Fottea, Olomouc, 19(2): 138–150, 2019
DOI: 10.5507/fot.2019.005

Three new subaerial *Achnanthidium* (Bacillariophyta) species from a karst landform in the Guizhou Province, China

Qingmin You[1], Yue Cao[1], Pan Yu[1], J. P. Kociolek[2, 3], Lixuan Zang[1], Bo Wu[1], R. Lowe[4] & Quanxi Wang[1*]

[1] *College of Life Sciences, Shanghai Normal University, Shanghai 200234, P. R. China; *Corresponding author e–mail: wangqx@shnu.edu.cn*
[2] *Museum of Natural History, University of Colorado, Boulder, CO 80309, USA*
[3] *School of Life Science, Shanxi University, Taiyuan, 030006, P.R. China*
[4] *Department of Biological Sciences, Bowling Green State University, Bowling Green, OH, USA*

Abstract: Three new subaerial species of *Achnanthidium* are examined and described from a karst landform of central–south China based on light and scanning electron microscopy observations, and are compared with similar taxa worldwide. *A. mediolanceolatum* sp. nov. is elliptical–lanceolate, not linear–lanceolate as is more typical in this genus, as well as having a bow–tie shaped central area on the raphe valve and a large lanceolate axial area on the rapheless valve, features which together make it easy to distinguish this species from others. *A. parvulum* sp. nov. and *A. guizhouensis* sp. nov. are linear–elliptical in shape, which is more common for *Achnanthidium* and they differ from other species mainly in size, raphe, density of striae and shape of the central area. We compared these three new species with morphologically–similar taxa, and present their ecological settings and distributions as well. The relationship between *Achnanthidium* and *Psammothidium* is discussed, and the data from these new species from Guizhou presented herein suggest the two genera are difficult to separate.

Key words: *Achnanithidium*, subaerial, monoraphid, new species, Bacillariophyta

Introduction

A generation ago, floristic manuals recognized two genera of monoraphid diatoms occurring in freshwater ecosystems, *Cocconeis* Ehrenberg and *Achnanthes* Bory (e.g. Patrick & Reimer 1975; Krammer & Lange–Bertalot 2004). Since that time, morphological evidence has grown to suggest several groups of monoraphid diatoms should be segregated from *Achnanthes* sensu stricto as typified by *A. adnata* Bory. The work of Bukhtiyarova & Round (1996) and others either resurrected names once forgotten such as *Achnanthidium* Kützing and *Eucocconeis* Cleve ex Meister, or proposed new taxa based on morphological evidence that was distinctive with light and scanning electron microscopy. These new taxa included genera such as *Planothidium* Round et Bukhtiyarova, *Karayevia* (Round et Bukhtiyarova) Round and *Lemnicola* Round et Basson or based on more subtle differences e.g. *Rossithidium* Round et Bukhtiyarova, *Psammothidium* Bukhtiyarova et Round and *Kolbesia* (Round et Bukhtiyarova) Round.

Since this work in the late 1990's establishing new monoraphid genera, studies have been undertaken on the relationships of the groups to one another, resulting in further dissection and circumscription of new taxa from these genera and, in some cases, raising concerns about whether the new taxa were warranted. Phylogenetic analyses have suggested that the monoraphid diatoms represent a grade of organization, not a monophyletic clade of closely related taxa (e.g. Thomas et al. 2016; Kulikovskiy et al. 2016), and that five or more lineages independently secondarily lost the raphe system on one valve (Kociolek et al., accepted). Within *Achnanthidium*, however, three morphological groups have been identified, recognized by their distinctive features of flexure of the external distal raphe ends and areolar structure (Karthick et al. 2017; Yu et al. 2018; Yu et al. 2019). Lange–Bertalot (in Krammer & Lange–Bertalot 2004) established the genus *Platessa* for species not easily assigned to *Psammothidium* or *Achnanthidium*. Kulikovskiy et al. (2013) established the genus *Gliwiczia* Kulikovskiy, Lange–Bertalot et Witkowski based on species that have a cavum, like those found in *Planothidium*, but occurring on both valves of a frustule. On the other hand, some have begun to question the distinctiveness of certain genera, with some species such as *Kolbesia suchlandtii* (Hustedt) Kingston (Kingston 2000) and *K.*

gessneri (Hustedt) Aboal (Aboal et al. 2003) also being assigned to the genus *Karyevia*. Monnier et al. (2007) have called into question whether *Psammothdium* can be separated from *Achnanthidum* based on species variation and the features used to circumscribe *Psammothdium* from *Achnanthidium*.

Achnanthidium species have been found throughout China, with over 60 taxa reported (Liu Y. et al. 2014, 2015, 2016; Wang & Deng 2017; Yu et al. 2017a, 2018, 2019; Zhu & Chen 2000 et al.). Only six species of the genus have been described from China, however, including *A. sinense* Liu et Blanco (Liu B. et al. 2016) from the Wuling Mountains, *A. longissimum* Yu (Yu et al. 2018) from Jiuzhai Valley, Southwestern China, and another three species from Taiping Lake (Yu et al. 2019).

While working on the diatom biodiversity of a karst landform in Guizhou, we observed many interesting diatom species, resulting in the description of one new genus and eleven new taxa (Kociolek et al. 2016a, b, 2019; Lowe et al. 2017; You et al. 2016, 2017, 2019; Yu et al. 2017b). The aim of this article is to describe three new *Achnanthidium* species, based on light microscopy (LM) and scanning electron microscopy (SEM) of cleaned materials from this same karst landform. We also provide a comparison with morphologically similar taxa, as well as ecological habitats and distribution for each of the new species.

Materials and Methods

Diatom samples were collected from two sampling areas, Daqikong (Big Seven holes) scenic spot and Maolan Nature Reserve, in Libo county, Guizhou Province on Oct. 3th, 4th, 2015. This region is located in the middle of the subtropical zone and is typical for karst landforms. Daqikong is famous for its steep hills and natural canyon, the Mengtang (Dagou) River flows through canyon, there are many tourists throughout the year. Maolan Nature Reserve is protected by the Chinese government and international agreements through inclusion as part of International Man and Biosphere Reserve Network (UNESCO) (You et al. 2017), and consequently it is less affected by human factors. These two areas are adjacent, and the distance between sampling sites is ca. 30 km. The collection habitats in this study are mainly on wet stonewalls at the base of hills, wet walls near caves, rock scrapes from a variety of lentic habitats and other subaerial environments. Elevation at the localities is ca. 400–500 a.s.l. Details on the collections used in this study can be found in Table 1. In the laboratory, samples were processed as described by You et al. (2016). Terminology for the morphological description follows Round et al. (1990), Bukhtiyarova & Round (1996), Monnier et al. (2007), Manoylov (2007) and Potapova (2010, 2012).

Table 1. Locality data and habitat for samples studied, as well as species distribution.

Sample No.	Location	Habitat	Collection Date	Collector	Distribution of three new species		
					A. mediolanceolatum	*A. parvulum*	*A. guizhouensis*
GZ1510048	Daqikong scenic spot	Wet stone wall, with *Nostoc* spp.	10.3. 2015	Rex Lowe	+	–	–
GZ1510049	Daqikong scenic spot	Wet stone wall, with *Nostoc* spp.	10.3. 2015	Rex Lowe	+	+	+
GZ1510051	Daqikong scenic spot	Wet stone wall	10.3. 2015	Rex Lowe	+	–	+
GZ1510056	Daqikong scenic spot	Wet stone wall, closed cave	10.3. 2015	Rex Lowe	+	–	–
GZ1510062	Maolan Nature Reserve	River rock, with Bryophytes	10.4. 2015	Rex Lowe	+	–	–
GZ1510063	Maolan Nature Reserve	Stone wall, waterfall splash zone,	10.4. 2015	Rex Lowe	+	+	+
GZ1510064	Maolan Nature Reserve	Wet stone wall	10.4. 2015	Rex Lowe	+	–	–
GZ1510066	Maolan Nature Reserve	Wet stonewall above river	10.4. 2015	Rex Lowe	+	–	–
GZ1510068	Maolan Nature Reserve	Rock near cave	10.4. 2015	Rex Lowe	+	+	–

Note: "+" means the species is present in this sample; "–" indicates the species is not present in this sample.

Results

***Achnanthidium mediolanceolatum* P. Yu, Q–M. You et Kociolek, sp. nov. (Figs 1–32, LM; 105–116, SEM)**

Description: Light microscopy (LM) (Figs 1–32): Valves lanceolate–elliptical, with blunt, not protracted,

Fottea, Olomouc, 19(2): 138–150, 2019
DOI: 10.5507/fot.2019.005

rounded apices. Valve length 11.5–18.5 µm, width 4–5 µm (n=100). On the raphe valve, axial area narrow linear, centrally expanded to form a large, bow–tie–shaped central area, symmetrical, and extending to the margins. Raphe filiform, with external proximal raphe ends straight, slightly expanded, external distal fissures obviously hooked in same direction. Transapical striae radiate throughout, straight, 18–20 in 10 µm. Areolae fine, not distinguishable. Striae near the apices on one side of the valve appear on a different focal plane compared to striae on the opposite side. Rapheless valve with short striae, resulting in axial areas large and wide, lanceolate in shape, occupying 2/3 of the valve breadth. Transapical moderately radiate throughout, 16–19 in 10 µm. Incompletely filled–in raphe slit commonly observed. Scanning electron microscopy (SEM) (Figs 105–116): On the raphe valve: Externally, raphe straight, filiform. Proximal raphe endings straight and slightly dilated (Fig. 106). Distal raphe endings hooked to same direction on the valve face, not reaching the margins (Figs 105, 107). Central area large, bow–tie shaped, expanded to the margins and bordered by one areola at most (Figs 105, 106). Striae uniseriate, straight (except near the central area), not continuing beyond the valve face/valve mantle junction, with one narrow hyaline area. Areolae not uniform, 1–4 (usually 2–3) per stria, small, rounded near the centre, elongated, slit–like near the apices and the valve face/valve mantle junction (Figs 105–107). On the side of the hooked distal raphe ends there are small depressions (Figs 105, 107). Internal raphe straight, proximal raphe endings slightly bent in opposite directions (Fig. 109), distal raphe endings terminate as helictoglossae, slightly bent in the same direction (Figs 108, 110). Areolae internally appearing as elongate ovals with occlusions positioned in the middle of the opening, with fine extensions to the edges of the areolae, giving an initial impression of double rows of narrow slits (Figs 108–110). These occur in the areolae of the face and mantle. (Figs 109, 110). On the rapheless valve: Both exterior and interior, striae uniseriate, short, composed of 1–4 areolae throughout the valve, axial area and central area forming a large, wide hyaline area on the entire valve axis (Figs 111, 114). Areolae same as raphe valve, externally small, rounded or elongate rounded (Figs 112, 113), internally large, elongate oval, occluded by individual hymenes (Fig. 116).

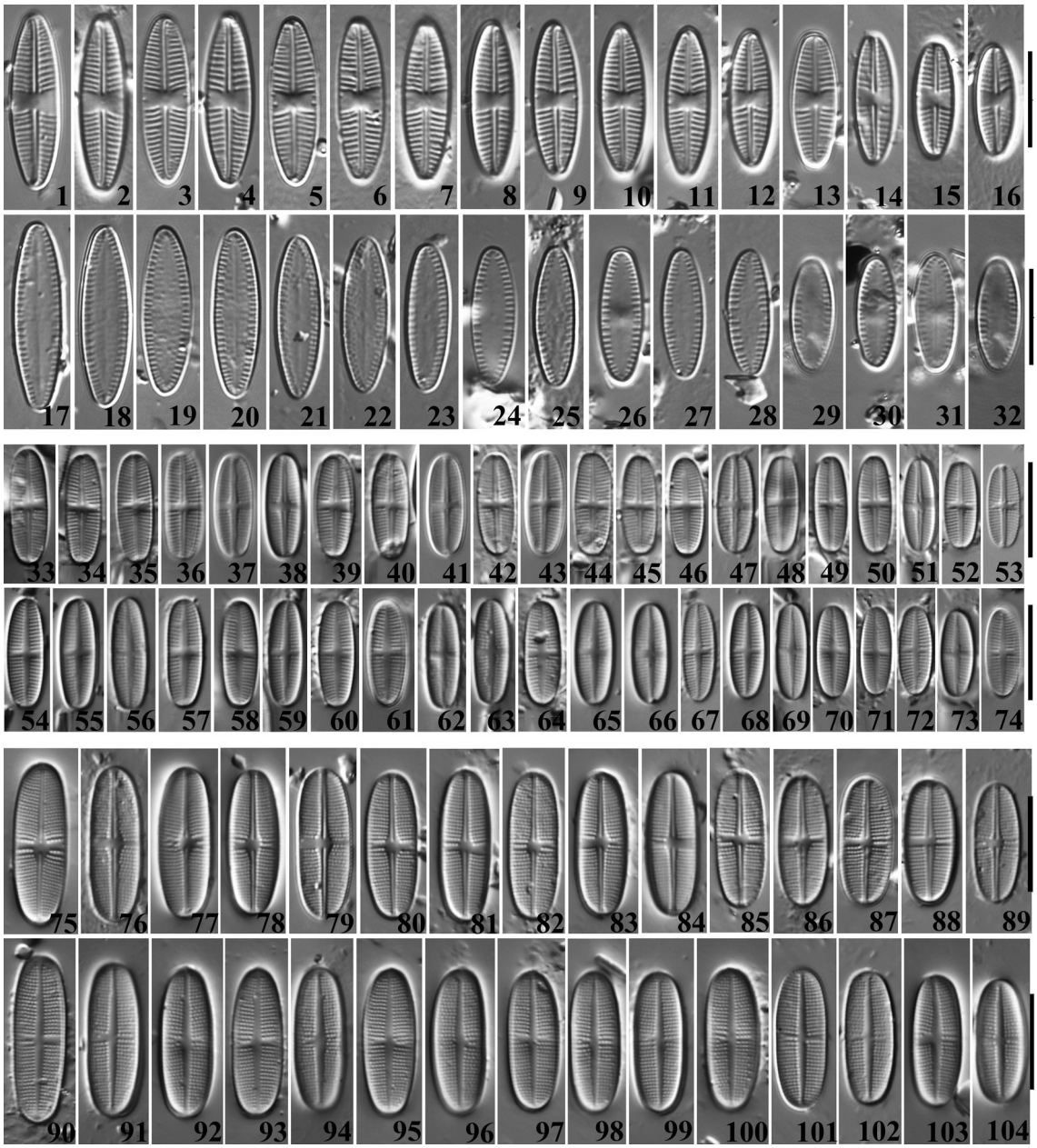
Holotype: SHNU! Material and slide GZ1510048, Biology Department Diatom Herbarium, Shanghai Normal University, China, here illustrated as figures 3, 19.
Isotype: COLO! Material 11114, Kociolek Collection, University of Colorado, Museum of Natural History Diatom Herbarium, Boulder, USA.
Type locality: CHINA. Guizhou Province: Big Seven Holes Scenic spot. The new species was found on the wet wall at the foot of the hill beside Mengtang River in the Big Seven Holes Scenic spot, Libo County, collected by R.L. Lowe, 3rd October 2015.

Etymology: The species is named for its lanceolate–elliptical outline.

Distribution: This species was present in collections GZ1510048, GZ1510049, GZ1510051, GZ1510056, GZ1510062, GZ1510063, GZ1510064, GZ1510066, GZ1510068. Detailed ecological information is presented in Table 1.

Remarks: The valve of *A. mediolanceolatum* is lanceolate–elliptical, this outline is not common in this genus and makes this new species easy to distinguish from others. This new *Achnanthidium* species is similar to *Psammothidium helveticum* (Hustedt) Bukhtiyarova et Round (Bukhtiyarova & Round 1996), *P. marginulatum* and *P. grischunum* in size and outline, especially for smaller specimens in the populations studied. However the new species can be easily distinguished by striae density and structure of the axial area on the rapheless valve. The striae of the new species are more coarse, less than 20 in 10 µm, as compared to ca. 18–30 in 10 µm in others (Hustedt 1933; Bukhtiyarova & Round 1996; Manoylov 2007). The axial area on the rapheless valve is lanceolate–elliptical and occupies the most valve, it is much larger than others. A comparison of these species is provided in Table 2.

***Achnanthidium parvulum* Q–M. You, P. Yu et Kociolek sp. nov. (Figs 33–74, LM; 117–124, SEM)**
Description: Light microscopy (LM) (Figs 33–74): Valves linear–elliptical, with broadly rounded apices. Valve length 9.0–12.5 µm, width 3.5–4.0 µm (n=160). On the raphe valve, axial area linear, slightly enlarged towards the central area. Central area narrow transverse rectangle formed by shortened striae. Transapical striae slightly radiate throughout, straight, 27–32 in 10 µm, indistinctly punctate. Aside from the lack of a raphe, features of the rapheless valve are similar to the raphe valve.
Scanning electron microscopy (SEM) (Figs 117–124): On the raphe valve: external views show straight raphe with proximal raphe endings straight, dilated, distal ends obvious curved in same direction on the valve face, not reaching the margins (Figs 117, 124). Central area narrow, forming a transverse rectangle, not reaching the margins (Fig. 117). Striae uniseriate, continuing to the valve face/valve mantle junction. Areolae not uniform, elliptical in the central part of the valve, 1–4 (usually 2–3) per stria, with one or two rows of slit–like areolae near the margin and one row of slit–like areolae on the mantle (Figs 117, 121, 122). Internally, raphe straight, with proximal raphe endings slightly bent in opposite directions, distal raphe endings terminate as helictoglossae. Areolae large, elliptical or subelliptical in shape, occluded with fine hymenate structures that include small openings around the periphery (Figs 118, 123). On the rapheless valve: both exterior and interior, axial area linear to narrowly–lanceolate, striae uniseriate, areolae round to elliptical, 27–32/10 µm, hymenate occlusions



Figs 1–32. *Achnanthidium mediolanceolatum* sp. nov. LM: (1–16) Raphe valves; (17–32) Rapheless valves; (3) Holotype, focus at raphe valve; (19) Holotype, focus at rapheless valve. Figs 33–74. *Achnanthidium parvulum* sp. nov.: (33–53) Raphe valves; (54–74) Rapheless valves; (34) Holotype, focus at raphe valve; (54) Holotype, focus at rapheless valve. Figs 75–104. *Achnanthidium guizhouensis* sp. nov.: (75–89) Raphe valves; (90–104) Rapheless valves; (75) Holotype, focus at raphe valve; (90) Holotype, focus at rapheless valve. Scale bar 10 μm.

with very small openings (Figs 119, 120).

Holotype: SHNU! Material and slide GZ1510049, Biology Department Diatom Herbarium, Shanghai Normal University, China, here illustrated as figures 34, 54.

Isotype: COLO! Material 11115, Kociolek Collection, University of Colorado, Museum of Natural History Diatom Herbarium, Boulder, USA.

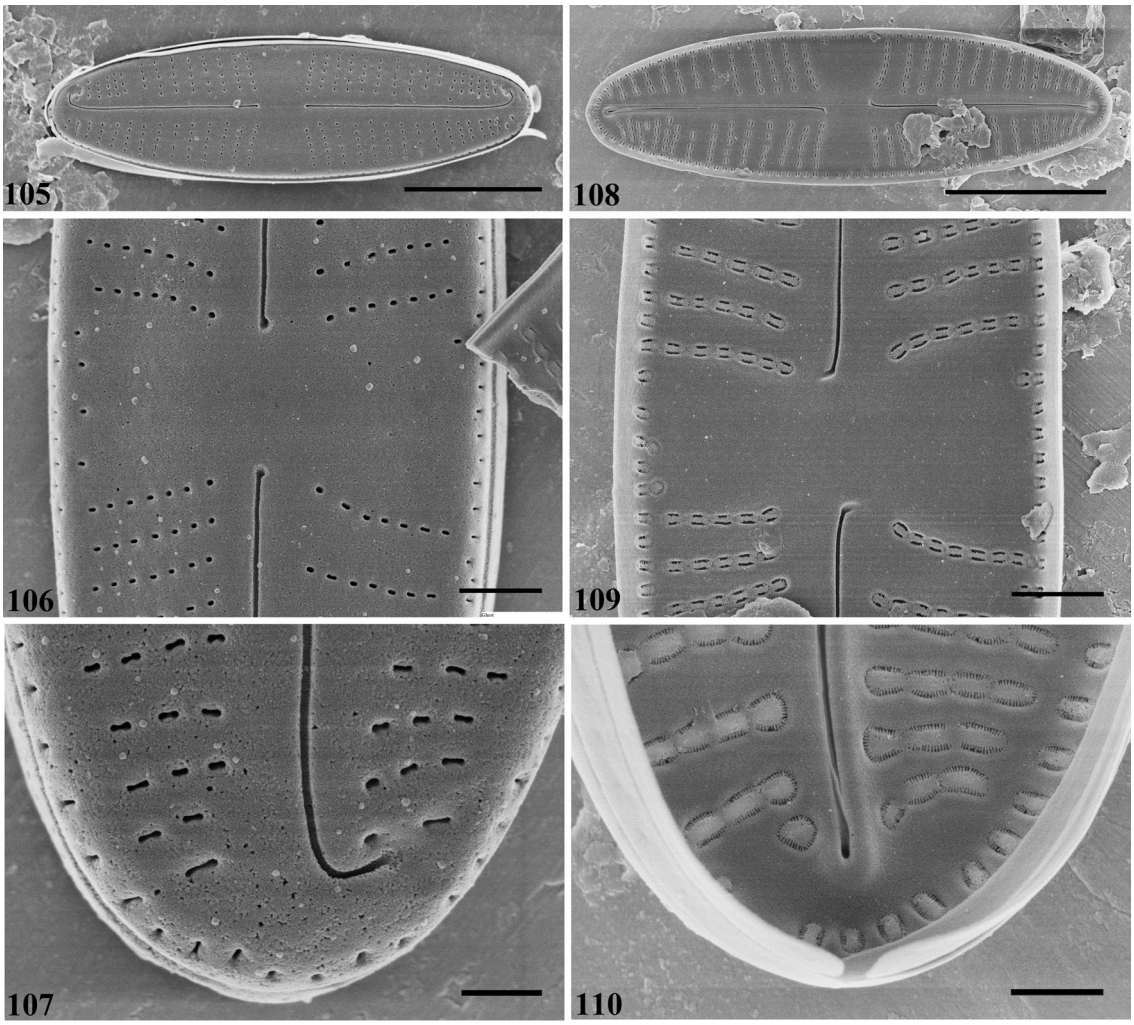
Type locality: CHINA. Guizhou Province: Big Seven Holes Scenic spot. The new species was found on the wet wall at the foot of the hill beside Mengtang River in the Big Seven Holes Scenic spot, Libo County, collected by R.L. Lowe, 3rd October 2015.

Etymology: The species is named for its small outline.

Distribution: This species was present in collections GZ1510049, GZ1510063 and GZ1510068. Detailed ecological information is presented in Table 1.

Remarks: This new small *Achnanthidium* species is similar in appearance to *Psammothidium curtissimum* (Carter) Aboal (Aboal et al. 2003), *P. semiapertum* (Hustedt) Aboal (Aboal et al. 2003), *P. levanderi* (Hustedt) Bukhtiyarova et Round (Bukhtiyarova & Round 1996) and *P. pennsylvanicum* Potapova (Potapova 2012), the length of these species do not exceed 13 μm. These species, however, are differentiated from one another mainly by features of valve width, striae density, and extent and

Fottea, Olomouc, 19(2): 138–150, 2019
DOI: 10.5507/fot.2019.005



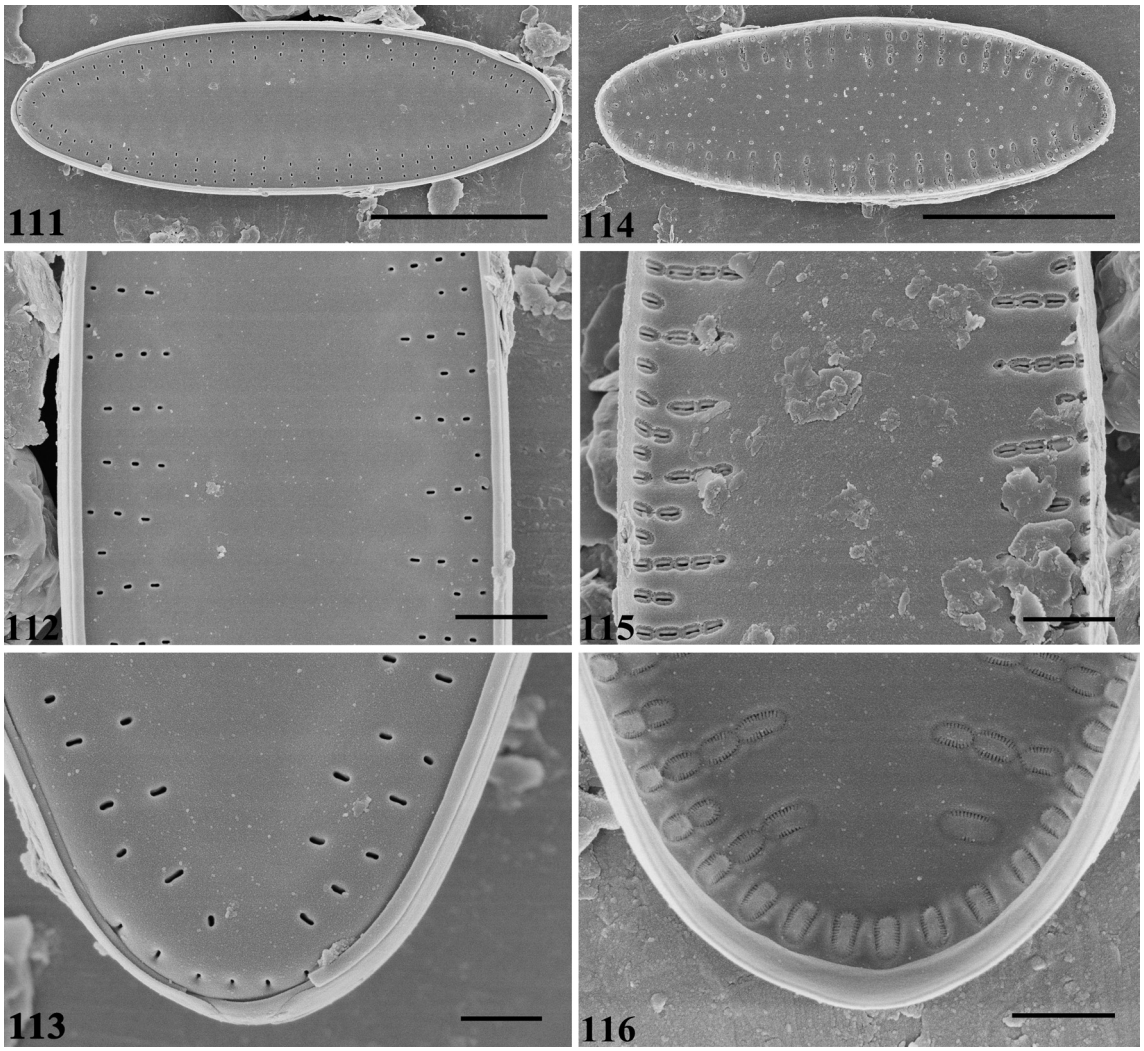
Figs 105–110. *Achnanthidium mediolanceolatum* sp. nov. SEM. Figs 105–107. External views of a raphe valve: (105) Entire valve view; (106) Central area of raphe valve, showing details of areolae, central area and proximal raphe endings; (107) Details of distal raphe end, strongly hooked, with slight depression on the side of the hooked raphe. Figs 108–110. Internal views of a raphe valve: (108) Entire valve view; (109) Central area of raphe valve, showing details of areolae, central area and proximal raphe endings; (110) Details of apex with helictoglossa. Scale bar 5 µm (105, 108), 1 µm (106, 109), 0.5 µm (107, 110).

shape of the axial and central areas. A comparison of these small species is provided in Table 3.

***Achnanthidium guizhouensis* P. Yu, Q–M. You et Kociolek sp. nov. (Figs 75–104, LM; 125–140, SEM)**

Description: Light microscopy (LM) (Figs 75–104): Valves linear–elliptical, with broadly–rounded apices. Valve length 13.0–18.0 µm, width 5.0–5.5 µm (n=100). On the raphe valve, axial area linear to narrowly linear–lanceolate, slightly enlarged towards the central area. Central area small, sometimes not obvious, usually asymmetrical, with an elongated stria included within the central area. Raphe straight, filiform. Transapical striae slightly radiate throughout, straight, 25–28 in 10 µm. Areolae can be distinguished in high resolution light microscopy. On the rapheless valve, the characteristics of axial area, central area and striae similar to the raphe valve.

Scanning electron microscopy (SEM) (Figs 125–140): On the raphe valve: external raphe straight (Fig. 125). Both proximal raphe endings and distal endings straight, barely expanded (Figs 126, 127). Central area small, variable, asymmetrical, sometimes not obvious. Striae uniseriate, straight, mostly not continuing beyond the valve face/valve mantle junction, with a distinct hyaline area at the margin (Figs 125–127). Areolae not uniform, 2–5 per stria, elliptical or subelliptical on most of the valve, occlusions in the interior of the valve can be seen from the exterior (Figs 125–128), with one or two rows of small, rounded areolae near the margin and one row small rounded areolae in the mantle (Figs 126, 127). Internal raphe straight, proximal endings slightly bent in opposite directions, distal raphe endings terminate as helictoglossae (Figs 129–131). Areolae elliptical or subelliptical in shape and occluded with fine hymenate structures that include small openings around the periphery (Figs 129–132). On the rapheless valve, on both the exterior and interior sides, striae uniseriate, not terminating on the valve face/valve mantle junction, with a narrow hyaline area at the margin (Figs 133–135, 137–139).



Figs 111–116. *Achnanthidium mediolanceolatum* sp. nov. SEM. Figs 111–113. External views of a rapheless valve: (111) Entire valve view; (112) Central area, showing details of areolae and central area; (113) Details of apex. Figs 114–116. Internal views of a rapheless valve: (114) Entire valve view; (115) Central area, showing details of areolae and central area; (116) Apex showing details of areolae. Scale bar 5 μm (111, 114), 1 μm (112, 115), 0.5 μm (113, 116).

The structure and arrangement of areolae similar to the raphe valve (Figs 136, 140).

Holotype: SHNU! Material and slide GZ1510051, Biology Department Diatom Herbarium, Shanghai Normal University, China, here illustrated as figs 75, 90.

Isotype: COLO! Material 11117, Kociolek Collection, University of Colorado, Museum of Natural History Diatom Herbarium, Boulder, USA.

Type locality: CHINA. Guizhou Province: Big Seven Holes Scenic spot. The new species was found on the wet wall at the foot of the hill beside Mengtang River in the Big Seven Holes Scenic spot, Libo County, collected by R.L. Lowe, 3rd October 2015.

Etymology: The species is named for the province where it was collected.

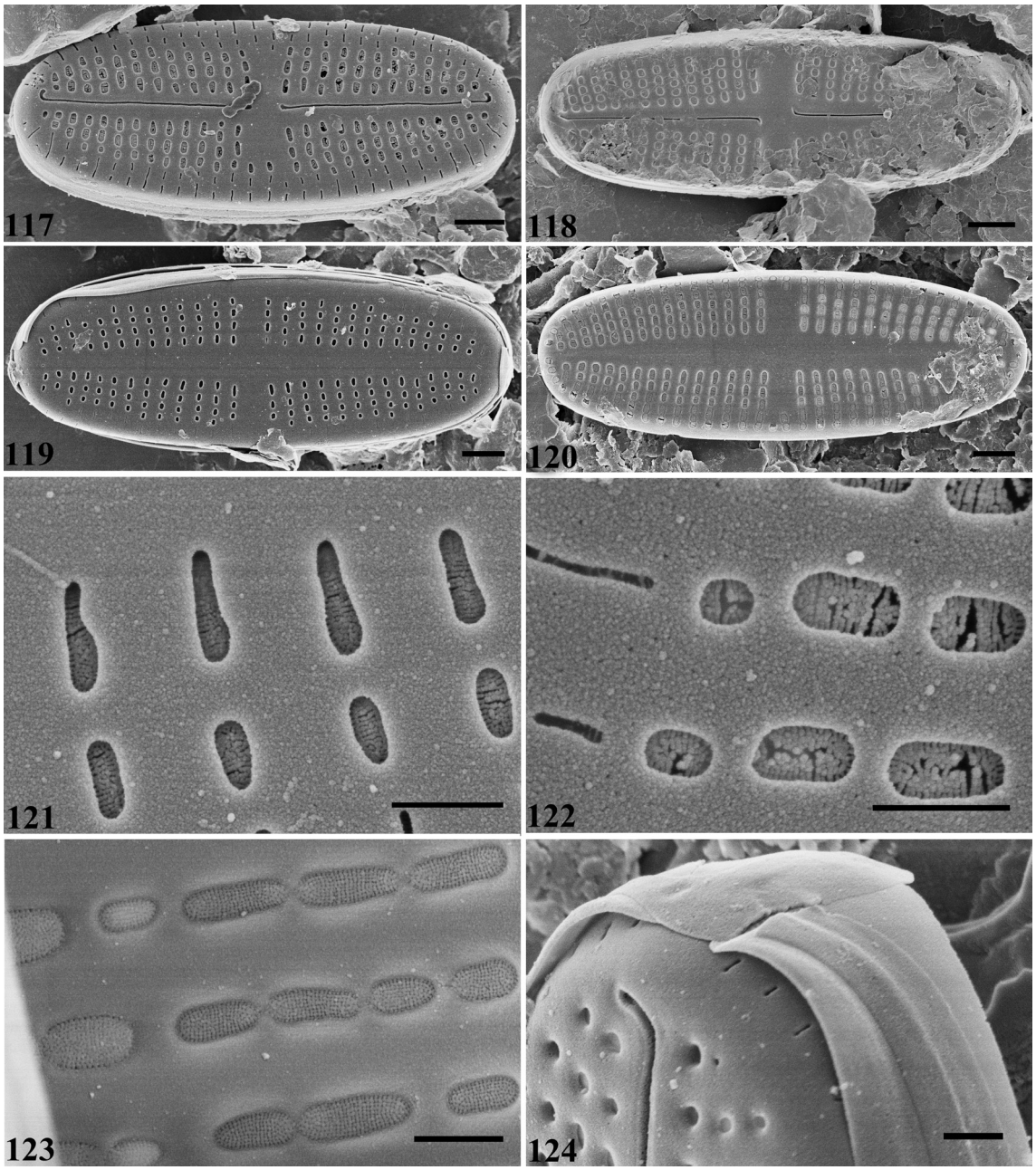
Distribution: This species was present in collections GZ1510049, GZ1510051 and GZ1510063. Detailed ecological information is presented in Table 1.

Remarks: This new *Achnanthidium* species is similar to *A. parvulum* sp. nov. in outline, however the size of *A. guizhouensis* sp. nov. is bigger, they do not overlap in overall size. *A. guizhouensis* sp. nov. is similar to *Psammothidium bristolicum* Bukhtiyarova et Round (Bukhtiyarova & Round 1996), *P. marginulatum* Bukhtiyarova et Round (Bukhtiyarova & Round 1996) and *P. chlidanos* Lange–Bertalot (Lange–Bertalot 1999) in terms of size and outline of the valves, but it is easy to differentiate them from each other based on striae density and the shape and extent of the axial and center areas. These species are compared in terms of their valve features in Table 4.

Discussion

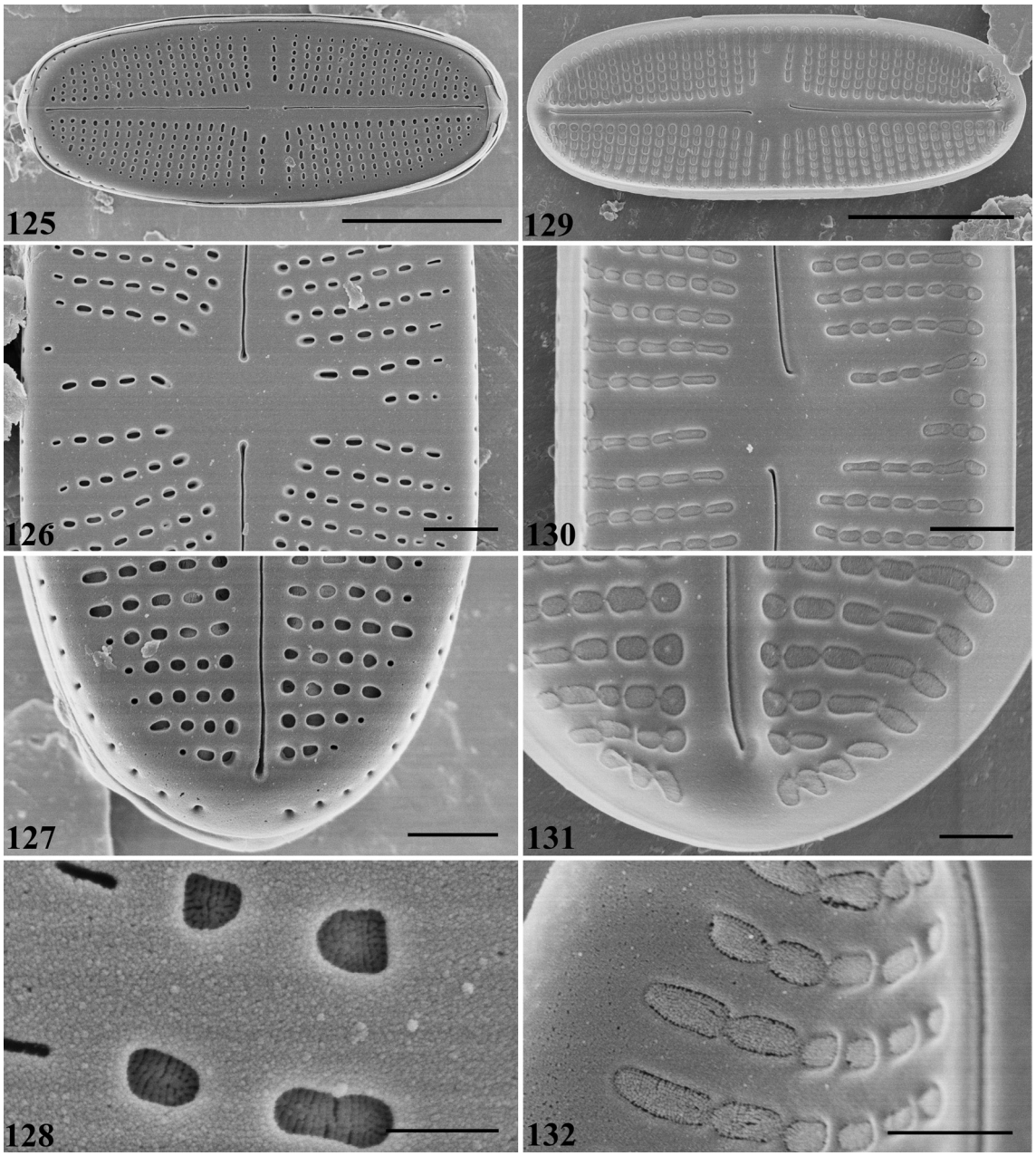
With the advent of better electron microscopes and the discovery and description of new species, we are beginning to more fully document the morphological diversity

Fottea, Olomouc, 19(2): 138–150, 2019
DOI: 10.5507/fot.2019.005



Figs 117–124. *Achnanthidium parvulum* sp. nov. SEM: (117) External view of a raphe valve; (118) Internal view of a raphe valve; (119) External view of a rapheless valve; (120) Internal view of a rapheless valve; (121, 122) Details of external view of areolae, internal areolar occlusions can be seen from the exterior; (123) Details of internal view of areolae, showing fine hymenate structures–small granules that include small openings around the periphery; (124) Details of distal raphe end. Scale bar Scale bar 1 µm (117–120), 0.3 µm (121–124).

exhibited by species of *Achnanthidium*. In our samples, for example, the three new species possess similar marginal regions, e.g. striae do not continue across the valve face/valve mantle junction, but instead are separated by a distinct marginal hyaline area. There are, however, some differences between the species. For example, there are two types of raphe morphology and areolae. The external raphe valves of *A. mediolanceolatum* sp. nov. and *A. parvulum* sp. nov. have straight raphes, with proximal endings straight and expanded, and distal endings curved in same direction on the valve face and not reaching the margins. In *A. guizhouensis* sp. nov., however, the raphe as well as the external proximal and distal endings are all straight. In terms of areolae, in *A. mediolanceolatum* sp. nov., the areolae are small, rounded or slit–like openings in external view, but internally the areolae are large, elongate ovals, occluded by individual hymenes. In *A. parvulum* sp. nov. and *A. guizhouensis* sp. nov., the external areolae are relatively large and elliptical along most of the valve, and the internal hymenate occlusions can be seen from the exterior with high magnification. The fine hymenate structures appear as small granules that include small openings around the periphery. These diagnostic characters are important for species

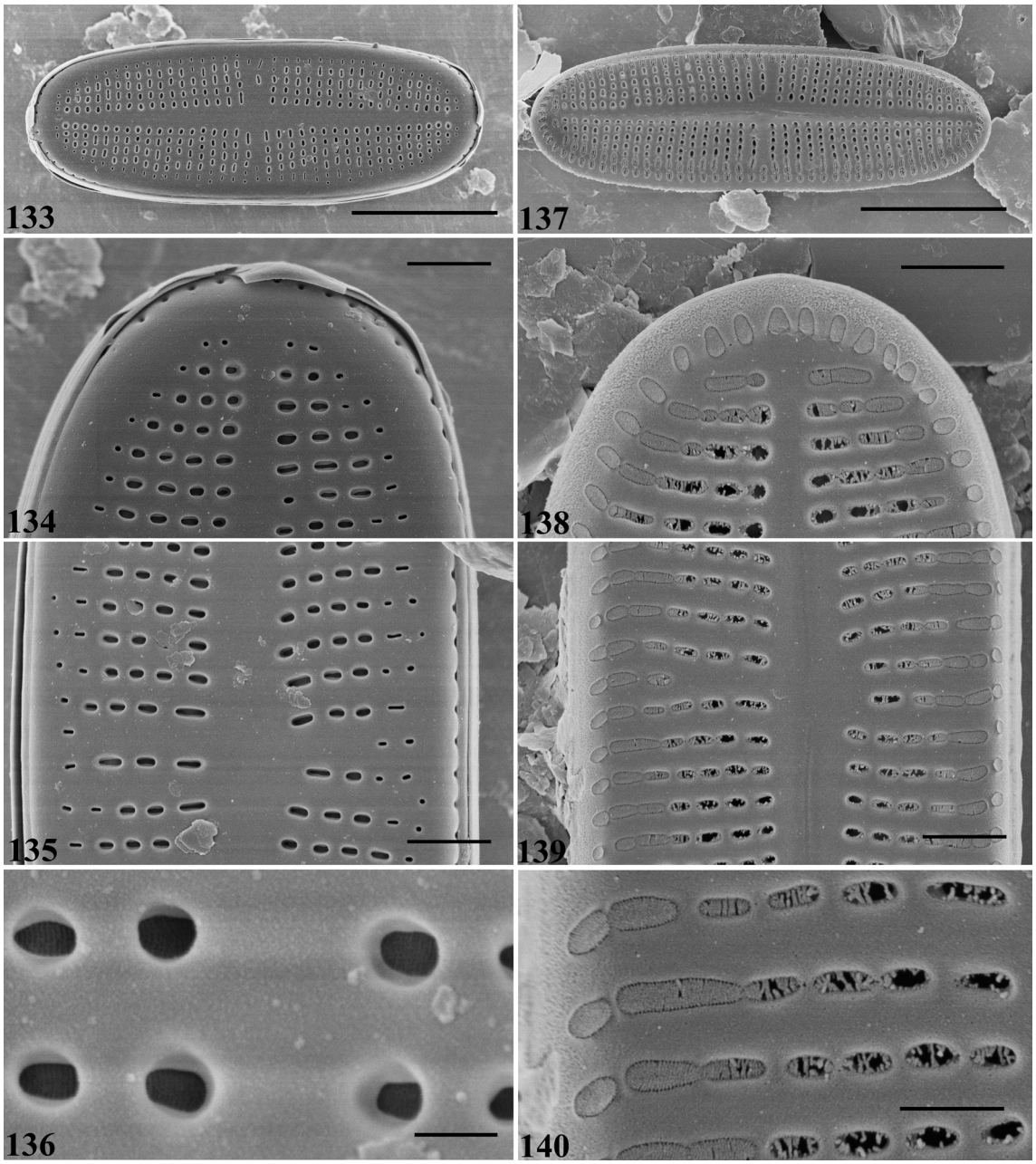


Figs 125–132. *Achnanthidium guizhouensis* sp. nov. SEM. Figs 125–128. External views of raphe valve: (125) Entire valve view; (126) Central area of raphe valve, showing details of areolae, central area and proximal raphe endings; (127) Details of distal raphe end; (128) Details of external view of areolae, occlusions of the areolae internally can be seen from the exterior. Figs 129–132. Internal views of interior of raphe valve: (129) Entire valve view; (130) Central area showing details of areolae, central area and proximal raphe ending; (131) Details of distal raphe end; (132) Details of areolae, showing fine hymenate structures–small granules that include small openings around the periphery. Scale bar 5 μm (125, 129), 1 μm (126, 127, 130), 0.2 μm (128), 0.5 μm (131, 132).

distinctions in our taxa, and similar characters also exist in some *Achnanthidium* spp. for example: *A. delmontii* Pérès, Le Cohu et Barthes (PÉRÈS et al. 2012), *A. pseudoconspicuum* var. *yomensis* Yana et Mayama (Yana & Mayama 2015), *A. linannulum* Karthick, Taylor et Hamilton (Karthick et al. 2017), *A. longissimum* Yu, You et Kociolek (Yu et al. 2018), *A. lacustre* Yu, You et Kociolek (Yu et al. 2019), *A. sublanceolatum* Yu, You et Kociolek (Yu et al. 2019), *A. taipingensis* Yu, You et Kociolek (Yu et al. 2019) et al.

Three morphological groups have been recognized within *Achnanthidium* (Karthick et al. 2017; Yu et al. 2018, 2019), and two of these three groups have representatives among the new taxa described here. *A. mediolanceolatum* sp. nov. and *A. parvulum* sp. nov. belong to the *A. pyrenaicum* complex, which have external distal raphe fissures deflected in the same direction, but areolae of *A. parvulum* sp. nov. are elliptical in shape, not lineate, which is the typical type of areolae found in this group. *A. guizhouensis* sp. nov. belongs to *A. minutissimum* complex, members of which have straight distal raphe endings and round to elliptical areolae.

Fottea, Olomouc, 19(2): 138–150, 2019
DOI: 10.5507/fot.2019.005



Figs 133–140. *Achnanthidium guizhouensis* sp. nov. SEM. Figs 133–136. External view of rapheless valve: (133) Entire valve view; (134) Details of apex; (135) Central area showing details of areolae and central area; (136) Details of areolae, internal occlusions can be seen from the exterior. Figs 137–140. Internal views of rapheless valve: (137) Entire valve view; (138) Apex showing details of areolae; (139) Central area showing details of areolae and central area; (140) Details of areolae, showing fine hymenate structures–small granules that include small openings around the periphery. Scale bar 5 μm (133, 137), 1 μm (134, 135, 138, 139), 0.2 μm (136), 0.5 μm (140).

Similarities in valve morphology between these *Achnanthidium* and *Psammothidium* taxa are striking, and provide more data to support Monnier et al.'s (2007) opinion that *Achnanthidium* and *Psammothidium* cannot be unambiguously separated on the basis of morphological criteria. The species described here lack most of the features proposed by Bukhtiyarova & Round (1996) to diagnose *Psammothidium*, including convex curvature of the raphe valve and raphe fissures in channels. Even the subjective feature of valve shape used to distinguish between these genera (linear valves representing *Achnanthidium* species, more elliptical valves representing *Psammothidium* species), seems less helpful in distinguishing between the genera, given these two genera cannot be ditinguished by morphological characters, eg. frustule outline, valve length, valve width, striae arrangement and density, and raphe structure. Therefore, given this situation, we have not assigned these new species to *Psammothidium*. Potapova (2012) thought the boundaries of recently established freshwater monoraphid genera should be questioned. It may be

Table 2. Comparison of morphological characteristics of *A. mediolanceolatum* and morphologically–similar *Psammothidium* taxa.

Species/Feature	***A. mediolanceolatum***	***P. marginulatum***	***P. helveticum***	***P. grischunum***
Valve length	11.5–18.5 µm	11–15 µm	10–12 µm	6–18 µm
Valve width	4–5 µm	5–6 µm	5.5 µm	4–5.5 µm
Valve outline	Lanceolate–elliptical	Lanceolate–elliptical	Elliptical–Linear elliptical	Oval to linear oval
Raphe valve				
Axial area/sternum	Linear	Lanceolate	Linear	Linear lanceolate
Central area	Bow–tie–shaped	Rectangular	Rectangular	Transapically oval
Raphe	Straight, filiform	Straight, filiform	Straight, filiform	Straight, filiform
Proximal raphe endings (external)	Straight and slightly expanded, simple	Straight, simple	Complex, with ridges and grooves	Complex, with ridges and grooves
Distal raphe endings (external)	Curved in same direction	Straight, short	Curved in opposite direction	Straight, slightly expanded
Density of striae	18–20 in 10 µm	27–30 in 10 µm	27–30 in 10 µm	18–27 in 10 µm
Rapheless valve				
Axial area	Lanceolate	Elliptical	Linear	Rhomboid
Central area	Large and wide	Wide	Rounded	Oval or rhombic
Density of striae	16–19 in 10 µm	27–30 in 10 µm	27–30 in 10 µm	18–27 in 10 µm
References	Current study	Bukhtiyarova & Round 1996	Hustedt 1933; Manoylov 2007	Bukhtiyarova & Round 1996

necessary to review the distribution of morphological features among the genera with smaller species and, through formal analyses of morphology and molecular data in a taxonomic and systematic revision and recognition of monophyletic groups (Kociolek & Williams 2015), consider the redrawing of generic boundaries among these taxa.

Acknowledgements

This research was funded and supported by National Natural Science Foundation of China (No. 31770222), National basic science and technology work (2013FY110400), and Shanghai Engineering Research Center of Plant Germplasm Resources (17DZ2252700). We are grateful for the comprehensive comments from two reviewers and editor in relation to scientific aspects, format and language.

References

Aboal, M.; Alvarez–Cobelas, M.; Cambra, J. & Ector, L. (2003): Floristic list of non marine diatoms (Bacillariophyceae) of Iberian Peninsula, Balearic Islands, and Canary Islands. Updated taxonomy and bibliography. – In: A. Witkowski (ed.): Diatom Monographs. – 639 pp., A.R.G. Gantner Verlag K.G., City.

Bukhtiyarova, L. & Round, F. (1996): Revision of the genus *Achnanthes* sensu lato. *Psammothidium*, a new genus based on *A. marginulatum*. – Diatom Research 11: 1–30.

Carter, J.R. (1963): Some new diatoms from British waters. – Journal of the Quekett Microscopical Club 29: 199–203.

Hustedt, F. (1933): Die Kieselalgen Deutschlands, Österreichs und der Schweiz unter Berücksichtigung der übrigen Länder Europas sowie der angrenzenden Meeresgebiete. – In: L. Rabenhorst (ed.): Kryptogamen Flora von Deutschland, Österreich und der Schweiz, Vol. 7, Part 2. – pp. 321–432, Akademische Verlagsgesellschaft m.b.h. Leipzig.

Hustedt, F. (1945): Diatomeen aus Seen und Quellgebieten der Balkan–Halbinsel. – Archiv für Hydrobiologie 40: 867–973.

Karthick, B.; Taylor, J.C. & Hamilton, P.B. (2017): Two new species of *Achnanthidium* Kützing (Bacillariophyceae) from Kolli Hills, Eastern Ghats, India. – Fottea 17: 65–77.

Kingston, J.C. (2000): New combinations in the freshwater Fragilariaceae and Achnanthidiaceae. – Diatom Research 15: 409–411.

Kociolek, J.P. & Williams, D.M. (2015): How to define a diatom genus? Notes on the creation and recognition of taxa, and a call for revisionary studies of diatoms. Proceedings of the 8th Central European Diatom Meeting. Zagreb, Croatia. – Acta Croatica Botanica 74: 195–210. DOI: 10.1515/botcro–2015–0018.

Kociolek, J.P.; You, Q–M.; Stepanek, J.G.; Lowe, R.L. & Wang, Q–X. (2016a): A new *Eunotia* (Bacillariophyta: Eunotiales) species from Karst formations of southern China. – Phytotaxa 265: 285–293.

Kociolek, J.P.; You, Q–M.; Stepanek, J.G.; Lowe, R.L. & Wang, Q–X. (2016b): New freshwater diatom genus, *Edtheriotia* gen. nov. of the Stephanodiscaceae

Table 3. Comparison of morphological characteristics of *A. parvulum* and morphologically–similar *Psammothidium* taxa.

Species/Feature	***A. parvulum***	***P. curtissimum***	***P. semiapertum***	***P. levanderi***	***P. pennsylvanicum***
Valve length	9.0–12.5 µm	4.9–8.5 µm	8.5–10.4 µm	7–11 µm	9–13 µm
Valve width	3.5–4.0 µm	3.5–4.0 µm	4.4–5.2 µm	4.5–5.3 µm	5.0–5.4 µm
Valve outline	Linear–elliptical	Elliptical–Linear elliptical	Elliptical	Elliptical–Linear elliptical	Elliptical
Raphe valve					
Axial area/sternum	Linear	Linear	Linear	Linear	Linear
Central area	Transverse rectangle	Transverse elongate	Transverse rectangle	Small and asymmetrical	Transverse rectangular, or elliptic
Raphe	Straight, filiform	Straight, filiform	Straight, filiform	Straight, filiform	Straight, filiform
Proximal raphe endings (external)	Straight and pore–like expanded	Straight, slightly expanded	Straight, slightly expanded	–	Straight, slightly expanded
Distal raphe endings (external)	Curved in same direction	Straight, slightly expanded	Straight, slightly expanded	–	Straight, slightly expanded
Density of striae	27–32 in 10 µm	27–31 in 10 µm	22–24 in 10 µm	24–30 in 10 µm	25–29 in 10 µm
Rapheless valve					
Axial area	Linear	Linear	Linear	Rhomboid	Linear
Central area	Narrow rectangle	Small transverse elongate	Transverse rectangle	Not differentiated from the axial area	Asymmetrical
Density of striae	27–32 in 10 µm	27–31 in 10 µm	22–24 in 10 µm	24–30 in 10 µm	25–29 in 10 µm
References	Current study	Carter 1963; Aboal et al. 2003	Hustedt 1945; Aboal et al. 2003	Hustedt 1933; Bukhtiyarova & Round 1996; Potapova 2010	Potapova 2012

Table 4. Comparison of morphological characteristics of *A. guizhouensis* and morphologically–similar *Psammothidium* taxa.

Species/Feature	***A. guizhouensis***	***P. bristolicum***	***P. marginulatum***	***P. chlidanos***
Valve length	13–18 µm	12–30 µm	11–15 µm	13.5–15.1 µm
Valve width	5.0–5.5 µm	5–11 µm	5–6 µm	5.7–6.2 µm
Valve outline	Linear elliptical	Linear to oval	Lanceolate/ elliptical	Elliptical
Raphe valve				
Axial area/sternum	Linear	Linear	Obvious lanceolate	Linear
Central area	Small, variable and asymmetrical	Transapically oval	Wide rectangle	Rectangle
Raphe	Straight, filiform	Straight, with ridges	Straight, filiform	Straight, filiform
Proximal raphe endings (external)	Straight, slightly pore–like expanded	Straight, slightly pore–like expanded	Straight, simple	–
Distal raphe endings (external)	Straight, slightly pore–like expanded	Curved in opposite directions	Simple, curve to one side	–
Density of striae	25–28 in 10 µm	25–30 in 10 µm	27–30 in 10 µm	28–32 in 10 µm
Rapheless valve				
Axial area	Linear	Linear–rhombic	Elliptical	Lanceolate
Central area	Small, variable and asymmetrical	Not differentiated from the axial area	Not differentiated from the axial area	Rectangle
Density of striae	25–28 in 10 µm	25–30 in 10 µm	27–30 in 10 µm	28–32 in 10 µm
References	Current study	Bukhtiyarova & Round 1996	Bukhtiyarova & Round 1996	Lange–Bertalot 1999; Manoylov 2007

(Bacillariophyta) from south–central China. – Phycological Research 64: 274–280.

Kociolek, J.P.; Williams, D.M.; Stepanek, J.; Liu, Q.; Liu, Y.; You, Q–M.; Karthick, B. & Kulikovskiy, M. (2019): Rampant homoplasy and adaptive radiation in pennate diatoms. – Plant Ecology and Evolution, Accepted.

Krammer, K. & Lange–Bertalot, H. (2004): Bacillariophyceae 4. Teil: Achnanthaceae, Kritische Erganzungen zu *Navicula* (Lineolatae), *Gomphonema*. Gesamtliteraturverzeichnis Teil 1–4 In: Süßwasserflora von Mitteleuropa. (Ettl, H. et al. Eds), 468 pp.

Kulikovskiy, M.; Lange–Bertalot, H. & Witkowski, A. (2013): *Gliwiczia* gen. nov. a new monoraphid diatom genus from Lake Baikal with a description of four species new for science. – Phytotaxa 109: 1–16.

Kulikovskiy, E.; Stepanek, J. & Kociolek, J.P. (2016): Historical and Current Perspectives on the Systematics of the 'Enigmatic' Diatom Genus *Rhoicosphenia* (Bacillariophyta), with Single and Multi–Molecular Marker and Morphological Analyses and Discussion on the Monophyly of 'Monoraphid' Diatoms. – PLoS One 11: e0152797. DOI:10.1371/journal.pone.0152797.

Lange–Bertalot, H. (1999): Neue Kombinationen von Taxa aus *Achnanthes* Bory (*sensu lato*). – Iconographia Diatomologica 6: 270–283.

Lowe, R.; Kociolek, J.P.; You, Q–M.; Wang, Q–X. & Stepanek, J. (2017): Diversity of the diatom genus *Humidophila* in karst areas of Guizhou, China. – Phytotaxa 305: 269–284.

Liu, Y.; Kociolek, J.P.; Wang, Q–X.; Tan, X. & Fan, Y–W. (2014): Two new species of monoraphid diatom (Bacillariophyceae) from South of China. – Phytotaxa 188: 31–37.

Liu, Y.; Fan, Y–W. & Wang, Q–X. (2015): Study on the Achnanthoid diatoms from the Great Xing'an Moutains. – Acta Hydrobiologica Sinica 39: 554–563.

Liu, Y.; Fan, Y–W. & Wang, Q–X. (2016): Newly recorded species of Achnanthidiaceae from Great Xing'an Mountains. – Acta Bot. Boreal.–Occident Sin. 36: 2339–2345.

Liu, B.; Blanco, S.; Hua, L.; Xu, J.J. & Jiang, X.Y. (2016): *Achnanthidium sinense* sp. nov. (Bacillariophyta) from the Wuling Mountains Area, China. – Phytotaxa 284: 194–202.

Manoylov, K.M. (2007): On some *Psammothidium* species from rivers in the United States. – Diatom Research 22: 317–327.

Monnier, O.; Lange–Bertalot, H.; Hoffmann, L. & Ector, L. (2007): The genera *Achnanthidium* Kützing and *Psammothidium* Bukhtiyarova et Round in the family Achnanthidiaceae (Bacillariophyceae): a reappraisal of the differential criteria. *Cryptogamie,* – Algologie 28: 141–158.

Patrick, R.M. & Reimer, C.W. (1975): The Diatoms of the United States, exclusive of Alaska and Hawaii, V. 2 Monographs of the Academy of Natural Sciences of Philadelphia, Philadelphia.

PÉRÈS, F.; Barthès, A.; Ponton, E.; Coste, M.; Ten–Hague,

Fottea, Olomouc, 19(2): 138–150, 2019
DOI: 10.5507/fot.2019.005

L. & R. Le–Cohu (2012): *Achnanthidium delmontii* sp. nov., a new species from French rivers. – Fottea 12: 189–198.

PÉRÈS, F.; Cohu, R.L. & Delmont, D. (2014): *Achnanthidium barbei* sp. nov. and *Achnanthidium costei* sp. nov., two new diatom species from French rivers. – Diatom Research 29: 387–397.

Potapova, M. (2010): *Psammothidium levanderi*. In Diatoms of North America. – Retrieved October 08, 2018, from https://diatoms.org/species/psammothidium_levanderi

Potapova, M. (2012): New species and combinations in monoraphid diatoms (family Achnanthidiaceae) from North America. – Diatom Research 27: 29–42.

Round, F.E. (1998): Validation of some previously published Achnanthoid genera. – Diatom Research 13: 181.

Round, F.E. & Basson, P.W. (1997): A new monoraphid diatom genus (*Pogoneis*) from Bahrain and the transfer of previously described species *A. hungarica* and *A. taeniata* to new genera. – Diatom Research 12: 71–81.

Round, F.E. & Bukhtiyarova, L. (1996): Four new genera based on *Achnanthes* (*Achnanthidium*) together with a re–definition of *Achnanthidium.* – Diatom Research 11: 345–361.

Round, F.E.; Crawford, R.M. & Mann, D.G. (1990): The diatoms. Biology and morphology of the genera. – 747 pp., Cambridge University Press, Cambridge.

Wang, Q–X. & Deng, G–P. (2017): Atlas of algae in Jiuzhaigou Nature Reserve. – 205 pp., Science Press, Beijing.

Wojtal, A.Z.; Ector, L.; Van de Vijver, B.; Moralies, E.; Lanza, S.B.; Piatek, J. & Smieja, A. (2011): The *Achnanthidium minutissimum* complex (Bacillariophyceae) in southern Poland. – Algological Studies 136: 211–238.

Yana, E. & Mayama, S. (2015): Two new taxa of *Achnanthidium* and *Encyonema* (Bacillariophyceae) from the Yom River, Thailand, with special reference to the areolae occlusions implying ontogenetic relationship. – Phycological Research 63: 239–252.

You, Q–M.; Kociolek, J.P.; Yu, P.; Cai, M–J.; Lowe, R.L. & Wang, Q–X. (2016): A new species of *Simonsenia* from a karst landform, Maolan Nature Reserve, Guizhou Province, China. – Diatom Research 31: 269–275.

You, Q–M.; Kociolek, J.P.; Cai, M–J.; Yu, P. & Wang, Q–X. (2017): Morphology and ultrastructure of *Sellaphora constrictum* sp. nov. (Bacillariophyta), a new diatom from southern China. – Phytotaxa 327: 261–268.

You, Q–M.; Yu, P.; Kociolek, J.P.; Wang Y–L.; Luo F.; Lowe R. & Wang, Q–X. (2019): A new species of *Achnanthes* (Bacillariophyta) from a freshwater habitat in a karst landform from south–central China. – Phycological research, In press.

Yu, P.; You, Q–M. & Wang, Q–M. (2017a): Newly recorded Monoraphidales (Bacillariophyta) species in Jiuzhaigou Valley, China. – Plant Science Journal 35: 326–334.

Yu, P.; You, Q–M.; Kociolek, J. P.; Lowe, R. & Wang, Q–X. (2017b): *Nupela major* sp. nov., a new diatom species from Maolan Nature Reserve, central–south of China. – Phytotaxa 311: 245–254.

Yu, P.; Kociolek, J.P.; You, Q–M. & Wang, Q–X. (2018): *Achnanthidium longissimum* sp. nov. (Bacillariophyta), a new diatom species from Jiuzhai Valley, Southwestern of China. – Diatom Research 33: 339–348.

Yu, P.; You, Q–M.; Kociolek, J.P. & Wang, Q–X. (2019): Three new freshwater species of the genus *Achnanthidium* (Bacillariophyta, Achnanthidiaceae) from Taiping Lake, China. – Fottea 19: 33–49.

Zhu, H–Z. & Chen, J–Y. (2000): Bacillariophyta of the Xizang Plateau. – 353 pp., Science Press, Beijing.

Received February 3, 2019
Accepted May 14, 2019