve end (Figs 36–38), central raphe ends hooked in opposite directions (Figs 36–38). Rimoportula well–developed, with protruding 'lips', adjacent to helictoglossa at each valve end (Figs 37, 38). Sternum evident, slightly raised internally, appearing diffuse towards valve centre, terminating and meeting helictoglossa (Figs 37, 38).

Holotype: HANU! Individual in slide YUNGL20210729 (Harbin Normal University, Heilongjiang, Harbin). Isotype deposited in the J.P. Kociolek Collection (COLO).
Type locality: Water samples of Guijiang River (24°15'23.89478' N, 110°46'2.05771" E, elevation 97.495 a.s.l), the tributary of Xijiang River.
Etymology: This taxon is dedicated to the Chinese ecologist, Prof. Dr. Yanling Liang.

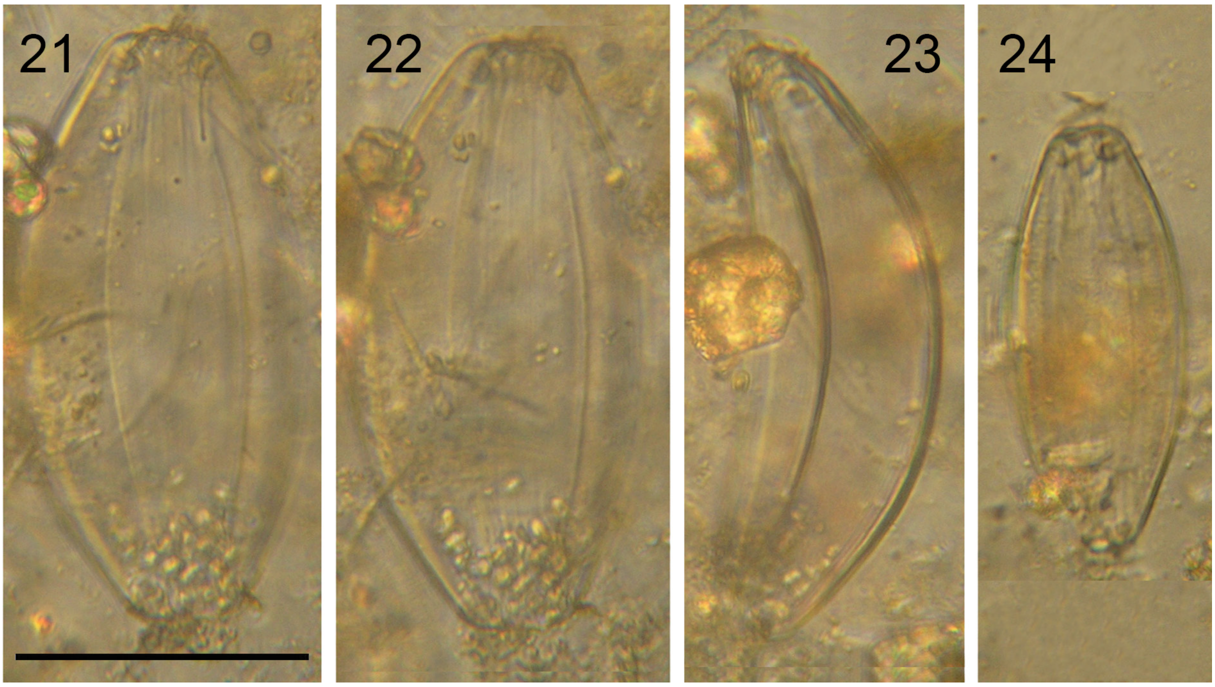
Ecology and confirmed distribution: So far this species has only been observed in a freshwater section of the Pearl River system. It was associated with *Achnanthes tumescens* A.R. Sherwood et R.L. Lowe (2009: 331), *Aulacoseira granulata* (Ehrenberg) Simonsen (1979: 58), *Cymbella turgidula* Grunow (Schmidt 1875: p. 9), *C. tumida* (Brébisson) van Heurck (van Heurck 1880: p. 64), *Fragilaria capucina* Desmazières (Desmazières 1830: p. 453), *F. tenera* (W. Smith) Lange–Bertalot (Lange–Bertalot 1980: p. 746), *Gomphonema minutiforme* Lange–Bertalot et E. Reichardt (Lange–Bertalot & E. Reichardt 1993: p. 61), *G. parvulum* (Kützing) Kützing (Kützing 1849: p. 65), *G. pumilum* (Grunow) E. Reichardt et Lange–Bertalot (Reichardt & Lange–Bertalot 1991: p. 528), *Karayevia clevei* (Grunow) Bukhtiyarova (Bukhtiyarov 1999: p. 94), *Navicula cryptotenella* Lange–Bertalot (Krammer & Lange–Bertalot 1985: p. 43), *Nitzschia palea* (Kützing) W. Smith (Smith 1856: p. 89), *Planothidium lanceolatum* (Brébisson ex Kützing) Lange–Bertalot (Lange–Bertalot 1999: p. 287), *Ulnaria ulna* (Nitzsch) Compère (Compère 2001: p. 100), and one unidentified species of *Sellaphora* C. Mereschkowsky (Mereschkowsky 1902).

Discussion

Morphology of the genus *Amphorotia*
The newly described species *Amphorotia liangyanlingii* fits well within the genus *Amphorotia* by virtue of a complex of morphological characters, notably the amphoroid shape of the frustule, details of the siliceous structure of the valve and girdle, and size and orientation of the raphe and rimoportulae. However, *A. liangyanlingii* differs

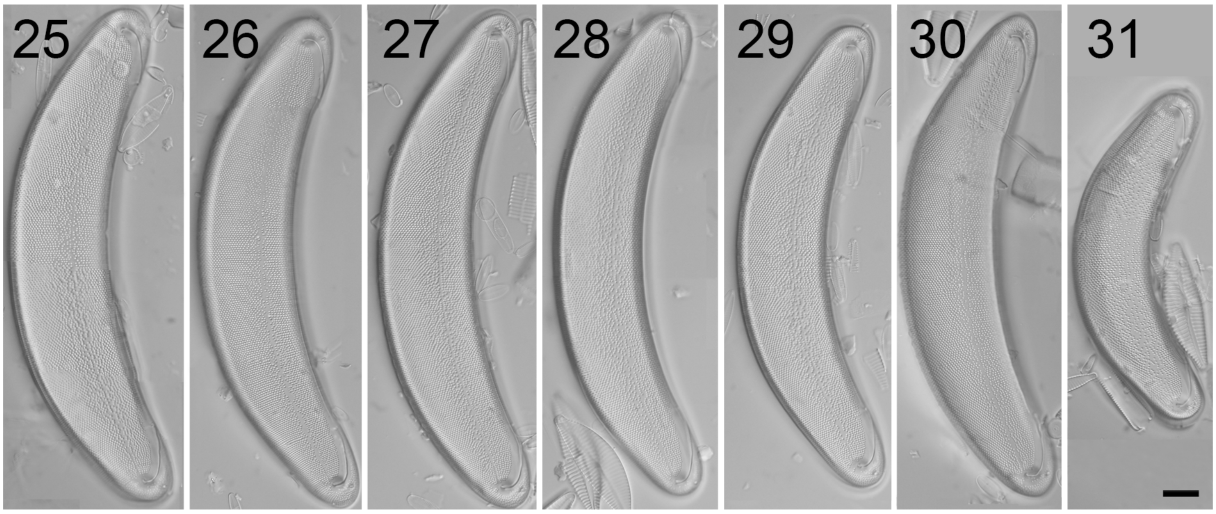


Figs 16–20. *Amphorotia curvata*, LM, DIC. Valve views, showing variability of the holotype population. Scale bar 10 μm.



Figs 21–24. *Amphorotia liangyanlingii* sp. nov. LM, DIC. Valve views, showing entire frustules. Scale bar 10 μm.

strikingly from the 21 other known species within the genus in four features: 1) the smaller size of the valves, 2) a different combination of valve shape and striation, 3) having longer or broken spines, and 4) the shape and direction of central raphe ends. Morphologically, the species is most similar to *A. zhujiangensis, A. mekonensis* and *A. baicalensis*, with which it shares an arcuate to lunate valve shape and bluntly rounded poles (Williams & Reid 2006; Wu et al. 2019). The characters found in *A. liangyanlingii* are compared with other five known species of the genus in Supplementary table 1. They are compared, contrasted and discussed below.



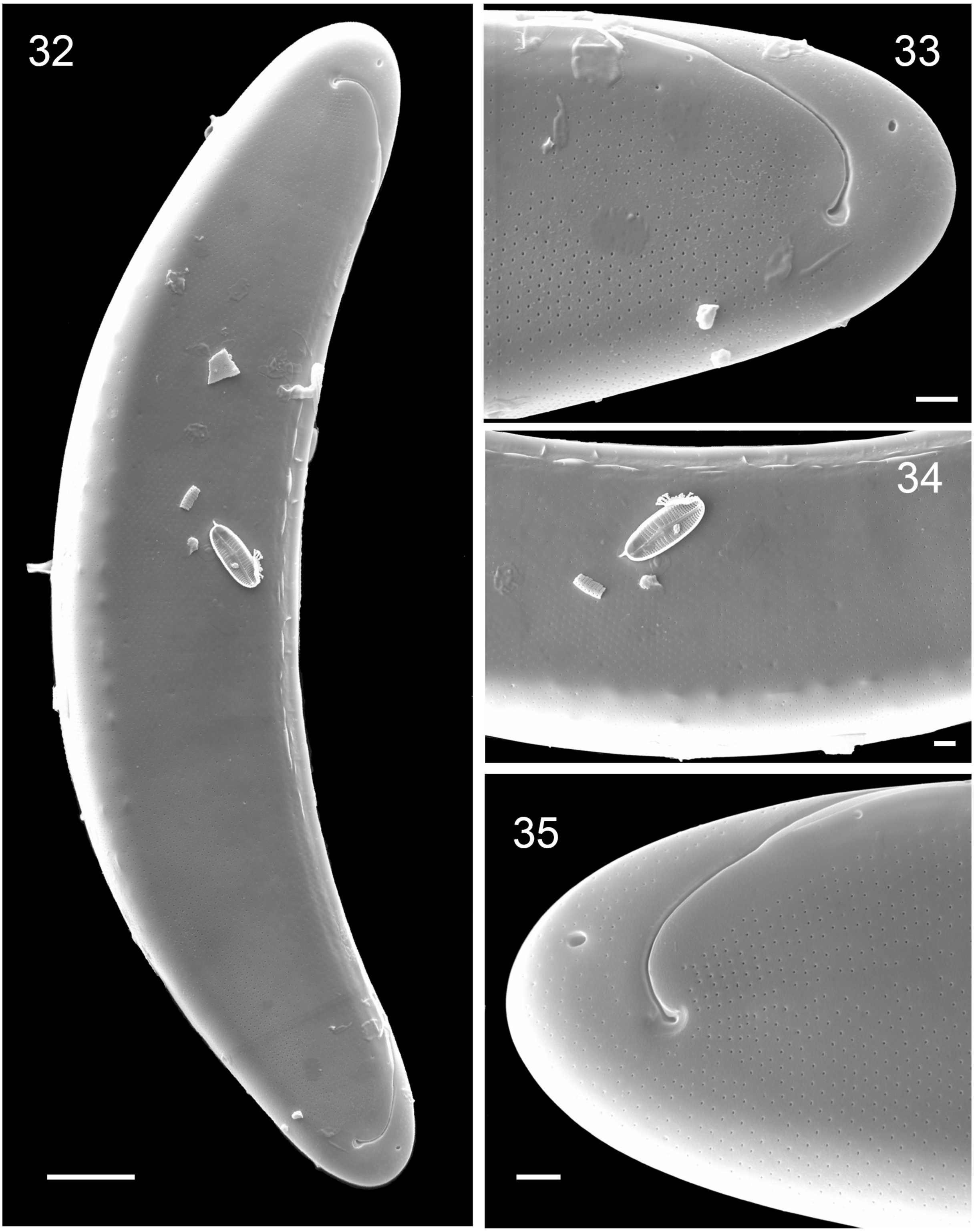
Figs 25–31. *Amphorotia liangyanlingii* sp. nov. LM, DIC. Valve views, showing variability of the holotype population. Fig. 26 is the holotype. Scale bar 10 μm.

The arrangement of striae is a distinguishing character for some taxa of *Amphorotia*. Taking into consideration stria density, only *A. baicalensis* can be considered a potentially related species to the taxa described here, but it differs in having arcuate valves versus the arcuate to lunate valves in *A. liangyanlingii* (Williams & Reid 2006). In terms of the shape of the valves, the *A. liangyanlingii* is similar to *A. zhujiangensis* and *A. mekonensis*, which share arcuate to lunate valves, but it differs from these other two species in that the degree of curvature of the valve margin is in between the other two species (Williams & Reid 2006; Wu et al. 2019). If the suite of characteristics of valve shape and striation are taken into consideration, the newly described species is morphologically most similar to *A. zhujiangensis*, but it differs from that taxon in the shape of raphe ends. For example, the central raphe ends are hooked in opposite directions from one another in *A. liangyanlingii* while they are undulate in *A. zhujiangensis*. The structure of the central raphe ends can also distinguish the newly described taxa from other members of the genus. It is also important to point out that *A. liangyanlingii* sp. nov. has longer (or sometimes broken) spines as compared to other three similar species (Wu et al. 2019).

Biogeography of the genus *Amphorotia*

Knowledge of biogeography is crucial for understanding the diversity, systematics, geographic range, and ecological role of species (Kociolek 2018). Williams & Reid (2005, 2006) have discussed the biogeography of *Amphorotia*, illustrating that *Amphorotia* has two basic patterns: (1) being present in the Northern Hemisphere, such as Siberia, Scandinavia, Russia and Mongolia (Hustedt 1913; Wislouch & Kolbe 1927; Skvortzov 1937a; Reid & Williams 2001; Edlund et al. 2010), (2) having a trans–Pacific distribution, being found in Indochina, China, Japan, Vietnam and United States (Skvortzov 1929; Qi et al. 1988; Shi 1991; Wang 1998). Hence, the discovery of known species in the Jianghan Plain resembles the distribution patterns of the other trans–Pacific taxa.

Summarizing previous studies from Europe and Asia, the genus *Amphorotia* has a distinct biogeographical distribution (Williams & Reid 2006; Wu & Flower 2016; Williams & Kociolek 2017; Wu et al. 2019). Fig. 39 provides the current distribution of the genus *Amphorotia* both fossil and recent occurences of *A. clevei* (Grunow) D.M. Williams et G. Reid (Scandinavia, Russia, Japan, USA, China). The taxa known only as recent species include: *A. baicalensis* (Skvortzov) D.M. Williams et G. Reid, *A. linearis* D.M. Williams et G. Reid, *A. lacusbaikali* (Skvortzov) D.M. Williams et G. Reid, *A. lunata* D.M. Williams et G. Reid, *A. hispida* (Skvortzov) D.M. Williams et G. Reid (all Lake Baikal endemics), *A. stoermeri* D.M. Williams et G. Reid (Mongolia endemic), *A. asiatica* (M. Voigt) D.M. Williams et G. Reid (Indochina, China), *A. sinica* (Skvortzov) D.M. Williams et G. Reid (China, Japan), *A. mekonensis* D.M. Williams et G. Reid (Mekong River, Vietnam, China) and *A. reimeri* (D.M. Williams et G. Reid) D.M. Williams et G. Reid (China). Taxa known exclusively as fossils: include *A. spinusnullosi* D.M. Williams et G. Reid (USA, Finland), *A. voigtii* D.M. Williams et G. Reid, *A. curvata* (Wang) D.M. Williams et G. Reid, *A. miocenica* (Li) D.M. Williams et G. Reid (all China), *A. americana* (Kain et Schultze) D.M. Williams et G. Reid (USA), *A. aculeata* (Moiseeva) D.M. Williams et G. Reid, *A. maculata* (Lupikina et Dolmatova) D.M. Williams et G. Reid and *A. penzhica* (Lupikina et Dolmatova) D.M. Williams et G. Reid (all Russia), *A. zhujiangensis* Wu, Williams et Flower (all China). In addition to the recent treatments on *Amphorotia* from Europe, areas such as United States, Japan and Russia are relatively well studied in terms of their *Amphorotia* species, but for other areas our knowledge of *Amphorotia* is very uneven (Williams & Reid 2006). As a result, only fossil

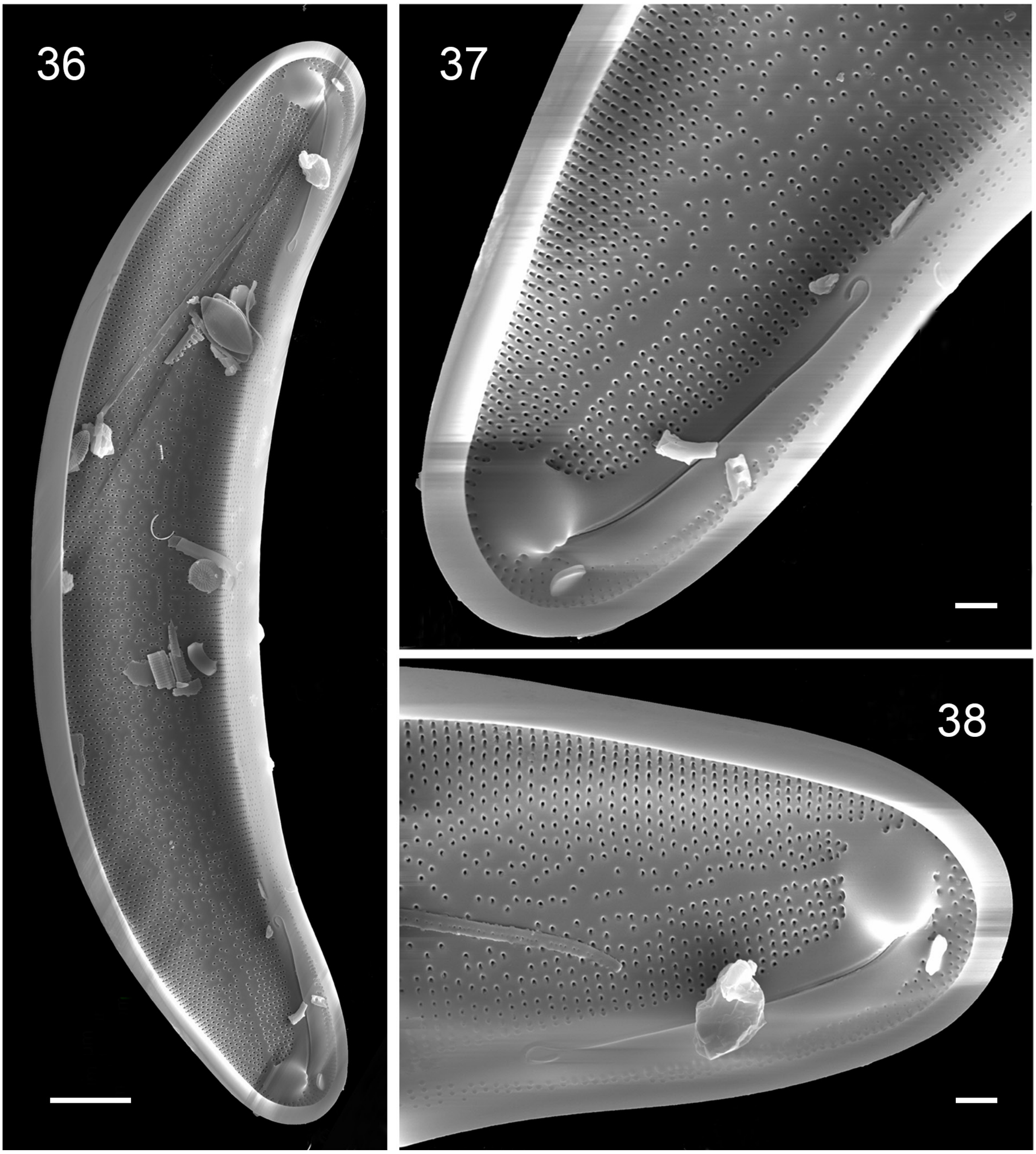


Figs 32–35. *Amphorotia liangyanlingii* sp. nov. SEM, external views: (32) external view of an entire valve; (33, 35) valve apices, the uniseriate striae with rounded areolae and a small pore near sternum terminus; (34) external view of valve center, the uniseriate striae with rounded areolae. Scale bars 10 µm (32), 2 µm (33–35).

diatoms of this genus have been found in China to date. Therefore, six species of the diatom genus *Amphorotia* were collected from Pearl River and Jianghan Plain B/H 47. Of these, one from the freshwaters of the Pearl River was described as new to science and formally described here. The other five known species from the sediments of Jianghan Plain were revised.

Ecology of the genus *Amphorotia*

Amphorotia species occupy environments with a wide range



Figs 36–38. *Amphorotia liangyanlingii* sp. nov. SEM, internal views: (36) internal view of an entire valve; (37, 38) valve near apex with helictoglossa and shortened raphe which ends hooked in opposite directions from one another. Scale bars 10 µm (36), 2 µm (37, 38).

of temperatures. There are species that occur in the cold boreal regions including Lake Baikal, Scandinavia, Russia and Mongolia (Hustedt 1913; Wislouch & Kolbe 1927; Skvortzov 1937a; Reid & Williams 2001; Edlund et al. 2010), yet there is a large number of species known from tropical and subtropical environments including the Pearl River and Jianghan Plain (Shi 1991, 1997; Chen et al. 2014; Wu & Flower 2016; Wu et al. 2019). The discovery of this genus in Guijiang River and Jianghan Plain area supports the idea that species emerged from the subtropical coastal areas and were possibly derived from the boreal species pool (Williams & Reid 2006; Williams 2011).

In addition to the fossil habitats in which *Amphorotia* species can be found, the genus also occurs in Recent freshwaters (Williams & Reid 2006). However, previous research has shown that only fossil diatoms have been found in China, not extant in water bodies (Shi 1991, 1997; Chen et al. 2014; Wu & Flower 2016; Wu et al. 2019). Since *Amphorotia* is mostly found in alkaline environments (Williams & Reid 2005), it seems to suggest that a strong boundary limited genera to low or higher pH levels. Further research is necessary to understand the biogeography and ecology of this genus through studies with a global perspective across environmental gradients.

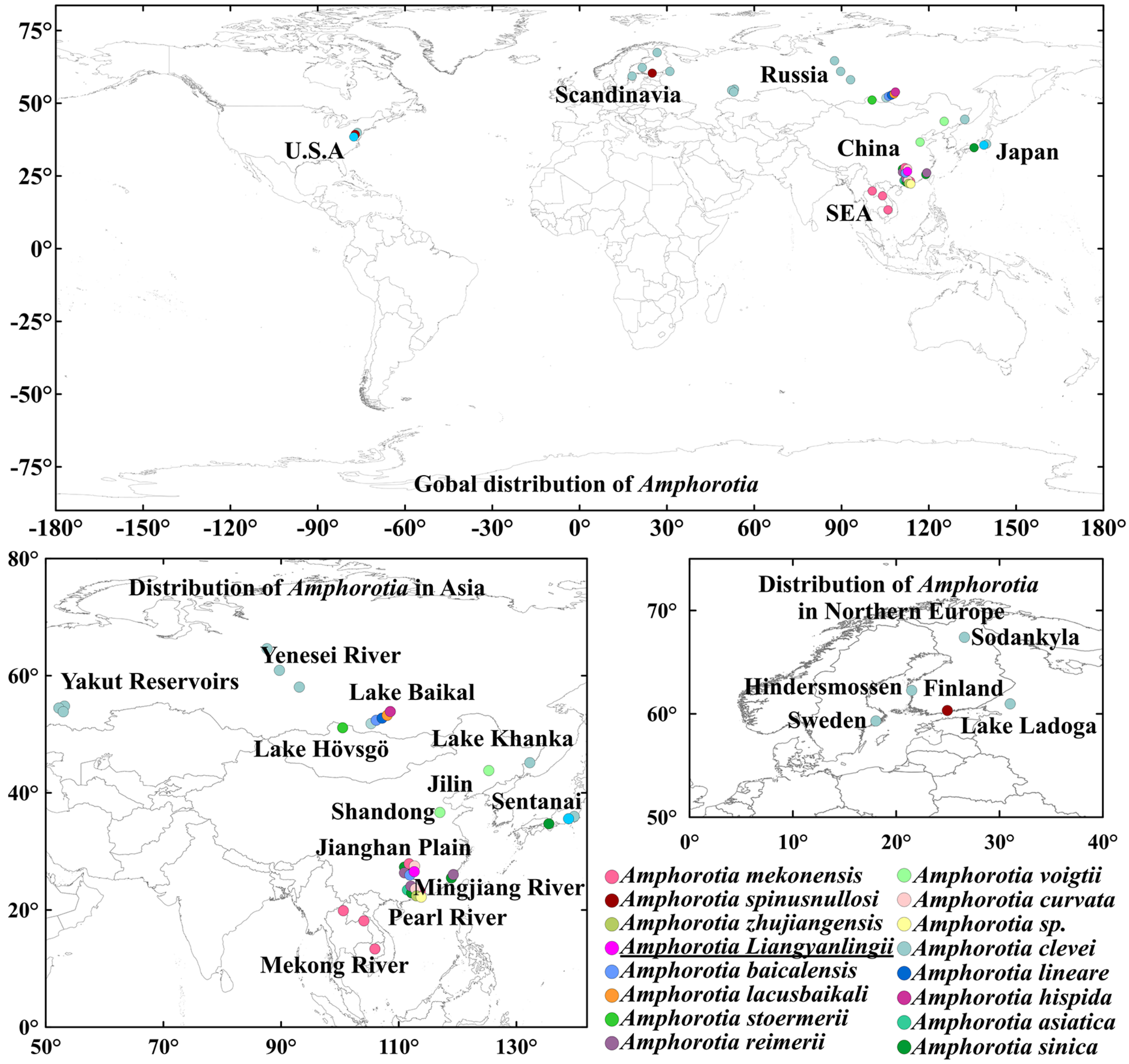


Fig. 39. Distribution of *Amphorotia* species across the Pacific and the Northern Hemisphere. The underlined taxon is *Amphorotia liangyanlingii* sp. nov.

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Supplementary material

The following supplementary material is available for this article:

Table 1. Comparison of Amphorotia species in this study.

This material is available as part of the online article (http://fottea.czechphycology.cz/contents)

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