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

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**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; Kulikovsky 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 *Platesa* for species not easily assigned to *Psammothidium* or *Achnanthidium*. Kulikovsky et al. (2013) established the genus *Gilwiczia* 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.*
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.
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. Transapically 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 helicostigmatid, 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 helicostigmatid. 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...
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...
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...
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
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. 2018), *A. taipingensis* Yu, You et Kociolek (Yu et al. 2018) 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.
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 Bukhtiyarov & 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 distinguished by morphological characters, e.g. 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
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.

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Achnanthes marginulatum

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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          | Linear        | Linear laceolate |
|                         | Central area        | Bow–tie–shaped | Rectangular   | Transapically oval |
|                         |                      |                 |               |               |
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|                         |                      |                 |               |               |
| Density of striae       | 18–20 in 10 µm       | 27–30 in 10 µm  | 27–30 in 10 µm | 18–27 in 10 µm |
| Raphe less valve        | Axial area           | Lanceolate      | Elliptical    | Linear        |
|                         | Central area         | Large and wide  | Wide          | Rhomboid      |
|                         |                      |                 |               |               |
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|                         |                      |                 |               |               |
|                         |                      |                 |               |               |
|                         |                      |                 |               |               |
| 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; Manylov 2007 | Bukhtiyarova & Round 1996 |

Table 2. Comparison of morphological characteristics of A. mediolanceolatum and morphologically–similar Psammothidium taxa.
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 | Husteedt 1945; Aboal et al. 2003 | Husteedt 1933; Bukhtiyarova & Round 1996; Potapova 2010 | Potapova 2012 |

References

- Current study
- Carter 1963; Aboal et al. 2003
- Husteedt 1945; Aboal et al. 2003
- Husteedt 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 |

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