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Yuzaoea gen. nov., a new biraphid diatom (Bacillariophyceae) genus and its phylogenetic significance

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Abstract

The flexed frustules in pennate diatoms are usually associated with monoraphid diatoms. Interestingly, we found a biraphid diatom species with flexed frustules in an offshore intertidal beach environment on Weizhou Island, Beihai City, Guangxi Zhuang Autonomous Region, China. Therefore, based on morphological characteristics, we described a new genus of diatoms *Yuzaoea sinensis* gen. et sp. nov. CH Li, HH Liu, YH Gao & CP Chen. The frustule of this genus is characterized by heterogeneous frustule with one concave valve and one convex valve, complete raphe on both valves, straight and moderately eccentric raphe, uniseriate striae and girdle bands with a single row of areolae. The most identifying feature of this genus was the flexed frustule, which is rare in biraphid diatoms and common in monoraphid diatoms. We compared the morphometric characteristics of genus *Yuzaoea* with genus *Rhoikoneis* and several genera within the family Rhoicospheniaceae, including *Rhoicosphenia*, *Campylopyxis*, and *Cuneolus*. Phylogenetic analyses based on SSU rRNA and *rbc*L showed that the genus *Yuzaoea* was the sister group to the clade of *Rhoicosphenia* with a high support value (bootstrap values = 100%), and the clade "*Yuzaoea*+*Rhoicosphenia*" was sister to the clade of monoraphid diatoms, in which the genera *Achnanthidium*, *Planothidium* and some *Cocconeis* with high support values (bootstrap = 100%). Morphologically, the genus *Yuzaoea* shares many morphological features with monoraphid diatoms like genera *Achnanthidium* and *Planothidium* and the members within the Rhoicospheniaceae. Therefore, based on a combined morphological studies and phylogenetic results we suggested that this branch may represented the evolution of one kind monoraphid diatoms, from biraphid diatoms (e.g. genus *Yuzaoea*), to incompleted biraphid diatoms (e.g. genera *Rhoicosphenia*, *Campylopyxis*), to monoraphid diatoms (e.g. genera *Achnanthidium* and *Planothidium*).

Key words: biraphid diatom, marine, new genus, Rhoicospheniaceae, taxonomy, *Yuzaoea*

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1 Introduction

The raphe is the slit-like opening in the diatom valve, which is related to the movement of diatoms (Round et al., 1990). Diatoms can secrete extracellular polymers through the raphe to help them move (Jin et al., 2018). Raphid diatoms have several types based on raphe systems, including biraphid diatoms, canal raphid diatoms and monoraphid diatoms (Round et al., 1990). The morphology and number of raphes are considered to be important features in diatom evolution (Kociolek et al., 2019). A biraphid diatom valve usually has two branches of raphe, and the position of raphe is usually in the center or at the edge of the valve (Ross et al., 1979). On the other hand, monoraphid diatoms have raphe on one valve and no raphe on the other, which are thought to have evolved from biraphid diatoms (Kociolek and Stoermer, 1986; Cox, 2010).

Compared with many monoraphid diatoms which usually have flexed frustules, few biraphid diatom genera have frustules with convex and concave valves. The biraphid diatom genus *Rhoikoneis* was established by Grunow (1863) to accommodate species flexed in girdle view similar to *Achnanthes* but could be distinguished by the presence of a central nodule on both valves. The genus included four species, i.e., *R. bolleana*, *R. garkeana*, *R. genuflexa* and *R. trinodis*. However, further study showed that taxa in *Rhoikoneis* were morphologically distinct and unrelated.

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R. genuflexa was moved to the genus *Rhoicosphenia* since it is an earlier synonym of *Rhoicosphenis adolfi* M. Schmidt. *R. trinodis* was placed in the genus *Achnanthes* (Van Heurck, 1880). Medlin (1985) reappraised the genus *Rhoikoneis* and described a new genus *Campylopyxis* based on *C. garkeana* (= *R. garkeana*). *Rhoikoneis* shares many morphological features with the genus *Navicula*, such as the raphe system and slit-like openings to the areolae, and is placed in the order Naviculales, the family Naviculaceae (Medlin, 1991). On the other hand, *Campylopyxis* and *Rhoicosphenia* are distinguished from *Rhoikoneis* by the type of areolae, the structure of the raphe and the morphology of the cingulum, belonging to the order Cymbellales, the family Rhoicospheniaceae (Round et al., 1990).

During the survey of epipsammic diatom flora from the marine sandy beach in southern China, an unknown taxon flexed in the pervalvar axis was analyzed and could not be ascribed to any established genera in the diatom literature. Therefore, a new genus, *Yuzaoea* gen. nov. is described to accommodate the new species. The new species *Yuzaoea sinensis* sp. nov. is introduced based on morphological examination with light microscopy (LM) and scanning electron microscopy (SEM). Their phylogenetic relationships among the genera and families in raphid diatoms are also investigated and discussed.

2 Materials and methods

The sandy samples were collected from the intertidal zone of Weizhou Island (21°01′31″N, 109°08′07″E), Guangxi Zhuang Autonomous Region, China. Weizhou Island, the largest volcanic island in China, is located in the central part of the Beibu Gulf, South China Sea. It has a broad intertidal zone and coral distribution and a subtropical monsoon climate with an average annual sea surface temperature of 24.6℃. Beibu Gulf is located in the northwestern South China Sea, which is a semienclosed bay. It is located in the tropical and subtropical zone with rich resources and is one of China’s excellent fishing grounds (Chen et al., 2013).

The sand sample was first treated by ultrasound to make the epipsammic diatoms fall off, and the diatoms were diluted and cultured in the 96 multi-well culture plates with f/2 medium. Cultured diatom samples were collected, concentrated hydrochloric acid was added, and the samples were boiled in a water bath to obtain clean diatom frustules. They were then rinsed several times with distilled water to remove the hydrochloric acid and salts. For LM, the treated diatom sample was fixed with Naphrax to make permanent slides. For SEM, the acid-cleaned frustules were adhered to SEM stubs by using electroconductibility adhesive tape and covered with gold (Cocquyt, 2004; Chen et al., 2019).

LM observation was performed using an Olympus BX51 microscope (Japan) or an Olympus CKX41 inverted microscope (Japan) with a DP70 digital camera system or Canon 60D camera. SEM observation was performed under 10–20 kV conditions using JEOL JSM-6390A and FEI Quanta 650 FEG analytical scanning electron microscopy at Xiamen University (Taylor et al., 2007). Slides with at least 30 valves for morphological data measurement were stored in the Biology Department Herbarium, Xiamen University (AU: Amoy University), China.

For DNA extraction, the cells were obtained by centrifugation for 10 min at 4 000 × *g* with 5 mL of cultured cell samples from the middle stage of logarithmic growth. Total DNA was extracted with the SteadyPure Plant Genomic DNA Kit (Accurate Biotechnology, Changsha, China) according to the manufacturer’s instructions. Primers from Zimmermann et al. (2011) and Ruck and Theriot (2011) were used to amplify the 18S rDNA fragment and part of the *rbc*L plasmid gene, respectively. PrimeSTAR premade mix (Takara, China) was used for PCR amplification. The conditions of amplification for 18S rDNA fragments were as follows: predenaturation at 95℃ for 5 min; 35 cycles at 94℃ for 30 s, 52℃ for 30 s, and 72℃ for 50 s; and a final extension at 72℃ for 10 min. The conditions of amplification for part of the *rbc*L plasmid gene were as follows: 95℃ for 5 min; 36 cycles at 95℃ for 30 s, 58℃ for 30 s, and 72℃ for 1 min; and a final extension at 72℃ for 5 min. The results of PCR amplification were demonstrated by 1% agarose gel electrophoresis, stained by GelStain. DNA products were sent to Sangon Biotech Company for product purification using SanPrep Column PCR Product Purification Kit (Sango Biotech, Shanghai, China) and sequencing using ABI 3730xl DNA Analyser.

The resulting sequences were checked and first aligned using the mafft V7.110 online program (http://mafft.cbrc.jp/alignment/server/) and the default settings. We manually checked the alignment using BioEdit v.7.0.9 (Hall, 1999). The maximum likelihood (ML) analysis was carried out by Raxml V7.2.6 (Stamatakis and Alachiotis, 2010) using the Model GTRMM in T-rex web servers (Boc et al., 2012). The bootstrap values were obtained by making 1 000 replicates of the ML analyses for each branch node of the phylogenetic tree.

3 Results

***Yuzaoea* CH Li, HH Liu, YH Gao & CP Chen, gen. nov.**

3.1 *Description*

Frustule heterovalvate, flexed in girdle view, cells can be linked together to form a colony. Valve elliptical to linear-elliptical with rounded apices. Raphe straight, moderately eccentric with expanded proximal raphe ends. Terminal raphe fissures hooked towards the same sides. Internally, helictoglossae well developed, and proximal raphe ends deflected towards the same sides. Striae uniseriate, parallel or slightly radial, composed of small areolae and internally occluded by hymenes. Girdle bands with one row of pore.

TYPE SPECIES. *Yuzaoea sinensis* CH Li, HH Liu, YH Gao & CP Chen, sp. nov.

ETYMOLOGY. The genus is named after Professor Yuzao Qi (Jinan University, China) in recognition of his outstanding contributions to the study of diatoms and aquatic biology in China. The specific epithet “*sinensis*” refers to China, where the specimen was found.

Yuzaoea sinensis CH Li, HH Liu, YH Gao & CP Chen, sp. nov. (Figs 1–4)

LM: Valve elliptical to linear, with rounded apices, 2.6–7.9 μm

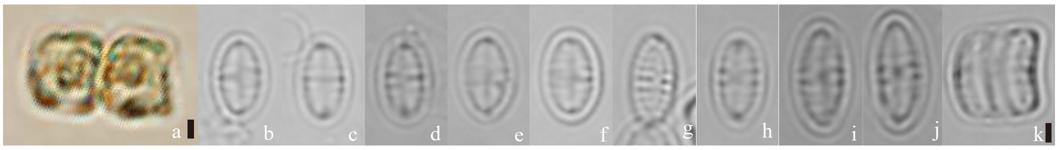

Fig. 1. LM micrographs of *Yuzaoea sinensis* gen. & sp. nov. Scale bar = 1 μm.

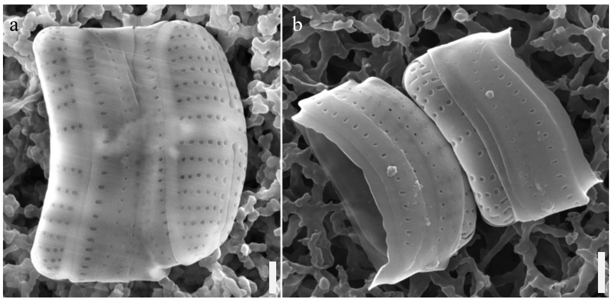

Fig. 2. SEM images of *Yuzaoea sinensis* gen. & sp. nov. Girdle view. Flexed frustule (a). Two valves joined together, showing a girdle band (b). Scale bars = 1 μm.

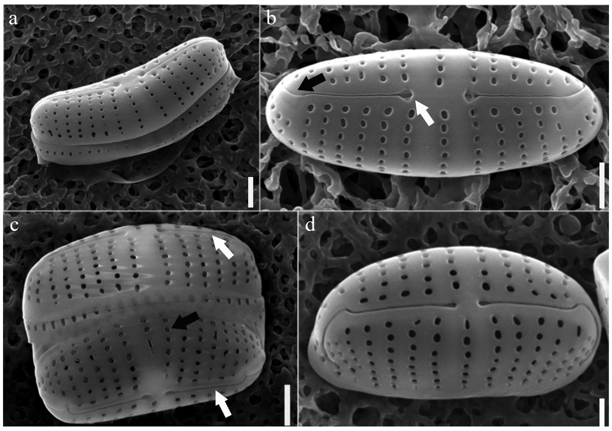

Fig. 3. SEM images of *Yuzaoea sinensis* gen. & sp. nov. Concave valve in girdle view (a). The external view of the whole valve showing drop-shaped proximal raphe ends (white arrow) and hook-shaped distal raphe ends (black arrow) (b). The external view of two valves of one frustule showing that both valves have complete raphe (white arrow) and irregular circular areolae are covered by a hymen (black arrow) (c). External view of a valve showing high mantle (d). Scale bars in a–c = 1 μm; d = 0.5 μm.

long, and 1.8–2.7 μm wide. Striae parallel or slightly radial, 17–29 in 10 μm. Raphe straight and filiform. Axial area narrowly linear (Figs 1b–j). Valves connected to form a short chain (Fig. 1a). Frustules heterovalvar, bends to one side in girdle view, and several girdle bands can be observed (Fig. 1k).

SEM: In girdle view, frustule flexed (Fig. 2a), several girdle bands with transapically elongated or small rounded pores (Figs 2a, b). Valves connected to form a short chain (Fig. 2b). One valve concave and the other convex (Figs 3a, 4a). Raphe simple, moderately eccentric, proximal raphe ends enlarged in droplet shape, and distal raphe fissures bent to the same sides in hook shape, ending in mantle (Fig. 3b). Both valves of the frustule have complete raphe systems (Fig. 3c). The striae uniseriate, asymmetrical. Areolae irregularly circular and internally occluded by hymenes (Figs 3b, c). The density of striae at the ends was similar to that in the middle of the valve (Figs 3b, c). The mantle is high (Fig. 3c). In internal views, helictoglossae are strongly raised at both ends of raphe (Fig. 4c). The proximal ends of raphe hooks to the same side (Fig. 4d).

3.2 *Molecular phylogenetics*

Two molecular markers, SSU rRNA and *rbc*L, were used to build ML phylogenetic analysis trees. The *Y. sinensis* taxon is a sister group to the clade of *Rhoicosphenia* with a high support value (bootstrap = 100%) (Fig. 5). *Yuzaoea sinensis* and *Rhoicosphenia* form a single branch that is sister to part of *Cocconeis* (except for *Cocconeis stauroneiformis*) and part of the Achnanthidiaceae clade, including *Achnanthidium* and *Planothidium* with a high support value (bootstrap = 100%). These sequence data have been submitted to the GenBank databases under accession number OM453684.1 and OM287439.1.

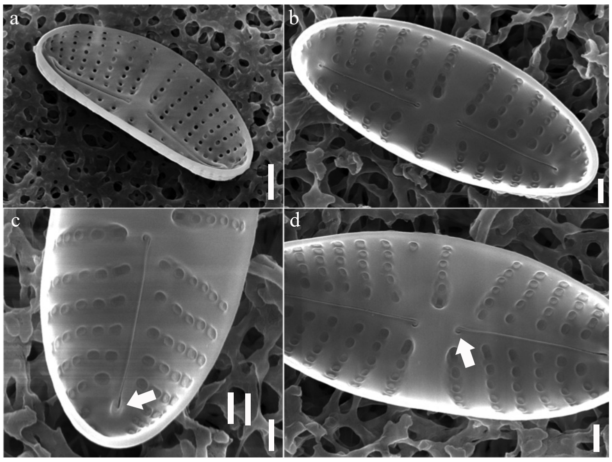

Fig. 4. SEM images of *Yuzaoea sinensis* gen. & sp. nov. Internal view of concave valve (a). Internal view of the whole valve (b). Internal view of the apices showing strongly raised helictoglossae (white arrow) (c). Internal view of the center of the valve showing raphe hooked in the same direction (white arrow) (d). Scale bars in a = 1 μm; b-d = 0.5 μm.

Holotype (here designated): Slide GX202012-6(AU, Biology Department Herbarium, Xiamen University). The holotype specimen is shown in Fig. 1b.

Isotype. Slide GX202012-6 deposited in the School of Life Sciences, Xiamen University, Xiamen, People's Republic of China.

Type locality: The intertidal zone of Weizhou Island, Guangxi Zhuang Autonomous Region, China, 20 December 2020, collector Lang Li.

Distribution: The type specimens were found at Weizhou Island, Guangxi Zhuang Autonomous Region, China. Later, we also found this species on the beaches of Nan'ao Island, Guangdong Province, and Gouqi Island, Zhejiang Province, China.

Etymology. The specific epithet "sinensis" refers to China, where the specimen was found.

4 Discussions

Under LM, *Y. sinensis* can be easily mistaken for raphe valves in members of *Achnanthidium*, such as *Achnanthidium rivulare* Potapova & Ponader and *Achnanthidium atomoides* Monnier, Lange-Bertalot & Ector (Potapova and Ponader, 2004; Morales et al., 2011), due to its linear-elliptical outline, bent girdle view and raphe system, as in *Y. sinensis*. *Yuzaoea sinensis* and *A. rivulare* differ mostly by the shape of the central area, which is indistinct in *Y. sinensis* but broader and lanceolate in *A. rivulare*. *Achnanthidium atomoides* often has spaced wider and short striae in the central portion of the valve and is denser towards the apices, while striae are more evenly and wider spaced in *Y. sinensis*.

Based on morphological structure, *Y. sinensis* is most likely aligned with taxa within the Rhoicospheniaceae, a family that includes the genera *Rhoicosphenia*, *Campylopyxis*, *Cuneolus*, *Gom-*

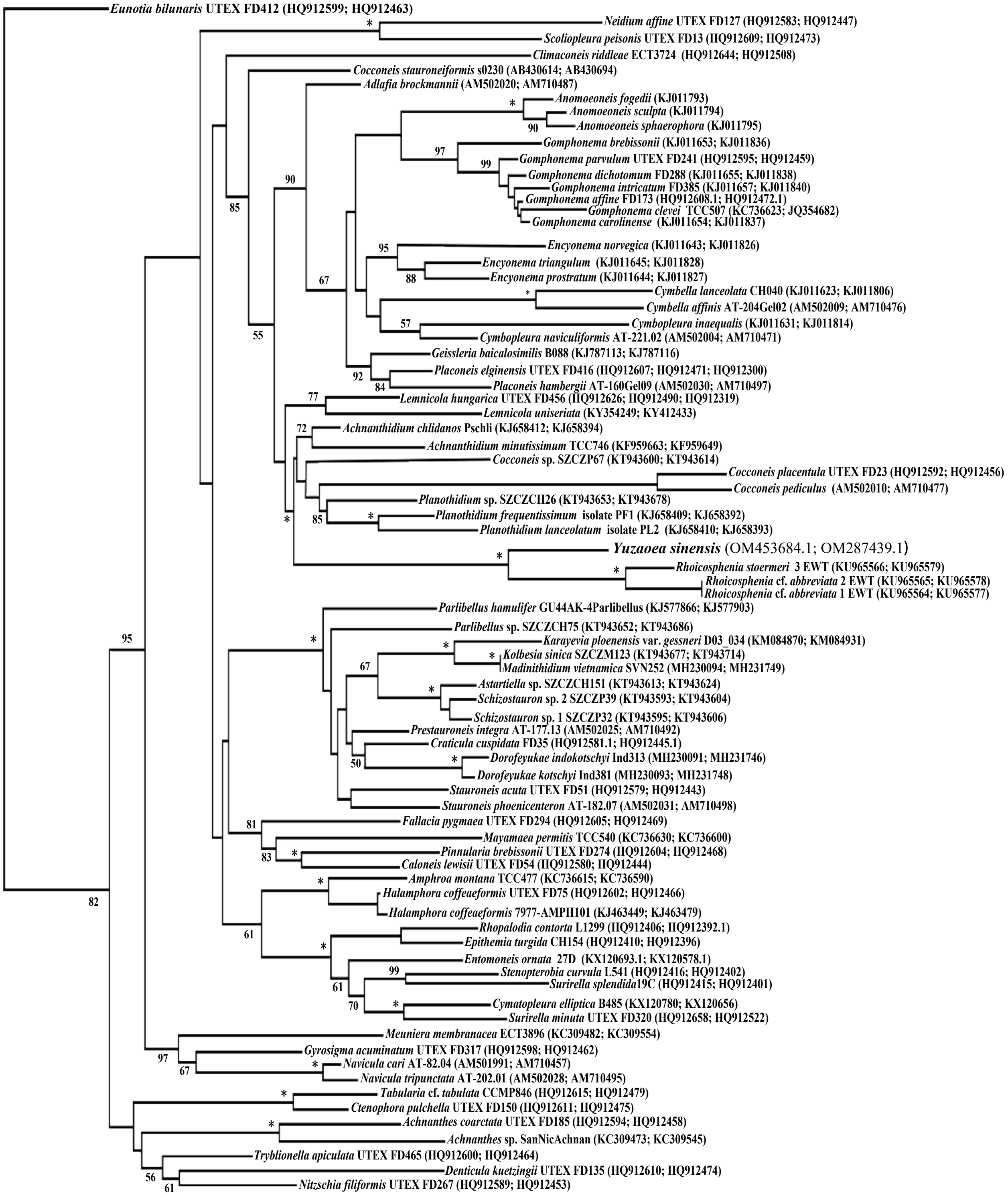

Fig. 5. The Maximum Likelihood (ML) phylogenetic tree based on the *rbc*L and SSU rRNA gene datasets shows the phylogenetic position of the *Yuzaoea sinensis* gen. & sp. nov. The values of the bootstrap analysis on the branches (<50% are not shown, *is 100% statistical support). *Eunotia bilunaris* was used as an outgroup.

phoseptatum, *Gomphonemopsis*, and *Gomphosphenia* (Round et al., 1990). It is interesting that members within Rhoicospheniaceae showed highly diverse frustule morphology, such as isopolar and heteropolar valves in the genera *Rhoicosphenia* and *Gomphosphenia* and frustules bent in the girdle view in the genus *Rhoicosphenia* (Table 1). The Gomphonemoid marine diatom genera *Gomphoseptatum* and *Gomphonemopsis* were revealed to be completely unrelated to *Gomphonema sensu stricto* (Medlin and Round, 1986). *Gomphoseptatum* is similar to *Rhoicosphenia* in its heteropolar valve, pseudoseptum or septum on the pole and areolae occluded by hymemes. *Gomphonemopsis* and *Gomphosphenia* have similar valve outlines, transapically elongate areolae and absence of terminal fissures. *Cuneolus* belongs to Rhoicospheniaceae because it shares many features with

Table 1. Morphological and inferred ecological characteristics of *Y. sinensis* in relation to some genera within Rhoicospheniaceae and genus *Rhoikoneis* (Medlin, 1985, Medlin and Round, 1986, Round et al., 1990)

	Frustule morphology	Areolae	Raphe	Cingula	Habitat	Literature
Yuzaoea gen. nov.	isopolar, flexed in girdle view	round poroids occluded internally by hymenes	a complete raphe system	open bands with elongate poroids	marine	
Campylopyxis Medlin	isopolar, flexed in girdle view	round poroids occluded internally by hymenes	concave valve with a complete raphe system, convex valve with reduced raphe system	open bands with elongate poroids	marine	(Medlin, 1985)
Rhoicosphenia Lange-Bertalot	heteropolar or isopolar, flexed in girdle view	apically elongate poroids colsed by hymenes	concave valve with a complete raphe system, convex valve with reduced raphe system	open bands with poroids or plain	brackish to fresh water	(Round et al. 1990)
Cuneolus Medlin	Slightly heteropolar, straight or slightly bent in girdle view	round poroids occluded by hymenes	a complete raphe system	open bands with poroids	marine	(Medlin and Round, 1986)
Rhoikoneis Grunow	isopolar, flexed in girdle view	apically elongate poroids colsed by hymenes	a complete raphe system	plain and open bands	marine	(Round et al., 1990)

Rhoicosphenia, namely, the areolae and internal raphe structure, the presence of pseudosepta and septa, and the girdle band construction (Medlin and Round, 1986). In terms of frustule and valve ultrastructure, *Campylopyxis* has several features that resemble *Rhoicosphenia*, including the heterovalvy of the frustule, the striae, the central internal and external raphe endings and the girdle bands (Medlin, 1985).

Among genera within the Rhoicospheniaceae, the valve structure of genus *Yuzaoea* is most closely aligned with *Campylopyxis* (Medlin, 1985). Both of these genera have isopolar valves and flexed cells in the girdle view, as opposed to isopolar/heteropolar valves and straight cells in the girdle view or heteropolar valves and flexed cells in the girdle view in other genera within Rhoicospheniaceae. Round poroids in the valve face and elongated poroids in valvocopula of *Y. sinensis* are similar to those found in the valve face and valvocopula of *C. garkeana*, respectively. No pseudosepta were obeserved both in the genera *Campylopyxis* and *Yuzaoea*. There are many differences that serve to distinguish *Yuzaoea* from *Campylopyxis*. First, *Yuzaoea* has an asymmetrical valve face about the apical axis as opposed to a naviculoid symmetric valve face about the apical axis in *Campylopyxis*. Second, the genus *Yuzaoea* has a complete raphe system with deeply indented terminal fissures, as opposed to concave valves with a complete raphe system and convex valves with a reduced raphe system in *Campylopyxis*. Third, the central area is indistinct in the genus *Yuzaoea* compared to the elliptical central area with occasional isolated puncta in *Campylopyxis*.

The genus *Yuzaoea* also shares features with the epiphytic diatom genus *Cuneolus*, another genus closely aligned with *Rhoicosphenia* but having an isovalvar frustule (Medlin and Round, 1986). As with *Rhoicosphenia* and *Yuzaoea*, valves of *Cuneolus* also have expanded external central endings and hooked internal central endings (Medlin, 1985). The poroids of *Cuneolus* are round and covered by hymenes, similar to those on the valve face of the genus *Yuzaoea*. However, unlike the genus *Yuzaoea*, the cells of *Cuneolus* are naviculoid in valve view, and the central area expands and thickens into a stauros. In addition, valve mantles in *Cuneolus* are produced into slight pseudosepta at either end (Round et al., 1990). It is worthing to note that pseudosepta is absent in the genera *Gomphonemopsis* and *Yuzaoea*. The genus *Rhoikoneis* with flexed frustule is worth mentioning. Similar to *Rhoicosphenia*, *Campylopyxis* and *Cuneolus*, *Rhoikoneis* is a marine diatom attached to seaweed. Although it has an idental raphe system with deeply indented terminal fissures superficially resembling that found in the genus *Yuzaoea*, *Rhoikoneis* is distinguished from the genus *Yuzaoea* by some aspects, such as the presence of internal raphe fissures with a thin, raised siliceous rib and accessory ribs, slit-like openings to the areolae and well-developed interstriae.

It is interesting that the molecular phylogenetic results in this study suggest that the genus *Yuzaoea* has a close relationship with *Rhoicosphenia* and the monoraphid genera (*Achnanthidium*, *Planothidium*, *Cocconeis*). These results are consistent with Cleve's hypothesis about the phylogenetic affinity of *Rhoicosphenia* to monoraphid diatoms (Cleve, 1895; Kulikovskiy et al., 2020). The derivation of monoraphid diatoms from biraphid diatoms is generally accepted (Kociolek and Stoermer, 1986; Cox, 2006, Cox and Williams, 2006). One piece of evidence for this is the study of the ontogeny of monoraphid diatoms, which shows the existence of raphe on both valves during the early formation of the valve (Mayama and Kobayasi, 1989). With the formation of the valve, one raphe was gradually filled with silica to form a valve called the Sternum Valve (SV). The valve with the raphe is called the Raphe Valve (RV). There is no such process in araphid diatoms, so it is inferred that monoraphid diatoms originate from biraphid diatoms. In addition to ontogenetic studies, taxonomists have also attempted to compare the morphological characteristics of monoraphid diatoms with those of biraphid diatoms to prove their genetic relationship (Kociolek and Stoermer, 1986, Cox, 2006).

In addition, many studies show that monoraphid diatoms do not form a monophyletic group but that instead monoraphy evolved independently on at least three separate occasions (Cox, 2006; Davidovich et al., 2017). The first group includes *Achnanthes sensu stricto*, the second group has *Achnanthidium, Planothidium*, *Cocconeis*, and Davidovich et al. (2017) revealed a third lineage of monoraphid diatoms formed by *Schizostauron*, *Astartiella*, *Kolbesia* and *Karayevia*. Phylogenetic analysis by Kulikovskiy et al. (2019) showed that there were at least five independent branches of monoraphid diatoms in the phylogenetic tree.

The biraphid genera within the Cymbellales (*Gomphonema*, *Cymbella* and their allies) are confirmed to be sister to the second group of monoraphids (Bruder and Medlin, 2008; Kermarrec et al., 2011). However, few morphological or cytological apomorphies could be found between the second group of monoraphids and the members within the Cymbellales (Kociolek and Stoermer, 1986; Nakov et al., 2014). Our results suggested that the genus *Yuzaoea* and members within Rhoicospheniaceae are the possible origins of the second group of monoraphid diatoms which contains the majority of *Cocconeis* and *Achnanthidiaceae*. The genera *Yuzaoea*, *Rhoicosphenia* and *Campylopyxis* have genuflexed shapes that are similar to the monoraphid group within *Achnanthidium* and *Planothidium* (Medlin and Round, 1986; Bąk and Lange-Bertalot, 2014; Pinseel et al., 2017). Some species in the genera *Rhoicosphenia* and *Campylopyxis*, i.e., *Rhoicosphenia genuflexa*, *Rhoicosphenia kolbei*, *Rhoicosphenia lesothensis* and *Campylopyxis garkeana* have the same apically transapically symmetrical frustule that occurs in the genera *Achnanthidium* and *Planothidium* (Medlin and Fryxell, 1984; Tseplik et al., 2021). These genera system evolution usually have round areolae and simple raphe (Round et al., 1990; Kulikovskiy et al., 2011; Wetzel et al., 2013; Marquardt et al., 2021). The complete raphe system in the genus *Yuzaoea* and the reduced raphe system in the genera *Rhoicosphenia* and *Campylopyxis* confirm their close affinities to monoraphid diatoms. However, the copulae in *Yuzaoea* and members within the Rhoicospheniaceae are open and perforated compared to girdles without areolae in the genera *Achnanthidium* and *Planothidium* (Bukhtiyarova, 2007; Lai et al., 2021).

In summary, *Yuzaoea sinensis* gen. & sp. nov. was described in the present paper and placed within the family Rhoicospheniaceae. Based on the morphological and phylogenetic results, the clade "*Yuzaoea+Rhoicosphenia*" is sister to the monoraphid diatoms, suggesting possible distinct monoraphe system evolution.

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