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REGULAR PAPER

Analysis of the type material of *Achnanthes minutissima* var. *macrocephala* (Bacillariophyta) and description of two new small capitate *Achnanthidium* species from Europe and the Himalaya

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Background and aims – Two unknown benthic diatom species belonging to the genus *Achnanthidium* Kütz., and found in French and Nepalese freshwater habitats, were investigated. Both species are here described as new and compared with the original material of *Achnanthes minutissima* var. *macrocephala* Hust. [≡ *Achnanthidium macrocephalum* (Hust.) Round & Bukht.] from Indonesia.
Methods – The morphology of three small and capitate *Achnanthidium* species was investigated using light microscopy (LM) and scanning electron microscopy (SEM).
Key results – *Achnanthidium coxianum* sp. nov. (from the Himalaya) belongs to the group of species with hooked terminal raphe endings, while *Achnanthidium peetersianum* sp. nov. (from France) has variable terminal raphe endings which are usually slightly bent. *Achnanthidium macrocephalum* is a much rarer species and illustrations concerning its identity in the literature do not conform to the type studied here.
Conclusions – The three species are similar in LM but clearly distinct in SEM. The shape of the areolae and terminal raphe endings separate the species. *Achnanthidium macrocephalum* has often been misidentified in studies from many areas of the world. It is similar to the new species in valve outline and in its small dimensions.

Key words – *Achnanthaceae*, diatom, France, Indonesia, Nepal, new species, SEM, ultrastructure.

INTRODUCTION

Achnanthidium Kütz. is one of the most abundant and common diatom genera in freshwater ecosystems worldwide (e.g. Lange-Bertalot & Krammer 1989, Krammer & Lange-Bertalot 1991, Ponader & Potapova 2007, Potapova & Hamilton 2007). The group of species that are similar to *Achnanthidium minutissimum* (Kütz.) Czarn. is one of the most complex of non-marine diatoms whose taxonomy and nomenclatural history has been the subject of intensive debate and revisions over several decades (Lange-Bertalot & Ruppel 1980, Lange-Bertalot & Krammer 1989, Krammer & Lange-Bertalot 1991, 2004, Round & Bukhtiyarova 1996, Potapova & Hamilton 2007, Ector 2011, Hlúbiková et al. 2011, Van de Vijver et al. 2011a, 2018, Novais et al. 2015, Marquardt et al. 2017, Krahn et al. 2018).

Based on the terminal raphe endings of the raphe valve, the genus has been historically sub-divided into two main groups of species: the complex around *Achnanthidium minutissimum* with straight terminal raphe fissures and a second one which comprises species around *Achnanthidium pyrenaicum* (Hust.) H.Kobayasi with clearly deflected or hooked distal terminal raphe fissures (Czarnecki 1994, Round & Bukhtiyarova 1996, Kobayasi 1997, Van de Vijver et al. 2011a, 2011b, Yu et al. 2018, 2019). However, recent

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examples have shown that the shape of the terminal raphe ends is not a synapomorphic character for *Achnanthidium* (e.g. Moser et al. 1995, 1998, Karthick et al. 2017), or other 'monoraphid' genera such as *Psammothidium* (Kulikovskiy et al. 2016).

The *Achnanthidium minutissimum* species complex is characterized by a usually slender, linear to linear-lanceolate valve outline, and by relatively short cells with a very fine and dense striation pattern (Van de Vijver et al. 2011a). The striae are usually radiate or almost parallel, uniseriate and wider spaced in the valve centre, especially on the raphe valve. One valve has a simple central raphe hardly expanded at the centre, with terminal fissures straight or deflected to the secondary side at the valve. On the valve mantle a single row of (slightly) elongated areolae is present (Round & Bukhtiyarova 1996).

Several recent investigations were carried out to define morphological boundaries hard to observe using light microscopy and several species have been described as new in both 'traditional' groups of species (e.g. Kobayasi 1997, Potapova & Ponader 2004, Cantonati & Lange-Bertalot 2006, Monnier et al. 2007, Jüttner & Cox 2011, Jüttner et al. 2011, Kulikovskiy et al. 2011, Novais et al. 2011, 2015, Van de Vijver et al. 2011b, Wojtal et al. 2011, Gassiole et al. 2013, Pérès et al. 2014, Olenici et al. 2017). Despite these efforts to delineate species boundaries using morphological characters, many species remain undescribed due to the lack of ultrastructural analysis of the type materials, and the difficulties in recognising subtle morphological differences. Most recently, molecular phylogenies were used in combination with a morphological analysis to reveal several distinct lineages in the *Achnanthidium minutissimum* complex (Pinseel et al. 2017).

Achnanthes minutissima var. *macrocephala* Hust. (Hustedt 1937: 193, pl. 13, figs 50–53) was described from Lake Toba (Sumatra, Indonesia) and records of the species are reported from many different regions of the world (e.g. Patrick & Reimer 1966, Krammer & Lange-Bertalot 1991, Vyverman et al. 1995, Metzeltin & Lange-Bertalot 2002, Cremer 2006, Potapova & Hamilton 2007, Blanco et al. 2008, Coste et al. 2009, Taylor et al. 2009, Straub 2013). Despite frequent records of specimens which were assigned to *A. minutissima* var. *macrocephala* no morphological studies were carried out on the ultrastructure of the valves. The transfer to the genus *Achnanthidium* and its elevation to the status of species was made by Round & Bukhtiyarova (1996: 349) without observation of the original material which remains unstudied with scanning electron microscopy. The main objective of this paper was to (1) study in detail French and Nepalese *Achnanthidium* species which were initially identified as *A. macrocephalum* using light and scanning electron microscopy, and (2) to elucidate their identities through comparison to the original material from Indonesia.

MATERIAL AND METHODS

Original unmounted material from Indonesia (Sumatra) deposited at the Hustedt collection [Alfred-Wegener-Institut für Polar- und Meeresforschung (BRM) Bremerhaven, Germany] was used. New slides and stubs were prepared with the following material.

- Sample AS849 in Hustedt Collection Bremerhaven (BRM). Sumatra, Lake Toba. TB1c, westlich Balige, Algenwatten, 5.4.1929, leg. Ruttner. Lectotype slide MA2-46 designated in Simonsen (1987: 211).
- Sample AS902 in Hustedt Collection Bremerhaven (BRM). Sumatra, Lake Toba, TW3e, W-Ufer Samosir, N Sigaol, heiße Quelle, 11.4.1929, leg. Ruttner.

Two samples (from France and the Himalaya) containing the species initially identified as *A. macrocephalum* were observed in LM and SEM:

- Periphytic sample collected at the Sauvigny River at Perrigny-sur-Loire, Bourgogne-Franche-Comté region (France). This sampling site has been monitored by French water agencies and its main chemical parameters, sampled monthly from 13/01/2010 until 05/04/2011 (n = 16), are summarized in fig. 4.
- Periphytic sample from Lake Donag (4839 m a.s.l.). Oligotrophic lake in Nepal's Sagarmatha (Everest) National Park, Fourth Lake within the Gokyo lakes series.

All samples were oxidized using standard methods (hot hydrogen peroxide [35%] and diluted HCl [37%]) in order to obtain a suspension of clean frustules. Permanent slides were mounted in Naphrax. Light microscopical (LM) observations were performed using a Leica® DMRX microscope with 100 x oil immersion objective. Photographs were taken with a Leica® DC500 camera. Samples selected for scanning electron microscopy (SEM) analysis were filtrated through polycarbonate membrane filters with a pore diameter of 3 µm, mounted on stubs using double-sided carbon tape, air dried and sputtered with platinum (30 nm) using a Modular High Vacuum Coating System (BAL-TEC MED 020) and studied with a Hitachi SU-70, operated at 5.0 kV and 10 mm distance. Micrographs were digitally manipulated and plates with LM and SEM pictures were arranged using Corel Draw X8®. Morphological terminology follows Ross et al. (1979), Round et al. (1990) and Krammer & Lange-Bertalot (1991). For comparison, the main publications consulted were: Lange-Bertalot & Ruppel (1980), Lange-Bertalot & Krammer (1989), Krammer & Lange-Bertalot (1991), Ivanov & Ector (2006), Ponader & Potapova (2007), Potapova & Hamilton (2007), Morales et al. (2009), Hlúbiková et al. (2011) and Van de Vijver et al. (2011a, 2011b).

RESULTS AND DISCUSSION

Achnanthidium macrocephalum (Hust.) Round & Bukht.

Figs 1A–M & 2A–L

≡ *Achnanthes minutissima* var. *macrocephala* Hust. (Hustedt 1937: 193, pl. 13, figs 50–53).

Type material – Indonesia, Balige, Lake Toba, Sample AS849 in Hustedt Collection Bremerhaven (AS849) (lecto- : BRM, slide MA2-46 designated in Simonsen 1987: 211).

Observations – Valves linear-elliptic with convex margins and broadly capitate, rounded apices (fig. 1B–L). Frustules in girdle view slightly arched (fig. 1M). Valve dimensions: 7–12 µm long and 2.5–3.2 µm wide. Rapheless valve with expanded axial area widening towards central area (fig. 2A–G). Central area bordered by 1 or 2 usually more widely spaced striae composed of larger elongate areolae; smaller, slit-like areolae often present at margin between central striae. Transapical striae radiate in central section of valve, becoming parallel towards valve ends, c. 38 striae in 10 µm unresolvable in LM. Striae composed of 1 (smaller valves) or 2 (rarely 3), transapically elongated, areolae of different length (fig. 2A–G). Smaller slit-like areolae irregularly present near valve margin. At valve face-mantle junction a pore-free area, strongly silicified, between striae on valve face and areolae on mantle. A single row of elliptic-elongated, and slit-like irregularly distributed, areolae on valve mantle (fig. 2E, G & K). Valve surface ornamented with irregularly orientated depressed fine lines (fig. 2A, B & D–G). Raphe valve with narrow linear axial area (fig. 2H–J). Central area very small, rounded, bordered by 1 or 2 slightly radiate striae on both sides composed of elongate areolae and short slit-like or elongate central striae (fig. 2H–J). Raphe straight, filiform, externally central raphe ends straight, very slightly expanded. Distal raphe ends straight externally or slightly deflected, ending in small depressions (fig. 2H & I). Transapical striae slightly radiate, becoming parallel near apices, 38–40 in

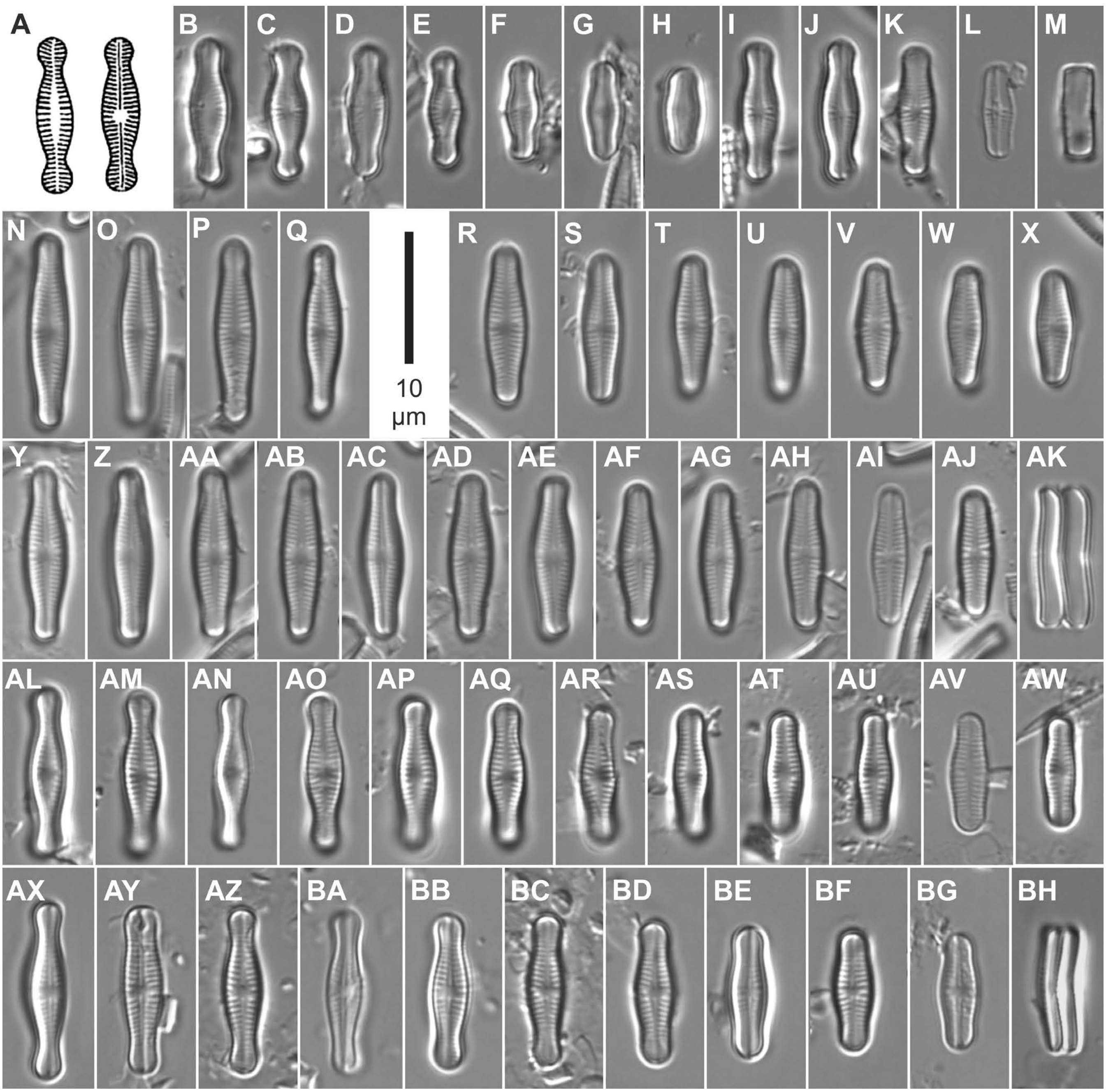

Figure 1 – *Achnanthidium* species. LM micrographs. A–M, *Achnanthidium macrocephalum* (Hust.) Round & Bukht. [≡ *Achnanthes minutissima* var. *macrocephala* Hust. (Lake Toba, Balige, Sumatra, holotype material AS849)]; A, reproduction of the original drawing by Hustedt (1937: 193, pl. 13, figs 50 & 51); N–AK, *Achnanthidium peetersianum* from the Bourgogne-Franche-Comté region, France; AL–BH, *Achnanthidium coxianum* from Nepal.

10 near valve centre. Striae composed of 1 or 2, rarely 3, transapically elongated, rarely slit-like, areolae of different length.

Remarks on distribution and similar species – After its description by Hustedt (1937) from Sumatra, Hustedt (1942) recorded the species in a sample from Bali (Bratan Lake) with the comment that the variety seems to be widespread also in the Indomalayan realm: "(…) die var. *macrocephala* wurde bisher nur auf Sumatra beobachtet, scheint also im indomalayischen Gebiet ebenfalls weiter verbreitet zu sein". After Hustedt's observations, the taxon was subsequently found in the USA by Hohn & Hellerman (1963) and later by Patrick & Reimer (1966). However, Potapova & Hamilton (2007) observed that specimens with a "capitate" outline from North America formed a group of species that, although similar to *A. macrocephalum*, could be distinguished from it by a slightly different valve outline, more radiate and denser striae near the valve ends *apud* Potapova & Hamilton (2007). North American populations also differed in their ecology and were present in nutrient-poor, slightly acidic waters, mostly in the south-eastern United States, while *A. macrocephalum* is an alkaliphilous species (Hustedt 1937), illustrating "the danger of making wrong conclusions about environmental conditions when specimens from taxonomically poorly studied areas are 'fitted' into historically recognized taxa" (Potapova & Hamilton 2007).

Some authors regarded *A. macrocephalum* as an important marker in some paleo-limnological studies (e.g. Abbott et al. 2000, Bigler & Hall 2002, Tapia 2008) and it supposedly occurred in many freshwater habitats around the world. However, we investigated all available illustrations in the bibliographic record and did not recognise the 'true' morphotype of *A. macrocephalum* in any of these images. There are records of *A. macrocephalum* from Africa (i.e. South Africa: Taylor et al. 2007, 2009, Harding & Taylor 2014, Musa & Greenfield 2018) and Madagascar (Metzeltin & Lange-Bertalot 2002). LM and SEM images were presented by Metzeltin & Lange-Bertalot (2002: pl. 17, figs 6–8) from a population with striae composed by several areolae (up to 4 or 5), and this clearly differs from the type investigated here. Taylor et al. (2007: pl. 23) presented specimens which are similar in outline, but also have a different areola arrangement (up to

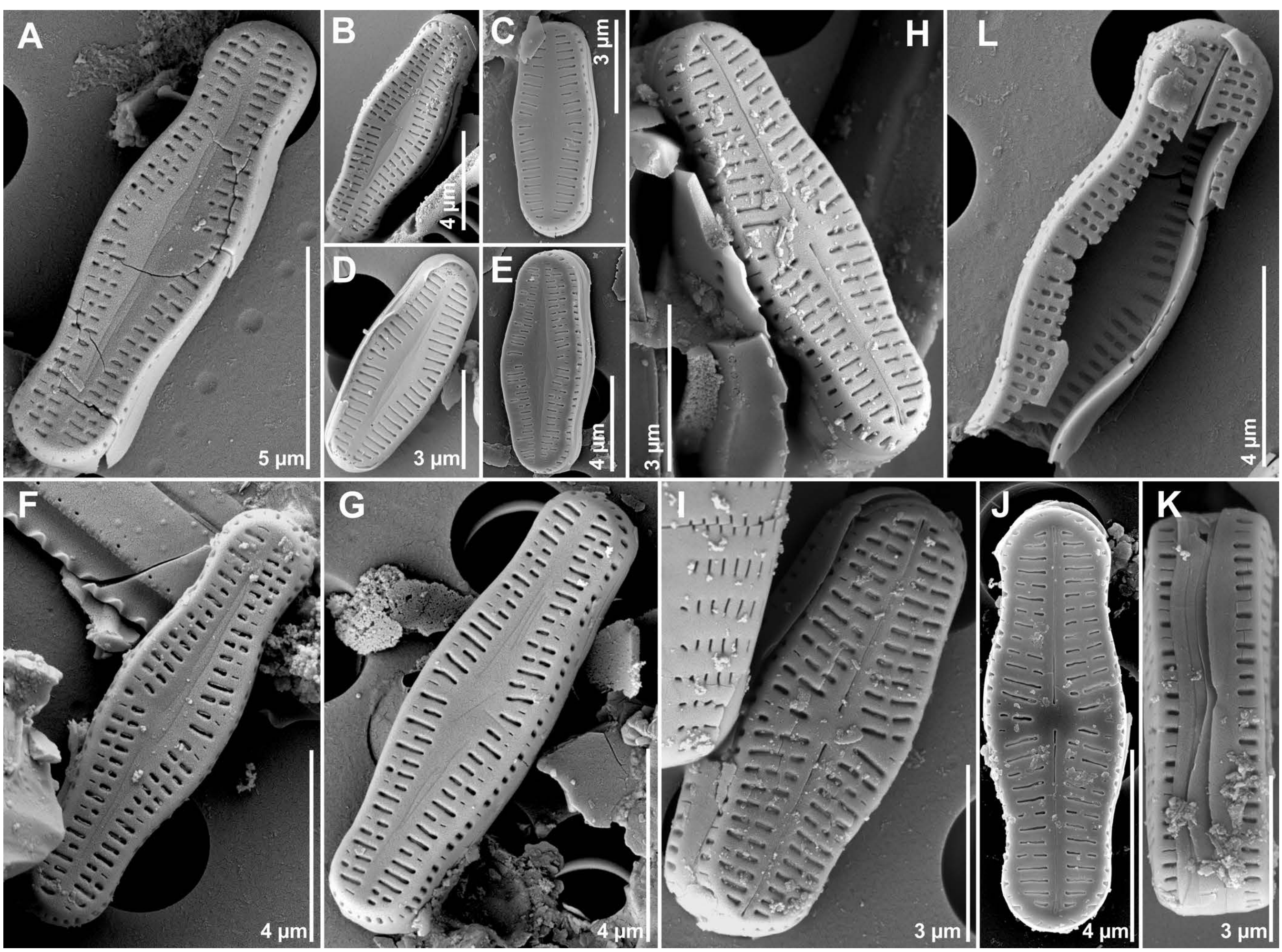

Figure 2 – SEM micrographs of the type material of *Achnanthidium macrocephalum*: A–G, external view of rapheless valves, note the open valvocopula (fig. B, white arrow); H–I, external view of raphe valves (tilted), J, external view of a raphe valve; K, girdle view of a frustule showing the different shapes of the mantle areolae and the girdle bands; L, external view of a broken frustule showing a higher number of areolae (up to 4) on a raphe valve.

6 areolae per striae) and higher stria density near the apices, and therefore also differ from the type. Specimens identified as *A. macrocephalum* were also recorded from Australasia (e.g. China, Japan, Nepal, Taiwan, and Tasmania) (Wang et al. 2009, Jüttner & Cox 2011, Shiao & Wang 2011). No publication has provided illustrations (e.g. Vyverman et al. 1995: 17, pl. 23, figs 8, 9, Ohtsuka & Tuji 1997: fig. 2, Kihara et al. 2009: 92, fig. 3) that agrees with the specimens from the original material from Lake Toba. In Europe, citations of *A. macrocephalum* exist from Estonia, France, Germany, Serbia, Spain and Switzerland (Cremer 2006, Linares Cuesta & Sánchez Castillo 2007, Morin et al. 2012, Straub 2013, Tekwani et al. 2013, Simić et al. 2015, Olenici et al. 2017). We could not confirm the identity of *A. macrocephalum* in any of these studies, either because SEM images were not provided or because the taxon shown did not conform to the type material from Indonesia.

Krammer & Lange-Bertalot (1991: 60, pl. 34, figs 7–9) provided LM images of specimens identified as *Achnanthes minutissima* var. *macrocephala* from Brunnsee (Upper Bavaria, Germany). These and SEM images from several lakes in Upper Bavaria (Lange-Bertalot & Krammer (1989: pl. 63, figs 6–10) show distinct morphological structures with respect to striation patterns (usually 3–5 rounded areolae) and valve outline. It is likely that these specimens belong to an independent and putative new taxon. Given this situation of likely misidentifications, the ecological information provided by Coste et al. (2009) for the taxon in Europe must be re-evaluated and a cautious approach adopted similar to that by Potapova & Hamilton (2007).

Achnanthidium macrocephalum was also reported from South America but, as elsewhere, these records do not match Hustedt's taxon. SEM images from Brazil (Marra et al. 2016: fig. 219) and Colombia (Sala et al. 2015: fig. 2 a–g) show specimens which clearly belong to a different species. Records from Argentina (Licursi & Gómez 2003), Peru (Tapia 2008), Brazil (Zorzal-Almeida et al. 2017, Bartozek et al. 2018) are also doubtful and most likely represent another species, based on the LM illustrations provided.

The most similar species with respect to the ultrastructure of the areolae is *Achnanthidium rosenstockii* var. *inareolatum* Lange-Bert. (in Krammer & Lange-Bertalot 2004: pl. 90, figs 1 & 2): the small valves have striae composed of

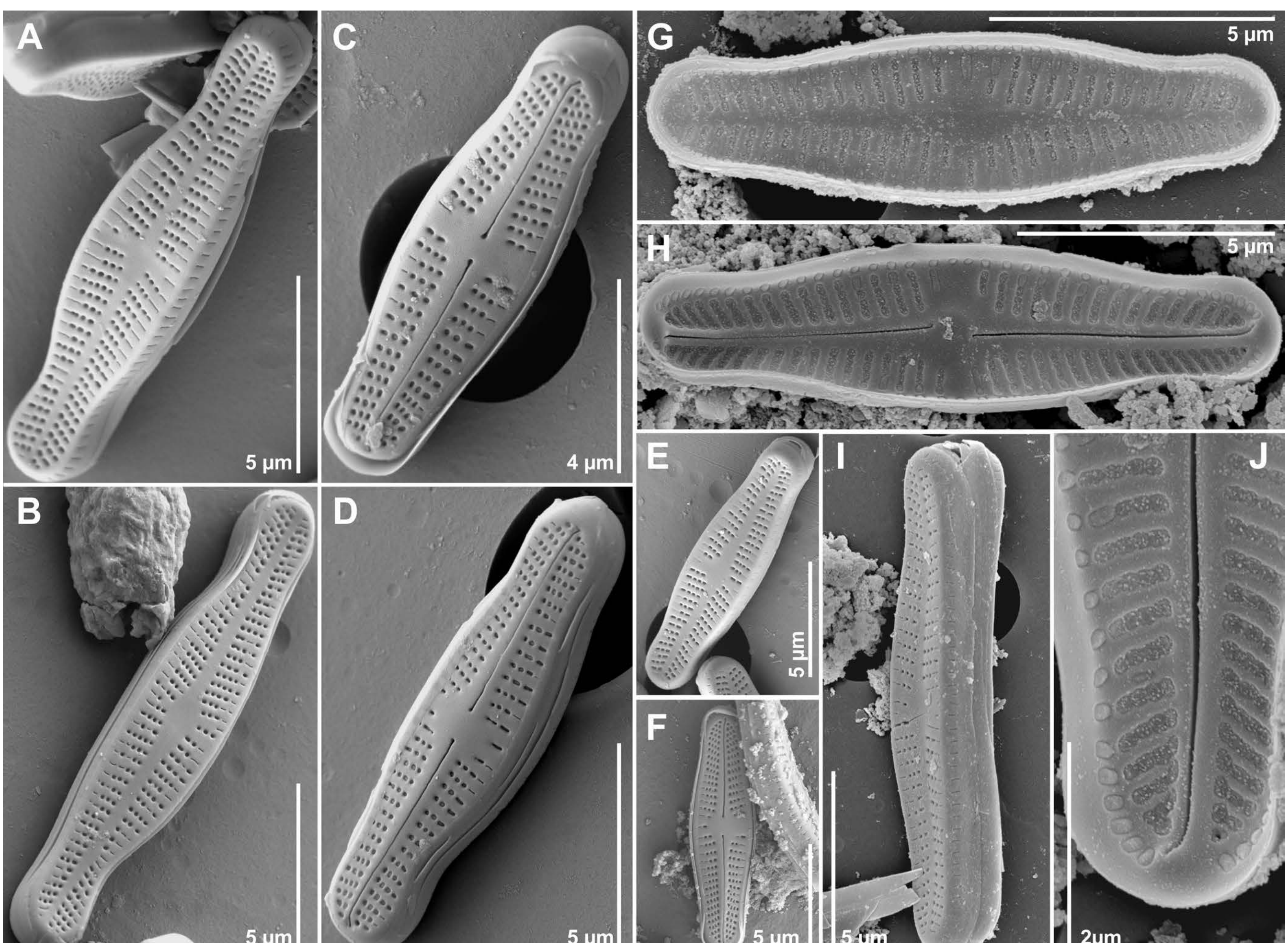

Figure 3 – SEM micrographs of *Achnanthidium peetersianum*: A, B & E, external view of rapheless valves; C–D & F, external view of raphe valves; G, internal view of rapheless valve; H, internal view of raphe valve showing the raphe, helictoglossae and occluded areolae; I, oblique view of a frustule; J, details of helictoglossa and internal view of occluded areolae.

single long areolae (as show in our fig. 2C, D). *Achnanthidium rosenstockii* (Lange-Bert.) Lange-Bert. (in Krammer & Lange-Bertalot 2004: 433) as illustrated (as *Achnanthes rosenstockii* Lange-Bert. in Lange-Bertalot & Krammer 1989: pl. 61, figs 1–17, pl. 63, figs 1–5) probably shows two different species: one with striae on both valves composed of single long areolae, and another with striae composed of mostly 4 areolae. Both taxa differ from *A. macrocephalum* also regarding valve outline, which are broader and have subcapitate poles.

Achnanthidium macrocephalum might be restricted to the Indomalayan archipelago based on the findings of Hustedt (1937, 1942). It is most likely that Hustedt (1937) included two morphotypes in his diagnosis based on his drawings (*pro parte*). We consider here the forms typified by Simonsen (1987: 211, pl. 325, figs 13–22) which are the specimens found in sample AS849 (i.e. figs 50 & 51 in Hustedt 1937).

Achnanthidium peetersianum C.E.Wetzel, Jüttner & Ector, **sp. nov.**

Figs 1N–AK & 3A–J

Type material – France, Bourgogne-Franche-Comté region, Le Sauvigny River at Perrigny-sur-Loire (46°32′15.8″N, 3°50′25.8″E), 11 Aug. 2010, *Valérie Peeters* (holo- : BR, slide BR-4551).

Description – Valves linear-elliptic with convex margins and broadly rounded subcapitate apices (fig. 1N–AJ). Frustules in girdle view slightly arched with slightly recurved apices (fig. 1AK). Valve dimensions 8.5–14.8 µm long and 2.8–3.3 µm wide. Rapheless valve slightly convex (fig. 3I) with narrow, linear axial area widening very slightly towards central area (fig. 3A, B & E). Central area indistinct or slightly expanded, bordered by 1 or 2 sometimes more widely spaced striae on both sides, often 1 central shortened stria present on both sides, composed of 1 often slit-like areola. Transapical striae radiate throughout entire valve, becoming slightly more radiate and denser near apices, 28–32 in 10 µm, up to 40 in 10 µm near apices, difficult to resolve in LM. Striae composed of 2–5 (rarely 6) round or slightly transapically elongated areolae. Areolae sometimes slit-like near valve margins. A single row of small, elongated or slit-like areolae on mantle separated from striae on valve face by a pore-free area (fig. 3A), not discernible in girdle view in LM (fig. 1AK). Raphe valve slightly concave with a narrow linear axial area, slightly expanded towards the centre. Central area small and rounded or elliptical (fig. 3C, D & F), bordered by 1 or 2 more widely spaced striae on both sides, sometimes central striae absent from one (fig. 3F) or both sides and central area forming a rectangular fascia (fig. 3C). Raphe straight, filiform, externally straight drop-shaped proximal raphe ends (fig. 3C, D & F), internally slightly deflected in opposite directions (fig. 3H). Externally distal raphe ends slightly bent to the same side (fig. 3C & D) or more or less straight (fig. 3F), terminating internally in a small helictoglossa (fig. 3H). Transapical striae weakly radiate throughout entire valve, becoming denser and more strongly radiate towards apices, 32 in 10 µm near valve centre, up to 40 in 10 µm near apices, difficult to resolve in LM. Striae composed of 3–5 rounded to slightly squared transapically elongated areolae.

Etymology – We dedicate the species to our colleague Valérie Peeters (DREAL Bourgogne-Franche-Comté, Dijon, France) for her excellent work on the diatoms of rivers in Burgundy.

Remarks on distribution and similar species – The ecology and distribution of this taxon cannot be determined at present because all small species with capitate apices were usually recorded under *A. minutissimum* or *A. macrocephalum*. The species has only recently been recognized as a taxon that is distinct from *A. minutissimum* s. lat. In France, mainly at its type locality in the Sauvigny River at Perrigny-sur-Loire, *A. peetersianum* was found in well oxygenated waters with slightly alkaline to neutral pH and relatively high conductivity values (130–320 µS cm^{-1}) (fig. 4). In Burgundy Peeters & Ector (2018: 60) published additional illustrations of the species as *Achnanthidium* sp. 3, a taxon with high relative abundances at the type locality (up to 55%).

The most similar species are *Achnanthidium minutissimum* and *A. microcephalum* Kütz., following the recent investigation of the type material by Potapova & Hamilton (2007),

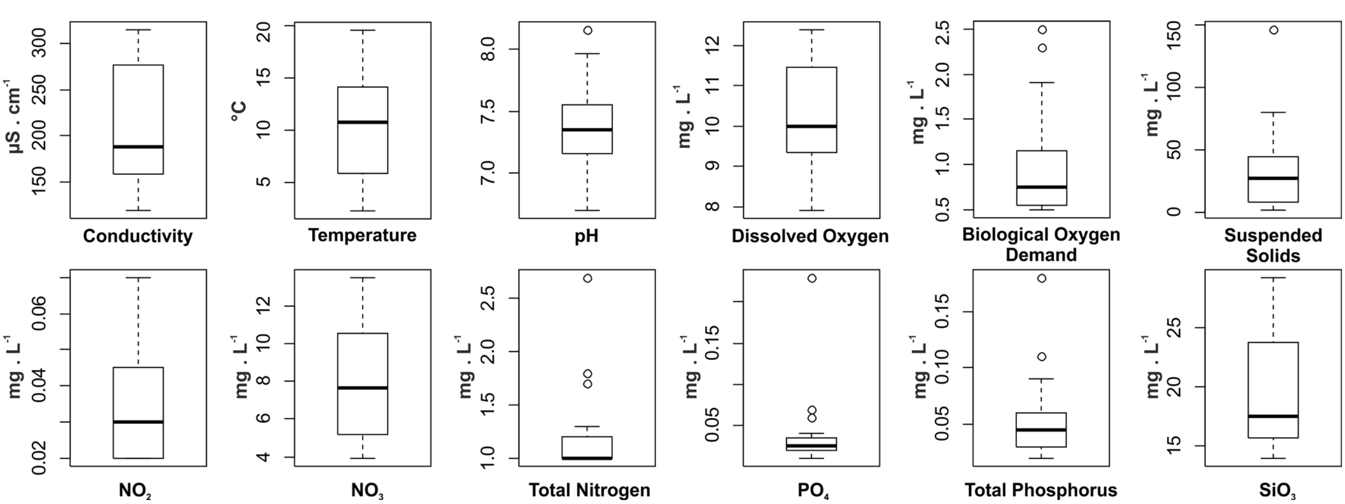

Figure 4 – Box-plots of environmental parameters recorded at locations in the Le Sauvigny River at Perrigny-sur-Loire, Bourgogne-Franche-Comté region, France, where *Achnanthidium peetersianum* was found in 2010.

Novais et al. (2015) and Marquardt et al. (2017). They differ in stria density, which is higher, and in valve outline, which is linear-elliptic with slightly rostrate or subrostrate valve ends rather than the subcapitate valve ends in *A. peetersianum*. Valves of *A. peetersianum* also rarely have a small, sometimes indistinct rectangular fascia (Novais et al. 2015, Peeters & Ector 2018). Similar taxa have been illustrated recently by Cantonati et al. (2014) who showed small capitated *Achnanthidium* populations with several deformities and teratology induced by metal contamination (copper, zinc, and antimony). However, it is difficult to determine whether they belong to the same taxon. *Achnanthidium jackii* Rabenh. (syn. *Achnanthidium neocryptocephalum* (Grunow) Novais & Van de Vijver; Potapova & Hamilton 2007: figs i, j, Novais et al. 2015: figs 80–125, 159–170, Van de Vijver et al. 2018: figs 1–22) has rostrate ends and a more distinct rectangular fascia on the raphe valve. *Achnanthidium affine* (Grunow) Czarn. (Czarnecki 1994: 156) is larger (8–30 µm long, 3.5–5 µm wide) and has linear-lanceolate to rhombic-lanceolate valves and a distinct central fascia on the raphe valve (see Bey & Ector 2013, p. 87). *Achnanthidium saprophilum* (H.Kobayasi & Mayama) Round & Bukht. (Round & Bukhtiyarova 1996: 349) has short and broader protracted, rostrate ends and its striae are composed of usually five areolae (Hlúbiková et al. 2011: figs 118–147). *Achnanthidium costei* Pérès & Le Cohu (Pérès et al. 2014: 390, figs 41–80) has higher stria density (32–35 in 10 µm) and a distinct rectangular central fascia on the raphe valve. *Achnanthidium polonicum* Van de Vijver et al. (Wojtal et al. 2011: 223, figs 131–154) is larger (11.4–21.5 µm long, 2.6–4.0 µm wide) and has distinct subcapitate ends.

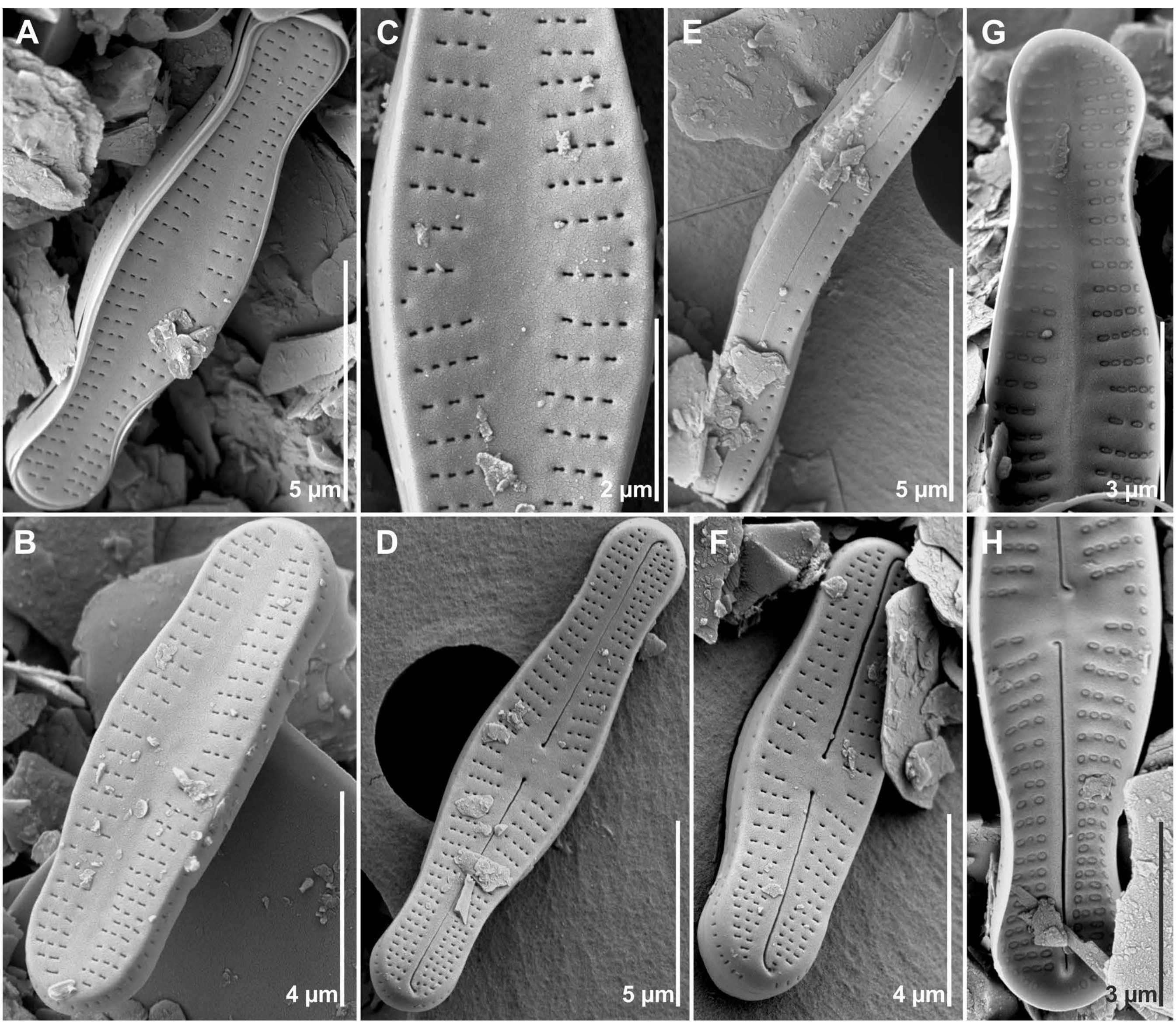

Figure 5 – SEM micrographs of *Achnanthidium coxianum*: A–C, external view of rapheless valves; D & F, external view of raphe valves; E, girdle view of a frustule showing short areolae on the mantle; G, internal view of rapheless valve showing expanded axial and central area, and occluded areolae; note the continuous row of areolae on the mantle at the apex; H, internal view of raphe valve showing proximal raphe ends curved to opposite sides, the helictoglossa and a gap in the mantle areolae at the apex.

Achnanthidium lusitanicum Novais & M.Morais (Novais et al. 2015: 129, figs 403–477) has protracted, broadly rounded rostrate ends and higher striae density (30–35 in 10 µm), and striae are difficult to resolve in LM. *Achnanthidium pseudolineare* Van de Vijver et al. (Van de Vijver et al. 2011a: 186, figs 208–256) is almost linear in shape with broad, subrostrate ends.

Achnanthidium coxianum Jüttner, Ector & C.E.Wetzel, **sp. nov.**

Figs 1AL–BH & 5A–H

Type material – Nepal, Donag Lake (Gokyo lakes series) at Sagarmatha (Everest) National Park, NMW.C.2009.003.401 G4 lake littoral (27°58′36.3″N, 86°40′49.6″E), 20 Oct. 2008, *Smriti Gurung & Ingrid Jüttner* (holo-: NMW, slide NMW.C.2009.003.401 G4 lake littoral; iso-: Kathmandu University/Department of Environmental Science and Engineering, slide NMW.C.2009.003.401 G4 lake littoral; BR, slide BR-4552).

Description – Valves linear-elliptic with convex margins and broadly rounded capitate apices (fig. 1AL–BG). Frustule slightly arched in girdle view with concave raphe valve and convex rapheless valve (fig. 1BH). Valve dimensions 8.1–12.9 µm long and 2.5–3.0 µm wide, 28–32 striae in 10 µm. On rapheless valve linear axial area widening towards the centre to form narrow elliptic central area. Striae in valve centre slightly radiate becoming parallel away from valve centre and near poles, sometimes more widely spaced at valve centre (figs 1AL–AW & 5A–C). On the raphe valve narrow axial area widening slightly towards small rounded central area. Raphe slit straight with drop-like external proximal raphe ends, distal raphe ends deflected to the same side, terminating on valve face near valve margin (figs 1AX–BG, 5D & F). Internally proximal raphe ends deflected in opposite directions, distal raphe ends terminating in small helictoglossae (fig. 5H). Striae radiate near valve centre becoming parallel away from valve centre and near poles, central striae are more widely spaced. Striae on both valves composed of (2)3–4 'dumbbell'-like shaped or small elongate areolae (fig. 5A–D & F). Mantle with one row of elongated areolae, separated from those on valve face by pore-free area along the valve face-mantle junction (fig. 5E & F). Internally areolae are occluded by hymenes perforated by delicate slits (fig. 5G & H).

Etymology – We dedicate the species to our colleague Dr. Eileen J. Cox as a token of respect for her impact and important contributions to diatom research.

Remarks on distribution and similar species – So far, the species was only found in the littoral of Donag Lake. Donag Lake is the forth lake in the series of the Gokyo lakes in the Gokyo Valley, Sagarmatha (Everest) National Park, Nepal. The lake is located at 4839 m a.s.l. on the moraine west of the Ngozumpa Glacier and has a surface area of 0.573 km^2. The sample was collected at the eastern side of the lake in a large flat area, which is inundated for short periods when the water level rises during and after the summer monsoon in the autumn, but falls dry during the pre-monsoon season in spring. The catchment is dominated by exposed bedrock and glacier debris of slow weathering gneiss and quartz-silicate rocks with vegetation comprising patches of dwarf shrubs and tundra grassland.

Achnanthidium modestiforme (Lange-Bert.) Van de Vijver (Van de Vijver et al. 2002: 17, figs 10–18, 21–22) is the most similar species but it has subcapitate ends, is larger (12–25 µm long, 2–4 µm wide), lacks a round central area and the areolae are rounded. *Achnanthes grimmei* Krasske (Krasske 1925: 30, figs 1, 10) has subcapitate ends and lower stria density (20 in 10 µm). *Achnanthidium rosenstockii* (Lange-Bert.) Lange-Bert. (Krammer & Lange-Bertalot 2004: 433) is wider (3–4.5 µm) and has broadly protracted, subcapitate ends. *Achnanthidium tepidaricola* Van de Vijver & M.de Haan (Van de Vijver et al. 2011b: 201, 202, figs 48–66) is slightly larger (12–14 µm long), has subcapitate ends and almost parallel valve margins in the central part of the valve. In valve view *Achnanthidium catenatum* (J.Bílý & Marvan) Lange-Bert. (Lange-Bertalot 1999: 277, see also Hlúbiková et al. 2011: figs 1–34, 148–155) is similar in shape, but ends are more broadly capitate, subcapitate or rostrate, the striae appear less distinct, the rapheless valve is concave, and the raphe valve convex. *Achnanthidium saprophilum* has short and broader protracted, rostrate ends and striae are composed of usually five, mostly rounded areolae (Hlúbiková et al. 2011: figs 118–147). *Achnanthidium acsiae* Wojtal et al. (2011: 226, 227, figs 155–184) has subrostrate to subcapitate ends, higher stria density (28–36 in 10 µm) and a small rectangular fascia on the raphe valve. *Achnanthidium palmeti* Gassiole et al. (Gassiole et al. 2013: 22, figs 1–27) is slightly wider (2.7–4.6 µm), the ends are rostrate or subcapitate, and the stria density is higher (32–35 in 10 µm) with striae rarely discernible in LM. *Rhossithidium nodosum* (Cleve) Aboal (Aboal et al. 2003: 178) has almost linear valves with hardly protracted ends.

CONCLUDING REMARKS

The three species observed may be difficult to distinguish at first glance. In SEM, differences in ultrastructure are clear, in particular with respect to the arrangement of the areolae, and there are subtle differences in the terminal raphe ends. Differences in LM are discrete; but differences in stria density, in the shape of the axial and central areas and in the shape of the poles allow identification also in LM. *Achnanthidium coxianum* has a more distinct elliptical central area on the rapheless valve, and the central area on the raphe valve is more distinct in both *A. coxianum* and in *A. peetersianum*. In *A. coxianum* the striae appear coarser compared to the other species, but the stria density is the same as in *A. peetersianum* (28–32 in 10 µm). In *A. macrocephalum* the striae are hardly resolvable in LM (38–40 in 10 µm), even using differential interference contrast microscopy. *Achnanthidium peetersianum* has subcapitate apices, whereas the other species have more distinct capitate apices.

It is likely that the three *Achnanthidium* species were overlooked in the past because of the broad species concept that was commonly applied until recently. *Achnanthidium peetersianum* has certainly been identified as *A. minutissimum* in France over the years. The distribution of these species is therefore unknown, but it is possible that *A. coxianum* and *A. macrocephalum* might have restricted distributions and are confined to Asia, and to the Himalaya and Indonesia in particular.

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