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The genera *Achnanthidium* Kützing and *Psammothidium* Bukhtiyarova *et* Round in the family Achnanthidiaceae (Bacillariophyceae): a reappraisal of the differential criteria

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Abstract – The diagnostic characteristics of the genera *Achnanthidium* and *Psammothidium*, the latter genus recently separated from other species of *Achnanthes sensu lato*, of the family Achnanthidiaceae D.G. Mann have been evaluated on the basis of a morphological study of eleven common species found in rivers and streams of Luxembourg. In light of these observations – supplemented by a literature review – it is concluded that the two genera cannot be unambiguously defined on the basis of morphological criteria. Furthermore, no ontogenetic or phylogenetic studies support any of the discriminating characteristics. On the basis of these results, *Achnanthes bioretii*, *A. daonensis*, *A. austriaca* var. *helvetica*, *A. lauenburgiana* and *Navicula subatomoides* have been transferred to *Achnanthidium*.

Achnanthidiaceae / *Achnanthidium* / Bacillariophyceae / *Psammothidium* / taxonomy

Résumé – **Les genres *Achnanthidium* Kützing et *Psammothidium* Bukhtiyarova *et* Round de la famille des Achnanthidiaceae (Bacillariophyceae) : une réévaluation des critères de distinction.** Les caractères de distinction des genres *Achnanthidium* et *Psammothidium*, ce dernier récemment séparé des autres espèces d'*Achnanthes sensu lato*, appartenant à la famille des Achnanthidiaceae D.G. Mann, ont été évalués sur la base de l'étude morphologique de onze espèces communes trouvées dans les cours d'eau du Luxembourg. A la lumière de ces observations – complétées par les données bibliographiques – il est conclu que ces deux genres ne peuvent être circonscrits sans ambiguïté sur la base des seuls critères morphologiques. De plus, aucune distinction n'a pu être validée par des études ontogénétiques ou phylogénétiques. En conséquence, *Achnanthes bioretii, A. daonensis, A. austriaca* var. *helvetica, A. lauenburgiana* et *Navicula subatomoides* ont été transférés dans *Achnanthidium.*

Achnanthidiaceae / *Achnanthidium* / Bacillariophyceae / *Psammothidium* / taxonomie

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INTRODUCTION

The taxonomy of *Achnanthes* Bory has undergone many changes in the last fifteen years. Although Round *et al.* (1990) broadly maintained the classification of Patrick & Reimer (1966) for higher taxonomic levels (classes to orders), they introduced intermediate levels (subclasses) and made significant changes to families and genera. Based on the large morphological variability reported in the Achnanthaceae Bory *sensu* Patrick & Reimer (1966), as well as the apparent polyphyly of the family (Kociolek & Stoermer, 1986), Mann recognised several new families (Mann, 1984a; Round *et al.*, 1990). One of these is Achnanthidiaceae D.G. Mann, which included *Eucocconeis* Cleve and *Achnanthidium* Kützing, the latter re-established as a genus (Round *et al.*, 1990), where previously it had been a subgenus of *Achnanthes* (*sensu* Reimer *in* Patrick & Reimer, 1966; *non sensu* Hustedt, 1959). Subsequently, *Achnanthidium* was emended (Round & Bukhtiyarova, 1996) along with the addition of numerous new genera: *Achnanthidium* Kützing, *Karayevia* Round *et* Bukhtiyarova, *Kolbesia* Round *et* Bukhtiyarova, *Lemnicola* Round *et* Basson, *Planothidium* Round *et* Bukhtiyarova, *Platessa* Lange-Bertalot, *Psammothidium* Buhhtiyarova *et* Round and *Rossithidium* Round *et* Bukhtiyarova (Round *et al.*, 1990; Bukhtiyarova & Round, 1996; Round & Bukhtiyarova, 1996; Round & Basson, 1997; Round, 1998; Krammer & Lange-Bertalot, 2004). However, with the exception of the generic "keys" provided by Compère (2000) and Carneiro (2003), no differential diagnosis – except for *Platessa* (Krammer & Lange-Bertalot, 2004: 442) – or tables for comparison are available for genera belonging to the Achnanthidiaceae. Furthermore, their establishment has raised questions about their delimitation and the relevance of particular diagnostic criteria.

As for most diatoms, genera in the family Achnanthidiaceae are 'morphogenera', based only on the structure of the frustule. Furthermore, species concepts in diatoms have often been interpreted too broadly; there are probably many more species than are currently recognised (Mann & Droop, 1996), even in areas of the world that are comparatively well known, such as Western Europe. Before any conclusions can be made regarding diatom biodiversity at the generic level, the concept of genera must be thoroughly refined, ideally reflecting the phylogeny as well as the degree of similarity between taxa.

Within the larger framework of a study on diatom diversity of Luxembourg's rivers and streams, a total of 454 taxa were identified with the light microscope, among which 39 belong in the family Achnanthidiaceae, in the genera *Achnanthidium*, *Psammothidium*, *Planothidium* and *Platessa*. In view of the unresolved taxonomy of this family, eleven of the more common species of *Achnanthidium* and *Psammothidium* were subjected to a detailed morphological investigation.

According to Bukhtiyarova & Round (1996), the differential criteria separating *Psammothidium* from *Achnanthidium* are: "(a) the shape of the valve, oval/elliptic (sometimes slightly capitate) as opposed to linear/linear capitate, (b) curvature of the raphe valve – convex as opposed to concave, (c) striae reach the sternum as opposed to marginal, (d) raphe fissures lying in channel (especially near the centre) as opposed to non-channeled and ending centrally in pin-hole expansions". The morphological features cited in the diagnosis of *Psammothidium* (Bukhtiyarova & Round, 1996) and the emended diagnosis of *Achnanthidium* (Round & Bukhtiyarova, 1996) are summarised in Table 1. Focusing on these criteria, gaps or continua among the genera studied were highlighted, in order to identify features that best differentiate taxa and to evaluate their taxonomic position.

Table 1. Diagnostic characters considered in genera diagnoses or emendations for *Psammothidium* and *Achnanthidium*, completed by personnal observations for characters not assigned by Bukhtiyarova & Round (1996) and Round & Bukhtiyarova (1996).

Character	*Psammothidium*	*Achnanthidium*
Frustule girdle	Concave-convex	Shallow-V-shaped
Raphe valve apical axis	Convex	Concave to convex
Raphe valve transapical axis	Convex	Concave to convex
Valve shape	Elliptical to lanceolate-elliptical	Linear-lanceolate to lanceolate-elliptical
Apices	Always rounded	Rounded to capitate
Length	*ca* 10-30 µm	10-20(30) µm
Width	Less than 10 µm	Less than 5 µm
Length/Width ratio	2(3-4)	3-6
Areolae on opposite valves	Similar	Similar or slightly different
Areolae inner openings	Small, closed by a cribrum	Small, closed by a membrane
Areolae external openings	Of varying shape	Of varying shape
Striae	Radiate, *ca* 30 in 10 µm	Radiate or almost transverse, *ca* 30 in 10 µm
Sternum	Narrowly linear to narrowly triangular	Narrow at apex, widening at centre
Central area	Variable	Of varying width and shape
Slit of the raphe	Straight	Fine, central
Raphe ends	Variably developed	Hardly expanded at centre, straight or turned to one side at apex
Raphe situation (internally)	In a rib	In a rib
Central pores (internally)	Slightly bent towards opposite sides	Slightly bent towards opposite sides
Helictoglossae	Slightly raised	Slightly raised
Sternums	Alike or dissimilar on both valves	Alike or slightly dissimilar on both valves
Mantle areolae	One row, separated from the valve face	One row, separated from the valve face

MATERIAL AND METHODS

Epilithic material collected from the rivers and streams of Luxembourg between 1994 and 2003 was investigated. The samples were treated with H_2O_2 and HCl, rinsed three times, then mounted on permanent slides with Naphrax® for light microscopy (Iserentant *et al.*, 1999). Optical observations, identifications, measurements and micrographs were made with a Leica® DMRB microscope with differential interference contrast. Treated samples were also mounted on stubs and sputtered with gold (40 nm) for scanning electron microscopy (SEM). Measurements and photographs were obtained with a Leica® Stereoscan 430i instrument, operated at 20 kV. Both optical and SEM measurements were used for the descriptions of taxa.

In the descriptions below, RV = raphid valve, AV = araphid valve.

OBSERVATIONS

Eleven taxa were identified from rivers in Luxembourg as belonging to the genera *Achnanthidium* and *Psammothidium*. These are briefly described below. Comments on each species are confined to particular features, those considered part of the generic diagnosis. The features of greatest relevance to the generic diagnosis of *Achnanthidium* and *Psammothidium* are summarised in Table 2.

Achnanthidium Kützing

1. ***Achnanthidium atomoides*** Monnier *et al.* (2004: 130, figs 1-72, 117-123) **Figs 1-8**
Notes: The primary differences, when compared to other taxa in *Achnanthidium*, are the concave RV and the convex AV along the transapical axis (Figs 6, 8 and Monnier *et al.*, 2004: fig. 121), the co-axial raphe branches inside the valve (Fig. 4), the striae pattern and striae and areolae densities are significantly different on both valves (Figs 3, 5) and the axial area of the AV is often slightly displaced towards one margin (Fig. 7).

2. ***Achnanthidium catenatum*** (Bílý *et* Marvan) Lange-Bertalot (1999: 277) **Figs 9-14**
Basionym: *Achnanthes catenata* Bílý *et* Marvan (1959: 35, pl. 8, figs 1-4).
References: Straub (2002: figs 1-10); Coste & Ector (2000: 380, pl. 1, figs 4-15); Druart & Straub (1993, figs 1-13); Krammer & Lange-Bertalot (1991: 62, pl. 34, figs 23, 24); Lange-Bertalot & Krammer (1989: 37, pl. 55, figs 30-32).
Notes: The primary difference, when compared to other taxa in *Achnanthidium*, is the purely convex curvature of the RV in smaller individuals (Fig. 9); larger specimens are slightly concave at the centre and strongly convex at the poles (Fig. 14).

3. ***Achnanthidium kranzii*** (Lange-Bertalot) Round *et* Bukhtiyarova (1996: 350) **Figs 15-22**
Basionym: *Achnanthes kranzii* Lange-Bertalot *in* Lange-Bertalot & Krammer (1989: 74, pl. 55, figs 13-21, pl. 62, figs 6-8).

References: Krammer & Lange-Bertalot (1991: 64, pl. 34, figs 25-33); Lange-Bertalot & Ruppel (1980: 25, pl. 11, figs 314-319).

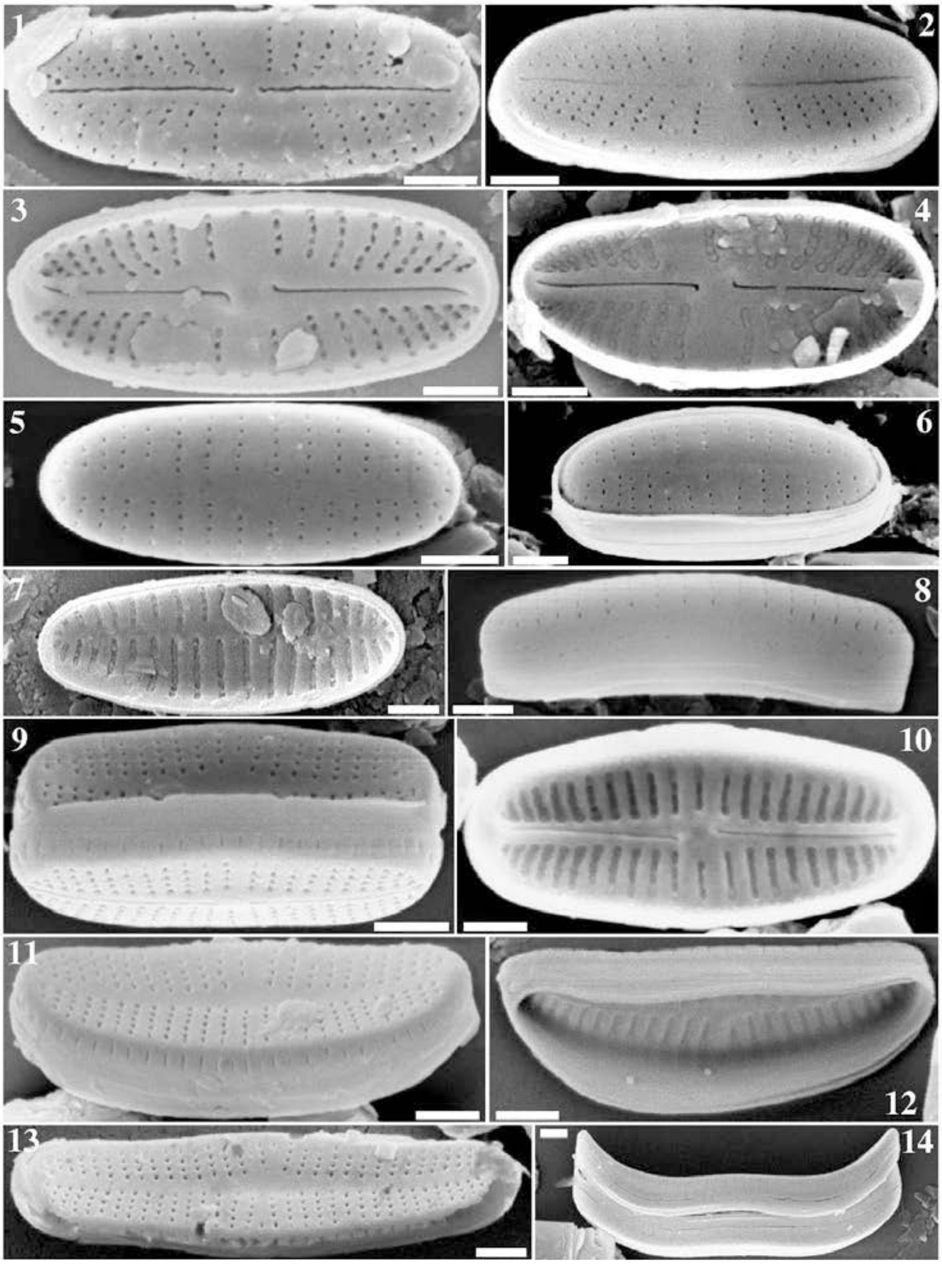
4. *Achnanthidium minutissimum* (Kützing) Czarnecki (1994: 157) **Figs 23-32**
Basionym: *Achnanthes minutissima* Kützing (1833: 578, fig. 54). **Synonym:** *Achnanthidium lineare* W. Smith (1855: 32, pl. 1, fig. 9) *pro parte* (syntype from Lasswade, Scotland, slide BM 445).

Table 2. Morphological criteria of the investigated species, considered as differential for *Psammothidium* by Bukhtiyarova & Round (1996).

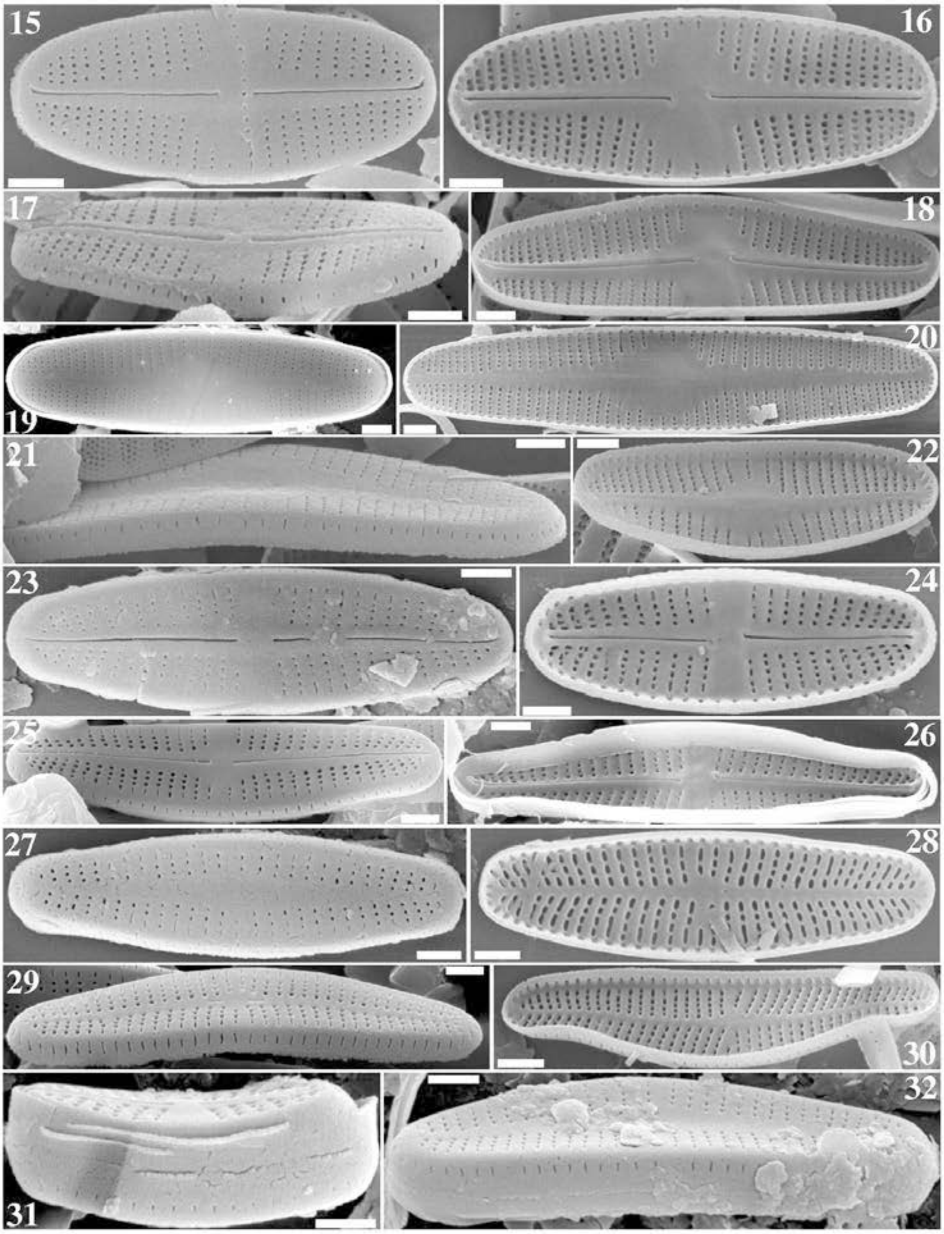
Taxon	*Valve shape*	*RV apical axis*	*RV transapical axis*	*Striae extension*	*Raphe slit*	*Central raphe ends*
Achnanthidium ***A. atomoides***	narrowly elliptic	concave	concave	valve face	simple	small pin-hole
A. catenatum	linear-lanceolate	convex to concave-convex	convex	valve face	simple	simple slit
A. kranzii	elliptic to elliptic-lanceolate	concave to concave-convex	convex	valve face	simple	simple slit
A. minutissimum	elliptic to linear-lanceolate	concave	convex	valve face	simple	simple slit
A. pyrenaicum	elliptic to linear-lanceolate	slightly concave	slightly convex	valve face	simple	drop
A. subatomus	elliptic to linear-elliptic	slightly concave	convex	valve face	furrow	drop
Psammothidium ***P. bioretii***	elliptic	concave-convex	centrally convex	on mantle	furrow and ridges	pin-hole
P. daonense	elliptic	concave-convex	centrally convex	valve face	furrow and ridges	pin-hole
P. helveticum	elliptic	concave-convex	convex	on mantle	furrow and ridges	drop
P. lauenburgianum	elliptic	concave-convex	convex	valve face	furrow and ridges	pin-hole
P. subatomoides	elliptic	concave-convex	slightly convex	valve face	furrow and ridges	pin-hole

References: Round & Bukhtiyarova (1996: 348, figs 1-6); Krammer & Lange-Bertalot (1991: 56, pl. 32, figs 1-24, pl. 35, fig. 1); Lange-Bertalot & Krammer (1989: 103, pl. 51, figs 1-20, pl. 52, figs 1-13, pl. 56, figs 1-4, pl. 57, figs 9-10).
Notes: An incipient vestigial raphe may be observed rarely (Fig. 29).

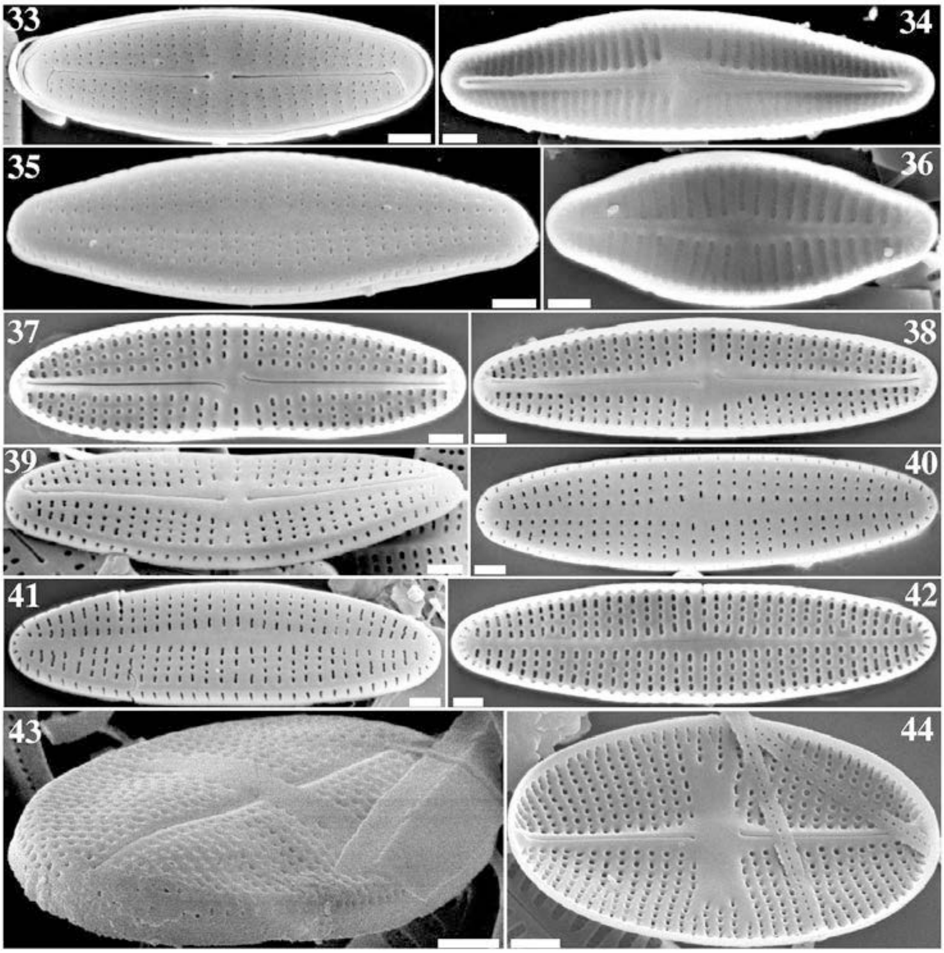
5. *Achnanthidium pyrenaicum* (Hustedt) H. Kobayasi (1997: 148, figs 1-18) **Figs 33-36**
Basionym: *Achnanthes pyrenaica* Hustedt (1939: 554, figs 5-10). **Synonyms:** *Achnanthes biasolettiana* Grunow *partim*, i.e. *sensu* Lange-Bertalot (Lange-Bertalot & Krammer, 1989: 26, pl. 57, figs 1-7); *Achnanthidium lineare* W. Smith (1855: 32) *pro parte* (syntype from Vaucluse, France, slide BM 623).



Figs 1-14. SEM. **1-8.** *Achnanthidium atomoides*. Specimens from a population of the river Ernz Blanche in Hessemillen, 27.09.2002. **1, 2.** RV, outside. **3, 4.** RV, inside. **5, 6.** AV, outside. **7.** AV, inside. **8.** Frustule, girdle. **9-14.** *Achnanthidium catenatum*. Specimens from a population of the streamlet Reideschbaach in Niederfeulen, 30.09.1996. **9.** RV, outside tilted, with a AV behind. **10.** RV, inside. **11.** AV, outside tilted. **12.** AV, inside tilted. **13.** AV, outside. **14.** Girdle view of two attached frustules. Scale bars = 1 µm.



Figs 15-32. SEM. **15-22.** *Achnanthidium kranzii*. Specimens from a population of the streamlet Breschterbaach in Pratz, 23.03.1995. **15.** RV, outside. **16.** RV, inside. **17.** RV, outside tilted. **18.** RV, inside tilted. **19.** AV, outside. **20.** AV, inside. **21.** AV, outside tilted. **22.** AV, inside tilted. **23-32.** *Achnanthidium minutissimum.* Specimens from different populations of Luxembourg, mainly of the river Ernz Blanche near Hessemillen, 27.09.2002. **23.** RV, outside. **24.** RV, inside. **25.** RV, outside tilted. **26.** RV, inside tilted. **27.** AV, outside. **28.** AV, inside. **29.** AV, outside tilted. **30.** AV, inside tilted. **31.** Frustule, strongly tilted. **32.** Frustule, tilted. Scale bars = 1 μm.



Figs 33-44. SEM. **33-36.** *Achnanthidium pyrenaicum.* Specimens from a population of the streamlet Rollingenbaach in Rollingen, 26.05.2002. **33.** RV, outside. **34.** RV, inside. **35.** AV, outside slightly tilted. **36.** AV, inside. **37-42.** *Achnanthidium subatomus.* Specimens from a population of the streamlet Stool in Brandenbourg, 19.07.1995. **37, 38.** RV, inside. **39.** RV, outside tilted. **40.** AV, outside. **41.** AV, outside slightly tilted. **42.** AV, inside. **43, 44.** *Psammothidium bioretii.* Specimens from a population of the streamlet Breschterbaach in Pratz, 23.03.1995. **43.** RV, tilted outside. **44.** RV, inside. Scale bars = 1 µm.

Reference: Simonsen (1987: 248, pl. 371, figs 9-17).
Notes: Mantle areolae are not interrupted at the terminal nodule (Fig. 34).

6. *Achnanthidium subatomus* (Hustedt) Lange-Bertalot (1999: 279) **Figs 37-42**
Basionym: *Achnanthes subatomus* Hustedt (1939: 554, figs 1-2).
Synonym: *Achnanthes biasolettiana* var. *subatomus* (Hustedt) Lange-Bertalot *in* Lange-Bertalot & Krammer (1989: 28, pl. 57, fig. 8, pl. 59, figs 1-11').
Reference: Simonsen (1987: 248, pl. 371, figs 1-4).
Notes: This species exhibits a coalescence of the foramina in the areolae (Figs 41, 42).

Psammothidium Bukhtiyarova *et* Round

1. ***Psammothidium bioretii*** (H. Germain) Bukhtiyarova *et* Round (1996: 9, figs 26-31) **Figs 43, 44**

Basionym: *Achnanthes bioretii* H. Germain (1957: 85, fig. 21). **Synonym:** *Navicula vanheurckii* Patrick (Patrick & Reimer, 1966: 491, pl. 46, fig. 22).

References: Krammer & Lange-Bertalot (1991: 19, pl. 12, figs 1-9); Lange-Bertalot & Krammer (1989: 30, pl. 20, figs 7-8, pl. 21, figs 19-35); Krammer & Lange-Bertalot (1985, pl. 24, figs 17-23, pl. 30, fig. 7).

Notes: This species has a slightly oblique raphe (Fig. 43). However, in the specimens under study the raphe is less oblique and sigmoid than those depicted in the original description (Germain, 1957: 85, fig. 21).

2. ***Psammothidium daonense*** (Lange-Bertalot) Lange-Bertalot (1999: 286) **Figs 45-52**

Basionym: *Achnanthes daonensis* Lange-Bertalot *in* Lange-Bertalot & Krammer (1989: 43, pl. 19, figs 27-32', pl. 25, figs 1-6, pl. 95, figs 1-13). **Synonym:** *Psammothidium grischunum* f. *daonense* (Lange-Bertalot) Bukhtiyarova *et* Round (1996: 12, figs 36-39).

Reference: Krammer & Lange-Bertalot (1991: 64, pl. 12, figs 10-20).

3. ***Psammothidium helveticum*** (Hustedt) Bukhtiyarova *et* Round (1996: 8, figs 20-25) **Figs 60-62**

Basionym: *Achnanthes austriaca* var. *helvetica* Hustedt (1933: 385, figs 831g-k). **Synonym:** *Achnanthes helvetica* (Hustedt) Lange-Bertalot (Kusber & Metzeltin, 2001: 632).

References: Lange-Bertalot & Krammer (1989: 63, pl. 19, figs 1-20, 26, pl. 20, figs 1-6, pl. 96, figs 6-11); Krammer & Lange-Bertalot (1991: 18, pl. 10, figs 12-27); Simonsen (1987: 133, pl. 220, figs 1-9); Kobayasi & Sawatari (1986: 260, figs 1-15); Le Cohu & Maillard (1983: 147, figs 113, 114).

Notes: The valve mantle may have two rows of areolae near the apices (Fig. 60).

4. ***Psammothidium lauenburgianum*** (Hustedt) Bukhtiyarova *et* Round (1996: 17, figs 62-65) **Figs 53-59**

Basionym: *Achnanthes lauenburgiana* Hustedt (1950: 394, pl. 36, figs 3-9).

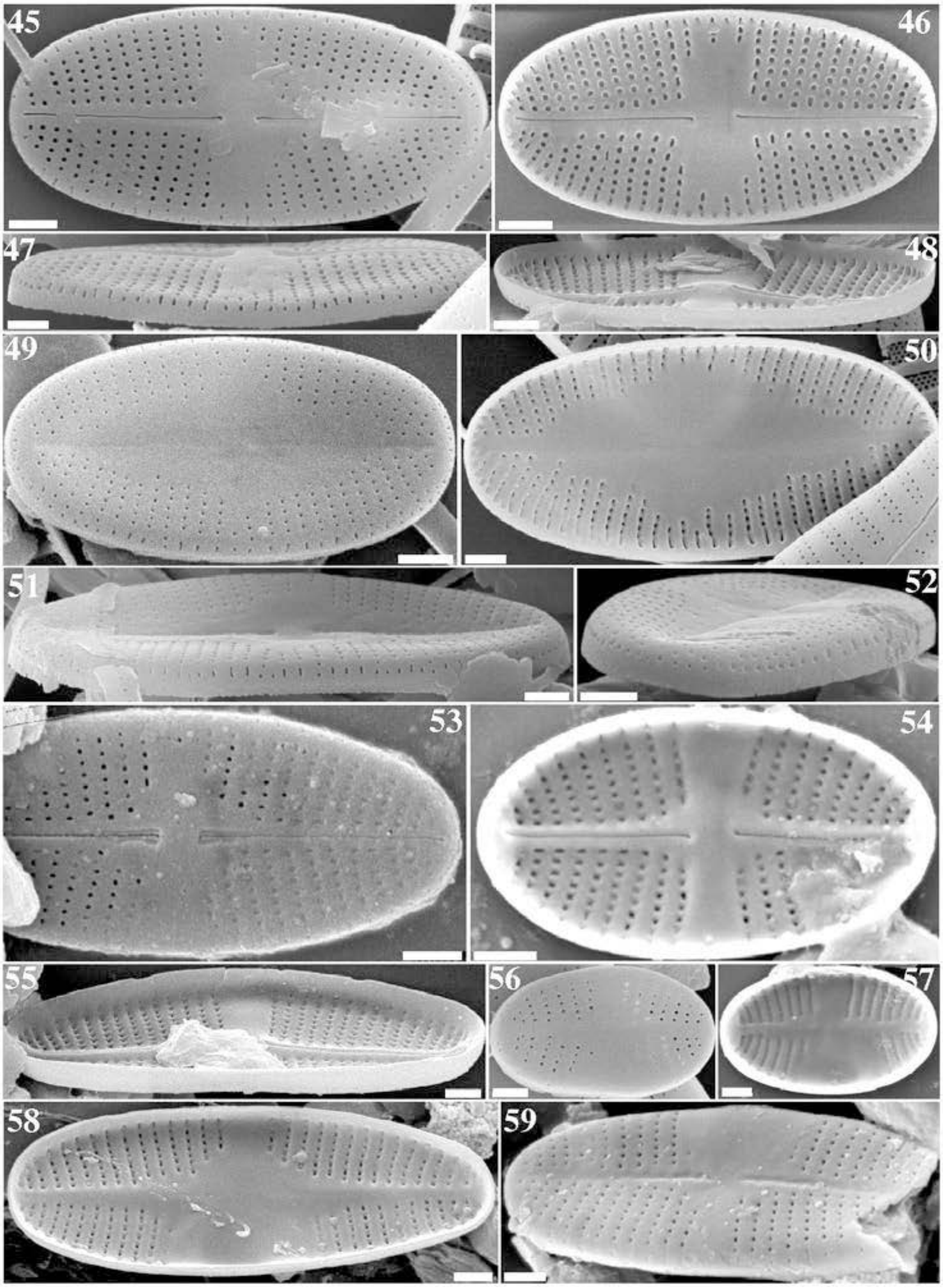
References: Krammer & Lange-Bertalot (1991: 26, pl. 4, fig. 3, pl. 14, figs 27-34); Lange-Bertalot & Krammer (1989: 94, pl. 28, figs 3-7, pl. 35, figs 1-10); Simonsen (1987: 358, pl. 543, figs 19-27).

Notes: The central area of the AV is unilaterally widened and has the 'horseshoe' shape (Figs 56, 58). The mantle areolae are interrupted at the level of the central area on both valves (Figs 55, 58).

5. ***Psammothidium subatomoides*** (Hustedt) Bukhtiyarova *et* Round (1996: 13, figs 48-51) **Figs 63-65**

Basionym: *Navicula subatomoides* Hustedt *in* A. Schmidt *et al.* (1936, pl. 404, figs 33-35). **Synonyms:** *Achnanthes subatomoides* (Hustedt) Lange-Bertalot *et* Archibald (Krammer & Lange-Bertalot, 1985: 9, 97); *Achnanthes detha* Hohn *et* Hellermann (1963: 274, pl. 2, figs 7, 8); *Achnanthes occulta* Kalbe (1963: 495, figs 2a, b).

References: Lange-Bertalot & Krammer (1989: 145, pl. 21, figs 1, 1', 11-14, 17, 18, pl. 22, figs 1-3, pl. 95, figs 22-23'); Krammer & Lange-Bertalot (1991: 24, pl. 14, figs 1, 2, 5, 6); Simonsen (1987: 199, pl. 308, figs 15-24); Kobayasi & Sawatari (1986: 261, pl. 2, figs 29-41, pl. 3, figs 42-45).



Figs 45-59. SEM. **45-52.** *Psammothidium daonense*. Specimens from a population of the streamlet Breschterbaach in Pratz, 23.03.1995. **45.** RV, outside. **46.** RV, inside. **47.** RV, outside tilted. **48.** RV, inside tilted. **49.** AV, outside. **50.** AV, inside. **51, 52.** AV, outside tilted. **53-59.** *Psammothidium lauenburgianum*. Specimens from a population of the streamlet Gander in Aspelt, 24.10.96. **53.** RV, outside. **54.** RV, inside. **55.** RV, inside tilted. **56.** AV, outside. **57.** AV, inside. **58.** AV, inside slightly tilted. **59.** AV, outside tilted. Scale bars = 1 µm.

The curvature of the RV along the apical axis, with reference to the external side of the RV, is extremely variable in the group of eleven taxa discussed above, ranging from concave (Fig. 31) to convex (Fig. 9) in *Achnanthidium* (Table 1). As far as the entire valve length is concerned, all possible intermediate shapes are encountered, from primarily concave, becoming slightly convex towards the apices (Fig. 17) to primarily convex and slightly concave at the centre (Fig. 14). As far as the central part of the valve is concerned, most species are concave (Table 1).

Valves also exhibit a variable **flexure perpendicular to the apical axis**. In most cases it is slightly convex (Figs 61, 39) or conversely concave, especially in *Achnanthidium* (Table 1), but some are raised at the centre and flat at the margin (Figs 43, 47), as in *Psammothidium*. As for the apical axis, the curvature is variable within a species, with the curvature along the transapical axis of the RV more or less opposite to that of the AV (Figs 9 & 12, 17 & 21, 25 & 32, 47 & 51).

The **shape of the valves** varies from narrow (Fig. 5) to broadly elliptical (Fig. 57) and elliptical-lanceolate (Figs 20, 36), especially in *Psammothidium* (Table 1), to linear-lanceolate (13), as in *Achnanthidium* (Table 1). In all taxa, small valves are primarily elliptical (Figs 2, 10, 15).

The **shape of apices** is round (Fig. 1) in *Psammothidium* and some members of *Achnanthidium* (Table 1) to subrostrate (Fig. 27) in other members of *Achnanthidium* (Table 1). Both genera have species with elliptical valves, but only some species of *Achnanthidium* have sub-rostrate poles.

Maximum **length/width ratios** conform to those given in the genera diagnoses (Table 1). However, the minimum values are lower in all species investigated in the genus *Achnanthidium*.

Cell thickness is always circa 2 µm.

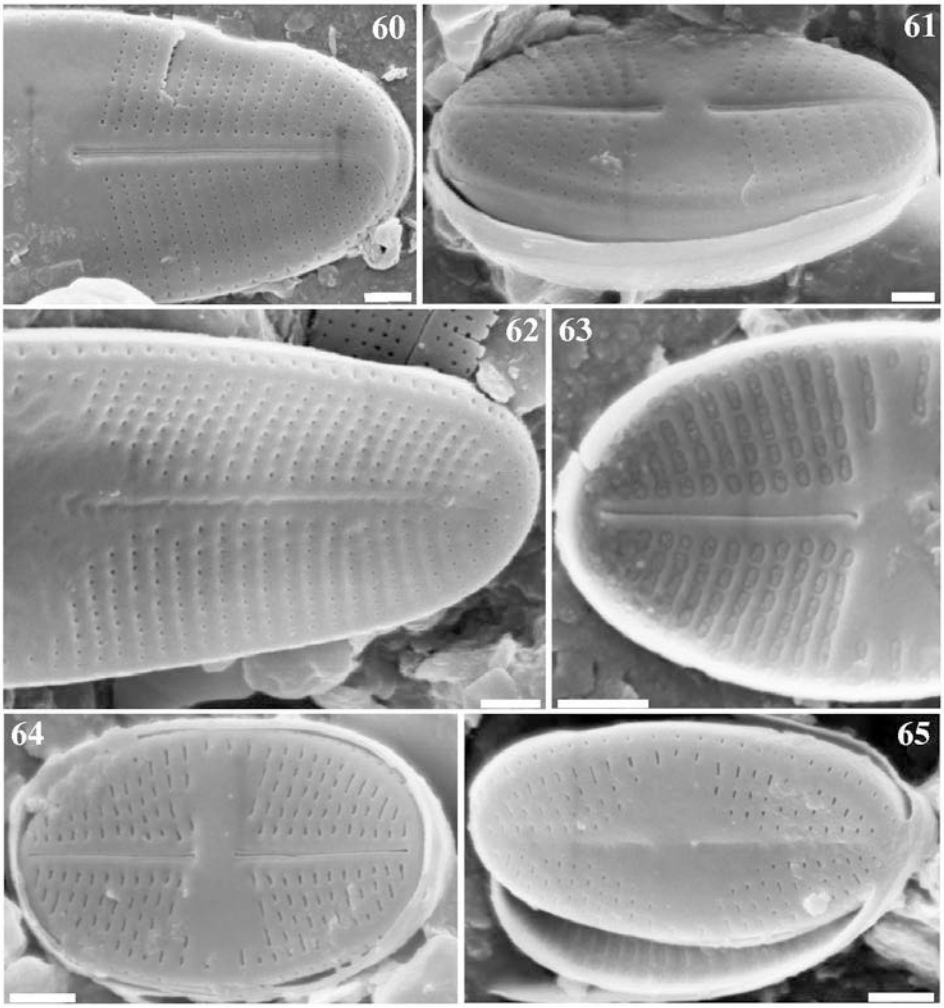
Most species exhibit co-axial **raphe branches** outside the valve (Figs 33, 45) with either more (Fig. 10) or less (Fig. 16) non co-axial branches within it.

The **raphe slit** is always narrow and rectilinear (Table 1). Additionally, it may extend proximally either in a furrow (Figs 39, 53) or not (Fig. 23), the furrow is occasionally furnished with ridges (Fig. 60). Inside the valve, there are no obvious differences in raphe morphology. It is always situated in a groove on the top of an arched rib (Table 1) in girdle view (Figs 26, 55) and branches are always terminated on their proximal and distal ends by a slightly raised nodule and helictoglossae (Fig. 34, Table 1).

The **distance between central raphe ends** is generally closer in *Achnanthidium* species.

The **form of raphe ends** is variable. Outside the valve, the proximal ends vary from a simple slit (Fig. 23) in some species of *Achnanthidium* (Table 1) to a variety of 'pin-hole' or 'drop-like', more or less expanded pores (Figs 1, 33, 45, 60) in some other species of *Achnanthidium* and *Psammothidium* (Table 1). The distal ends may be slit shaped (Fig. 2), 'pin-hole' shaped (Figs 45, 53), and are more (Fig. 33) or less (Fig. 15) turned to one side in some species of *Achnanthidium*, or turned to the other side in some species of *Psammothidium* (Fig. 61). Internally, the raphe ends are always slits, almost straight at the distal ends (Figs 24, 54) but proximal ends are curved to opposite sides (Figs 3, 37).

The **axial area of the RV** is always narrow, being either more (Fig. 38) or less (Fig. 64) linear-lanceolate. Conversely, the **central area of the RV** is extremely variable in both shape and width (Table 1), reaching the valve face/mantle junction (Figs 24, 54) or bordered by more (Fig. 44) or less (Fig. 64) long striae. Sometimes, it is just a slight central expansion of the axial area (Fig. 10).



Figs 60-65. SEM. **60-62.** *Psammothidium helveticum.* Specimens from a population of the streamlet Millebaach in Bigelbach, 25.07.1995. **60.** RV, outside. **61.** RV, outside tilted. **62.** AV, outside slightly tilted. **63-65.** *Psammothidium subatomoides.* Specimens from a population of the streamlet Millebaach in Bigelbach, 25.07.1995. **63.** RV, inside. **64.** RV, outside. **65.** AV, outside and RV behind, inside. Scale bars = 1 µm.

In some taxa, especially *Psammothidium*, the **axial and/or central areas of the AV** are not like that of the RV. A well-developed **vestigial raphe** can be consistently observed in species of this genus (Figs 59, 62, 65). Remnants of a similar feature may be weakly observed in some *Achnanthidium* species (Figs 21, 29).

Striae are uniseriate, straight (Fig. 60), slightly (Fig. 28) to strongly curved (Fig. 4) or slightly sigmoid (Fig. 44), parallel (Fig. 41) and more or less irregularly spaced (alternate) on the AV (Fig. 35). They may be arranged similarly (Figs 16 & 20) or differently (Figs 1 & 5) on both valves, slightly radiate at the centre, becoming closer and more radiate (Fig. 25) in *Psammothidium* (Table 1), or conversely almost transverse in a group of *Achnanthidium* species to slightly convergent (Figs 16, 34) towards the ends, extending from the sternum close to the margin of the valve (Fig. 39) or slightly on to the valve mantle (Fig. 43). The variability of striae pattern is greater in *Achnanthidium*.

Areolae openings (foramina) are generally small and round on the valve exterior (Table 1, Fig. 49), larger internally (Fig. 50) but may be occasionally (Fig. 40) or always (Fig. 64) elongated; they are closed internally by thin siliceous membranes (Figs 4, 63).

Sometimes, the **number of striae and/or areolae** differs between RV and AV in some *Achnanthidium* species.

Virgae are broad in the centre and thinner towards the ends of the valve (Figs 18, 30), slightly prominent on the internal valve face (Fig. 55).

Mantle areolae are generally elongated (Fig. 11), sometimes weakly so (Figs 2, 62) or round, interrupted at the terminal nodule (Fig. 43). Generally often separated from the striae (Table 1, Fig. 35), in some cases they are packed very close together or are barely discernible (Figs 8, 61). In some species of *Psammothidium*, they can be interrupted at the level of the central area or arranged in two rows towards apices.

DISCUSSION

Problems encountered in the classification of taxa belonging to either *Achnanthidium* or *Psammothidium* are best demonstrated by *Achnanthidium kranzii* (Figs 15-22) and *Psammothidium daonense* (Figs 45-52). Several features possessed by *Achnanthidium kranzii* support its placement in *Achnanthidium*, according to Round & Bukhtiyarova (1996): the size of the cells, uniseriate striae reduced and more widely spaced at the centre, denser towards the apices (Figs 16, 20), cells V-shaped in girdle view (Figs 17, 21), fine median raphe slit with unexpanded central endings and distal endings turned to one side (Fig. 15) and a narrow sternum expanded at the centre (Figs 16, 22). The RV is indeed concave but only at its centre; it is slightly convex at the poles (Fig. 17). In contrast, several other characters would place *A. kranzii* in *Psammothidium*, according to Bukhtiyarova & Round (1996): shape and thickening of the sternum on the inner side of the RV (Fig. 18), lower length/width ratio, apices always broadly rounded (Fig. 19), central pores internally deflected in opposite directions (Fig. 16), slightly prominent distal nodules (Fig. 18) and similarity of shape between the hyaline areas of both valves (Figs 16, 20). Moreover, the RV in girdle view is not convex, but slightly concave in the centre and slightly convex towards the apices (Fig. 47).

All these characters demonstrate many points of similarity between *Achnanthidium kranzii* and *Psammothidium daonense* (Figs 45-52); the two species differ only by the ridged raphe slit (Fig. 45) and a well-marked vestigial raphe (Figs 49, 51, 52) in *P. daonense*. Lange-Bertalot & Krammer (1989) also noted that the characteristic vegetative valve shape and appearance of *Achnanthes kranzii* closely resembles *Achnanthes grischuna* Wüthrich and *A. daonensis*, both of which were included in the genus *Psammothidium* by Bukhtiyarova & Round (1996).

Except for the small valves of *Achnanthidium catenatum* (Fig. 9), all specimens of each taxon in this study have a central concavity along the RV apical axis. All species of *Psammothidium* examined appear rather flat in girdle view, slightly concave at the centre and slightly convex towards the apices (Table 2). As in several species this feature is clearly related to the size of the individual valves and becomes variable especially towards the ends of valves, it is strongly recommended to evaluate this feature in relation to the central part of the valve.

The curvature along the transapical axis is convex in species of *Achnanthidium*, in most cases (Table 2). In fact, a continuum exists in the raphe curvature between species of *Achnanthidium* and *Psammothidium*. In taxa studied, the shape of the valve does not allow unambiguous allocation to one genus or another (Table 2). Thus, some species of *Psammothidium* are linear or elongate, e.g. *P. levanderi* (Hustedt) Bukhtiyarova *et* Round or *P. abundans* (Manguin) Bukhtiyarova *et* Round (Bukhtiyarova & Round, 1996: figs 71, 74). While others that are considered part of *Achnanthidium*, are elliptical or have a lower length/width ratio, e.g. *A. fulla* (Carter) Aboal, *A. subsalsum* (J.B. Petersen) Aboal or *A. straubianum* (Lange-Bertalot) Lange-Bertalot. There are no differences in striae position between *Achnanthidium* and *Psammothidium*, except for *P. bioretii* and *P. helveticum*, where they may slightly extend to the mantle. The path of the raphe fissure is quite variable in both genera and does not always lie in a channel, as stated by Bukhtiyarova & Round (1996), e.g. in *P. marginulatum* (Grunow) Bukhtiyarova *et* Round, the type of this genus (Bukhtiyarova & Round, 1996: figs 2, 7). Central raphe ends can be expanded in *Achnanthidium*, as in *A. pyrenaicum* (Fig. 33) and *A. subatomus* (Fig. 39).

With respect to taxa studied herein, the only observable difference between *Achnanthidium* and *Psammothidium* is the presence of ridges accompanying the raphe slit, especially on its proximal part. Some taxa do not have this feature, yet fit the diagnosis of *Achnanthidium* and should not be assigned to *Psammothidium*, e.g. *P. abundans* or *P. levanderi* (Bukhtiyarova & Round, 1996: figs 66, 67, 72-75). In addition, species in other genera belonging to the Achnanthidiaceae have their raphe slit in a furrow, accompanied by ridges, e.g. *Lemnicola* (Round & Basson, 1997: fig. 28) or *Platessa* (Krammer & Lange-Bertalot, 2004: pl. 93, fig. 2; Monnier *et al.*, 2003: fig. 24). However, these modifications of the external raphe fissure shape can occur at the later stage of valve morphogenesis (Cox, 1999), hence this criterion is primarily dependent of the degree of silicification during ontogenesis.

Another difference is the presence of a well marked vestigial raphe on the AV in taxa belonging to *Psammothidium* studied herein, a characteristic not specified by Bukhtiyarova & Round (1996), which is often but not always seen in taxa with a ridged raphe slit (Bukhtiyarova & Round, 1996: fig. 54). Vestigial raphes occur in other genera of the Achnanthidiaceae, e.g. *Planothidium* (Andrews, 1981: fig. 10; Monnier *et al.*, 2001: fig. I-4), *Platessa* (Monnier *et al.*, 2003: fig. 32) and in some species of *Achnanthidium*, e.g. *A. convergens* (Kobayasi) Kobayasi and *A. kryophilum* (Hustedt) Bukhtiyarova (Mayama & Kobayasi, 1989). However, Mayama and Kobayasi (1989) carried out investigations on valve development in *A. saprophilum* (Kobayasi *et* Mayama) Round *et* Bukhtiyarova and found that on the AV there was an initial raphe slit before filling occurred. This ontogenetic developmental trajectory of the axial area is found in other achnanthoid genera, e.g. *Cocconeis* Ehrenberg (Mann, 1984b) and *Achnanthes* Bory (Boyle *et al.*, 1984).

In addition to morphological criteria, Bukhtiyarova & Round (1996) consider that *Psammothidium* is generally adnate to the substrate, whereas *Ach-*

nanthidium is stalked. However, some species of *Achnanthidium* are not stalked but prostrate, e.g. *A. lineare* W. Smith *pro parte* (Planas *et al.*, 1989: figs 60a, b) or *A. japonicum* (Kobayasi) Kobayasi (Tanaka & Watanabe, 1990: pl. 1, fig. 1).

CONCLUSIONS

From our analysis of differential characteristics suggested by Bukhtiyarova & Round (1996), it follows that the structure of the raphe endings and the presence of a vestigial raphe cannot be used to separate *Psammothidium* from *Achnanthidium* at the generic level. As mentioned above, these two features are dependent on the stage of 'completeness' of frustule silicification. The resulting morphological variability of these characters appears not to have phylogenetic significance (Cox, 1999) and is thus deemed inappropriate for generic level identity (Cox & Reid, 2004). Thus, we believe, at the moment, it is impossible to unambiguously separate *Psammothidium* from *Achnanthidium*. Following discussion offered by Cox (2002) on the use of genera, subgenera and sections, we therefore reject *Psammothidium* as a genus. Nevertheless, some species still require separation from *Achnanthes sensu stricto* on the basis of further evidence, e.g. number of plastids (Round *et al.*, 1990). Thus the simplest option is to place them in *Achnanthidium*. Therefore we propose the following new combinations:

1. *Achnanthidium bioretii* (H. Germain) Monnier, Lange-Bertalot *et* Ector **comb. nov.**
Basionym: *Achnanthes bioretii* H. Germain, *Bull. Soc. Bot. Fr.* 104: 85, fig. 21 (1957).

2. *Achnanthidium daonense* (Lange-Bertalot) Lange-Bertalot, Monnier *et* Ector **comb. nov.**
Basionym: *Achnanthes daonensis* Lange-Bertalot, *Bibl. Diatomol.* 18: 43, pl. 19 figs 27-30, 32, 32', pl. 25, figs 1-3 (1989).

3. *Achnanthidium helveticum* (Hustedt) Monnier, Lange-Bertalot *et* Ector **comb. nov.**
Basionym: *Achnanthes austriaca* var. *helvetica* Hustedt, *Die Kieselalgen Deutschlands, Österreichs und der Schweiz*, p. 385, figs 831g-k (1933).

4. *Achnanthidium lauenburgianum* (Hustedt) Monnier, Lange-Bertalot *et* Ector **comb. nov.**
Basionym: *Achnanthes lauenburgiana* Hustedt, *Arch. Hydrobiol.* 43: 394, pl. 36, figs 3-9 (1950).

5. *Achnanthidium subatomoides* (Hustedt) Monnier, Lange-Bertalot *et* Ector **comb. nov.**
Basionym: *Navicula subatomoides* Hustedt *in* A. Schmidt *et al.*, *Atlas der Diatomaceen-kunde*, pl. 404, figs 33-35 (1936).

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REFERENCES

ANDREWS G.W., 1981 — *Achnanthes linkei* and the origin of monoraphid diatoms. *Bacillaria* 4: 29-40.

BÍLÝ J. & MARVAN P., 1959 — *Achnanthes catenata* sp. n. *Preslia* 31: 34-35.

BOYLE J.A., PICKETT-HEAPS J.D. & CZARNECKI D.B., 1984 — Valve morphogenesis in the pennate diatom *Achnanthes coarctata. Journal of phycology* 20: 563-573.

BUKHTIYAROVA L. & ROUND F.E., 1996 — Revision of the genus *Achnanthes sensu lato. Psammothidium*, a new genus based on *A. marginulatum* [Title in contents: "Revision of the genus *Achnanthes sensu lato* section *Marginulatae* Bukht. sect. nov. of *Achnanthidium* Kütz.]. *Diatom research* 11: 1-30.

CARNEIRO L.A., 2003 — *Ordem Achnanthales (Bacillariophyceae) de águas doces do estado de São Paulo: levantamento florístico*. Dissertação de Mestre em Ciências Biológicas, Universidade de São Paulo, Rio Claro, Brasil.

COMPÈRE P., 2000 — *Clé provisoire pour la détermination des genres de diatomées d'eau douce.* [http://perso.club-internet.fr/clci/ADLaF_Cle_des_genres.htm]. *Tentative key for the determination of freshwater diatom genera* [http://www.br.fgov.be/RESEARCH/EDITION/keydiato_BR.html].

COSTE M. & ECTOR L., 2000 — Diatomées invasives exotiques ou rares en France : principales observations effectuées au cours des dernières décennies. *Systematic and geography of plants* 70: 373-400.

COX E.J., 1999 — Variation in patterns of valve morphogenesis between representatives of six biraphid diatom genera (Bacillariophyceae). *Journal of phycology* 35: 1297-1312.

COX E.J., 2002 — Generic concepts and intrageneric variation in diatoms with particular reference to *Navicula* Bory. *In:* John J. (ed.), *Proceedings of the 15th International Diatom Symposium.* Ruggell, Gantner Verlag, pp. 289-304.

COX E.J. & REID G., 2004 — Generic relationships within the Naviculineae: a preliminary cladistic analysis. *In:* Poulin M. (ed.), *Proceedings of the 17th International Diatom Symposium.* Bristol, Biopress Limited, pp. 49-62.

CZARNECKI D.B., 1994 — The freshwater diatom culture collection at Loras College, Dubuque, Iowa. *In:* Kociolek J.P. (ed.), *Proceedings of the 11th International Diatom Symposium.* Memoirs of the Californian Academy of Sciences 17: 155-173.

DRUART J.C. & STRAUB F., 1993 — *Achnanthes catenata* Bílý & Marvan (Diatomophyceae), diatomée planctonique nouvelle pour les eaux douces françaises. *Cryptogamie Algologie* 14: 95-98.

GERMAIN H., 1957 — *Achnanthes bioretii* nov. sp. *Bulletin de la société botanique de France* 104: 85-86.

HOHN M.H. & HELLERMANN J., 1963 — The taxonomy and structure of diatom populations from three Eastern North American rivers using three sampling methods. *Transactions of the American microscope society* 82: 250-329.

HUSTEDT F., 1933 — Die Kieselalgen Deutschlands, Österreichs und der Schweiz. *Dr. L. Rabenhorsts Kryptogamenflora von Deutschland, Österreich und der Schweiz*, Band 7, Teil 2, Lief. 3: 321-432. Leipzig, Akademische Verlagsgesellschaft.

HUSTEDT F., 1939 — Diatomeen aus den Pyrenäen. *Berichte der Deutschen botanischen Gesellschaft* 56: 543-572.

HUSTEDT F., 1950 — Die Diatomeenflora norddeutscher Seen mit besonderer Berücksichtigung des holsteinischen Seengebietes. V-VII. Seen in Mecklenburg, Lauenburg und Nordostdeutschland. *Archiv für Hydrobiologie* 43: 329-458.

HUSTEDT F., 1959 — Die Kieselalgen Deutschlands, Österreichs und der Schweiz. *Dr. L. Rabenhorsts Kryptogamenflora von Deutschland, Österreich und der Schweiz*, Band 7, Teil 2, Lief. 6: 737-845. Leipzig, Akademische Verlagsgesellschaft.

ISERENTANT R., ECTOR L., STRAUB F. & HERNÁNDEZ-BECERRIL D.U., 1999 — Méthodes et techniques de préparation des échantillons de diatomées. *Cryptogamie, Algologie* 20: 143-148.

KALBE L., 1963 — Beitrag zur Kieselalgen-Flora der Tatragewässer. *Österreichische botanische Zeitschrift* 110: 489-497.

KOBAYASI H., 1997 — Comparative studies among four linear-lanceolate *Achnanthidium* species (Bacillariophyceae) with curved terminal raphe endings. *Nova Hedwigia* 65: 147-163.

KOBAYASI H. & SAWATARI A., 1986 — Some small and elliptic *Achnanthes. In:* Ricard M. (ed.), *Proceedings of the 8th International Diatom Symposium*, Paris, pp. 259-269.

KOCIOLEK J.P. & STOERMER E.F., 1986 — Phylogenetic relationships and classification of monoraphid diatoms based on phenetic and cladistic methodologies. *Phycologia* 25: 297-303.

KRAMMER K. & LANGE-BERTALOT H., 1985 — Naviculaceae. Neue und wenig bekannte Taxa, neue Kombinationen und Synonyme sowie Bemerkungen zu einigen Gattungen. *Bibliotheca diatomologica* 9: 1-230.

KRAMMER K. & LANGE-BERTALOT H., 1991 — Bacillariophyceae 4. Teil: Achnanthaceae. Kritische Ergänzungen zu *Navicula (Lineolatae)* und *Gomphonema*. Gesamtliteraturverzeichnis Teil 1-4. *In:* Ettl H., Gärtner G., Gerloff J., Heynig H. & Mollenhauer D. (eds), *Süsswasserflora von Mitteleuropa* 2/4, Stuttgart, Gustav Fischer Verlag.

KRAMMER K. & LANGE-BERTALOT H., 2004 (2nd edition) — Bacillariophyceae 4. Teil: Achnanthaceae. Kritische Ergänzungen zu *Achnanthes* s. l., *Navicula* s. str., *Gomphonema*. Gesamtliteraturverzeichnis Teil 1-4. *In:* Ettl H., Gärtner G., Gerloff J., Heynig H. & Mollenhauer D. (eds), *Süsswasserflora von Mitteleuropa* 2/4, Heidelberg, Spektrum Akademischer Verlag.

KUSBER W.H. & METZELTIN D., 2001 — Checklist of new diatom combinations, replaced names and validations published by Horst Lange-Bertalot until the year 2000 and additional validations. *In:* Jahn R., Kociolek J.P., Witkowski A. & Compère P. (eds), *Lange-Bertalot-Festschrift: Studies on Diatoms*, Ruggell, Gantner Verlag: 585-633.

KÜTZING F.T., 1833 — Synopsis Diatomacearum oder Versuch einer systematischen Zusammenstellung der Diatomeen. *Linnaea* 8: 529-620.

LANGE-BERTALOT H. & RUPPEL M., 1980 — Zur Revision taxonomisch problematischer, ökologisch jedoch wichtiger Sippen der Gattung *Achnanthes* Bory. *Algological studies* 60: 1-31.

LANGE-BERTALOT H. & KRAMMER K., 1989 — *Achnanthes*, eine Monographie der Gattung mit Definition der Gattung *Cocconeis* und Nachträgen zu den Naviculaceae. *Bibliotheca diatomologica* 18: 1-393.

LANGE-BERTALOT H., 1999 — Neue Kombinationen von Taxa aus *Achnanthes* Bory (sensu lato). *Iconographia diatomologica* 6: 276-289.

LE COHU R. & MAILLARD R., 1983 — Les diatomées monoraphidées des îles Kerguelen. *Annales de limnologie* 19: 143-167.

MANN D.G., 1984a — Structure, life history and systematics of *Rhoicosphenia* (Bacillariophyta). V. Initial cell and size reduction in *Rh. curvata* and a description of the Rhoicospheniaceae fam. nov. *Journal of phycology* 20: 544-555.

MANN D.G., 1984b — An ontogenic approach to diatom systematics. *In:* Mann D.G. (ed.), *Proceedings of the 7th International Diatom Symposium*. Koeltz Scientific Books, Koenigstein, pp. 113-144.

MANN D.G. & DROOP S.J.M., 1996 — Biodiversity, biogeography and conservation of diatoms. *Hydrobiologia* 336: 19-32.

MAYAMA S. & KOBAYASI H., 1989 — Sequential valve development in the monoraphid diatom *Achnanthes minutissima* var. *saprophila. Diatom research* 4: 111-117.

MONNIER O., BERTRAND J., LANGE-BERTALOT H. & GÜTTINGER W., 2001 — Observations préliminaires sur les diatomées en aquarium. *Symbioses* n. s. 5: 25-35.

MONNIER O., LANGE-BERTALOT H. & BERTRAND J., 2003 — La flore des diatomées d'un aquarium d'eau douce tropicale I : observations taxinomiques. *Bulletin de la société des sciences naturelles de l'Ouest de la France,* 2e supplément Hors Série: 125-165.

MONNIER O., LANGE-BERTALOT H., RIMET F., HOFFMANN L. & ECTOR L., 2004 — *Achnanthidium atomoides* sp. nov., a new diatom from the Grand-Duchy of Luxembourg. *Vie et milieu* 54: 129-138.

PATRICK R. & REIMER C.W., 1966 — The diatoms of the United States Vol. 1: Fragilariaceae, Eunotiaceae, Achnanthaceae, Naviculaceae. *Monographs of the academy of natural sciences of Philadelphia* 13: 1-688.

PLANAS D., LAPIERRE L., MOREAU G. & ALLARD M., 1989 — Structural organization and species composition of a lotic periphyton community in response to experimental acidification. *Canadian journal of fisheries and aquatic sciences* 46: 827-835.

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.* Cambridge, Cambridge University Press, 747 p.

SCHMIDT A., SCHMIDT M., FRICKE F., HEIDEN H., MULLER O. & HUSTEDT F., 1936 — *Atlas der Diatomaceen-kunde.* Heft 1-120, Tafeln 1-460, Leipzig, Aschersleben.

SIMONSEN R., 1987 — *Atlas and catalogue of the diatom types of Friedrich Hustedt.* Vol. 1: Catalogue, 525 p.; Vol. 2: Atlas, Pl. 1-395; Vol. 3: Atlas, Pl. 396-772. Berlin/Stuttgart, J. Cramer.

SMITH W., 1855 — Notes on an excursion to the south of France and the Auvergne in search of Diatomaceae. *The annals and magazine of natural history* 15: 1-9.

STRAUB F., 2002 — Note algologique II. Apparition envahissante de la diatomée *Achnanthes catenata* Bílý et Marvan (Heterokontophyta, Bacillariophyceae) dans le lac de Neufchâtel (Suisse). *Bulletin de la société Neufchâtelloise des sciences naturelles* 125: 59-65.

TANAKA S. & WATANABE T., 1990 — The colonization process of a typical epilithic algal community – *Homoeothrix janthina-Achnanthes japonica* community – in a less polluted river in Japan. *Japanese journal of phycology* 38: 167-177.