Scalariella a new genus of monoraphid diatom (Bacillariophyta) with a bipolar distribution

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Abstract: The identity of a small–celled diatom *Naviculadicta pseudofallacia* Witkowski, Metzeltin et Lange–Bertalot, originally described from Bear Island, southernmost island of the Norwegian archipelago Svalbard, is reconsidered. Observations of marine samples from the Kerguelen archipelago (Southern Ocean, Indian Ocean sector) revealed that this species also occurs in the Subantarctic region. The original classification within *Naviculadicta* was erroneous since this species is a monoraphid taxon and belongs to the Achnanthales. Its morphological features justify creating a new genus *Scalariella* Riaux–Gobin, which is distinguished from other achnanthoid genera by a peculiar raphe system, the stria structure of the sternum valve (each stria composed of a depressed macroareola), and the presence of a lateral solid area in the raphe valve, splitting each stria into two areolae. Based on light and electron microscopy, *N. pseudofallacia* is renamed *Scalariella pseudofallacia* (Witkowski, Metzeltin et Lange–Bertalot) Riaux–Gobin et Witkowski comb. nov. The genus also includes a second and rare species, observed in the Kerguelen material, *S. oblongella* Riaux–Gobin, Witkowski et Ruppel, which is described and illustrated, but which needs complementary observations. The morphology of *Scalariella* is compared to that of some genera split from the genus *Achnanthes* Bory. The biogeography of *Scalariella pseudofallacia*, a marine taxon probably misidentified in the past due to its small size, is reconsidered with respect to its affinity for subpolar, cold water habitats, in both hemispheres.

Key words: diatoms, Achnanthales, *Scalariella* gen. nov., *S. pseudofallacia* comb. nov., *S. oblongella* sp. nov., morphology, geographic distribution

Introduction

Naviculadicta pseudofallacia Witkowski, Metzeltin et Lange–Bertalot (Metzeltin & Witkowski 1996) is a small–celled marine diatom first described as a member of the genus *Naviculadicta* Lange–Bertalot (Lange–Bertalot & Moser 1994). *N. pseudofallacia* originated from the Bear Island in Sub–Arctic. The authors based their description on light and electron microscopy (SEM and TEM) observations. *Naviculadicta* was proposed as a taxon to hold a number of established or new taxa with morphological characters that excluded them from *Navicula* sensu stricto after other genera were separated from *Navicula* sensu lato (e.g. Cox 1987; Mann 1989; Mann & Stickle 1991; Round et al. 1990). Although the genus *Naviculadicta* was subsequently criticized by Kociolek (1996), it continues to be used (e.g. Metzeltin & Witkowski 1996; Lange–Bertalot & Genkal 1999; Van de Vijver et al. 2002; Metzeltin et al. 2005).

In the present report we demonstrate that *Naviculadicta pseudofallacia* is a heterovalvar, monoraphid diatom, belonging to the Achnanthales sensu Silva (1962). Its sternum valve (SV) was first observed during a survey of the genus *Cocconeis* from the Kerguelen Archipelago (Indian Ocean, Austral sector; Riaux–Gobin & Romero 2003). It was subsequently found again in some other Kerguelen samples from the same survey (Witkowski et al., pers. obs.).

The inclusion of this taxon in an existing genus appeared difficult, since several characteristics, or groups of characteristics, do not fit any existing genus. As part of the Achnanthales, the large and heterogeneous genus *Achnanthes* Bory has been subdivided,

beginning in 1990, with the aim of creating smaller, homogeneous genera. Although ROUND et al. (1990) re–erected *Achnanthidium* KÜTZING, and *Eucocconeis* CLEVE, further splitting was strongly advocated by two authors: BUKHTIYAROVA and ROUND. BUKHTIYAROVA & ROUND (1996) and ROUND & BUKHTIYAROVA (1996) redifined *Achnanthidium* and established several new genera, e.g. *Psammothidium* BUKHTIYAROVA et ROUND, *Rossithidium* ROUND et BUKHTIYAROVA, *Planothidium* ROUND et BUKHTIYAROVA, *Karayevia* ROUND et BUKHTIYAROVA and *Kolbesia* ROUND et BUKHTIYAROVA. Subsequently, some *Achnanthes* taxa have been transferred to *Eucocconeis* (LANGE–BERTALOT & GENKAL 1999; see also KRAMMER & LANGE–BERTALOT 2004). Finally it was proposed that *Kolbesia* be united to *Karayevia* (BUKHTIYAROVA 2006).

A group of taxa resembling *Achnanthes bahusiensis* was moved to another new genus *Astartiella* WITKOWSKI, LANGE–BERTALOT et METZELTIN (WITKOWSKI 1998), *Achnanthes taeniata* into the new genus *Pauliella* ROUND et BASSON, and *Achnanthes hungarica* into *Lemnicola* ROUND et BASSON (ROUND & BASSON 1997). Recently BUKHTIYAROVA (2008) summarized the subdivision of *Achnanthes* sensu lato. Despite major efforts by several research groups (e.g. ROUND et al. 1990; BUKHTIYAROVA & ROUND 1996; ROUND & BUKHTIYAROVA 1996; LANGE–BERTALOT & GENKAL 1999; WITKOWSKI et al. 2000; KRAMMER & LANGE–BERTALOT 2004; DIAZ & MAIDANA 2006), there are still numerous taxa that are either unique or constitute small clusters of taxa which need appropriate generic classification. This is the case for *N. pseudofallacia* and another similar taxon which we describe as a new species.

In this paper we describe *Scalariella*, a new genus of monoraphid diatoms, which includes a previously established species, i.e. *Naviculadicta pseudofallacia*. We characterize the genus based on light (LM) and electron microscopy [scanning (SEM) and transmission (TEM)]. A second, rare taxon (Table 1), belonging to the same genus and also discovered in Kerguelen is described and illustrated in SEM. We re–evaluate the biogeographic range of *Scalariella pseudofallacia* and the morphological characteristics of the new genus are compared to those of several achnanthoid genera, with a particular focus on *Karayevia* sensu lato (Table 2). Although several of these genera (Table 2) are exclusively fresh–water (such as *Nupela*), morphological comparisons can be made.

Another small–celled taxon, still classified under *Achnanthes*, i.e. *A. delicatissima* SIMONSEN (HINZ et al., in press), shows some characteristics close to those of *Scalariella* (Table 1) but also to *Achnanthidium* sensu lato (ROUND et al. 1990). Its type material is examined, illustrated and compared to *Scalariella*.

Material and Methods

Sediment samples were collected during four austral summers between 1985 and 1992 at different marine Kerguelen stations. The Archipelago is located to the north of the "Plateau des Kerguelen", between 49° and 50° S, near the Polar Front (see map *in* RIAUX–GOBIN & ROMERO 2003). All sediment samples (intertidal and subtidal) were formalin preserved (10% final dilution). A variety of habitats were sampled (from subtidal muds underlying the macroalgal belt, to exposed intertidal sandy beaches or estuarine shallow mud) and epipsammic, epipelic and epiphytic diatoms collected.

The monoraphid diatoms, some of which are of epiphytic origin (impressive *Macrocystis pyrifera* belts inhabit shores and fjords), are numerous on the subtidal shallow muds of Kerguelen. Two sites (see fig. A and table 2 in RIAUX–GOBIN & ROMERO 2003) were regularly sampled in the Morbihan Bay: Port–Aux–Français (12 m water depth; 49° 20' S, 69° 50' E) and Port–Raymond (10 m water depth; 49° 21' S, 70° 12' E). In addition the holotype of *N. pseudofallacia* was analyzed (slide No. 40–1 in Coll. LANGE–BERTALOT, Senckenberg Museum, Frankfurt am Main). Original material of *A. delicatissima* (SIMONSEN 1959, the western Baltic Sea) was also observed under LM and SEM.

For LM examination, the sediment was rinsed with distilled water, cleaned with concentrated H_2O_2, rinsed again with distilled water, gently centrifuged, alcohol–dehydrated, air–dried onto cover glasses, and mounted in Naphrax®. A Leica DM LB Photomicroscope, equipped with a PlanAPO x100 (i.d. 1.4) objective and Nikon camera (University of Szczecin, Poland), was used for slides observation.

For SEM examination, samples were collected onto 1 µm Nuclepore filters, rinsed twice with deionised water (milliQ) and air–dried. The filters were then mounted on stubs and coated with gold–palladium alloy using a sputter coater (EMSCOP SC 500 apparatus), and examined with a SEM HITACHI S–4500, operating at 10 kV (C2M University of Perpignan Via Domitia, France and the Botanical Institute of the J.–W. Goethe–University, Frankfurt am Main, Germany). The apparatus in Frankfurt am Main has been operating at 5–7 kV and the stubs were coated with gold (Agar–Sputter–Coater). Since no severe treatment was applied to the samples, the intact valve's

hymenes can be observed in SEM examination.

Results

***Scalariella* Riaux–Gobin gen. nov.**

Diagnosis: Valvae ellipticae ad oblongae–ellipticae, apicibus obtuse rotundis.

Sternumvalva : valva leniter convexa. Area axialis recta et moderate angusta. Striae transapicales parallelae, ad modice radiantes ad polos. Areolae latae, in totis striis locatae et marginem attingentes, hymeno delicato occlusae. Area centralis nulla.

Raphevalva : valva plana ad leniter concava. Raphe recta filiformis, extremis centralibus approximatis et parum deflectis ad primarium latus. Fissurae terminales duplo curvatae et ad idem latus deflectae. Area axialis anguste linearis. Striae moderate radiantes, cum aequalibus interstriis et in media parte interruptae a lunatis areis lateralibus apices non attingentibus.

Typus generis: *Scalariella pseudofallacia* (Witkowski, Metzeltin et Lange–Bertalot) Riaux–Gobin et Witkowski comb. nov.

Description: Heterovalvar and solitary diatom. Observed on marine sediments. Valves elliptic to linear elliptic with obtusely rounded to subrostrate apices.

Sternum valve (SV) convex, transapical striae in parallel rows in the central part of the valve to very slightly radiate in the apices (Figs 7–9, 1–2, 5). Striae formed of wide, very slightly depressed, scalar apertures or macroareolae (following the definition by Bukhtiyarova 2006) and occluded internally by a thin hymen without apparent slits (Fig. 6). Narrow linear sternum.

Raphe valve (RV) flat to very slightly concave, striae parallel at the centre of the valve to radiate at the apices (Figs 10–17). Striae regularly spaced. A hyaline lateral lunate–shaped area, not reaching the apices, divides the striae into two large and regular areolae/foramina (Figs 10–17). Areolae occluded by a thin uniform hymen (without visible slits, Fig. 17; see also TEM illustration in Metzeltin & Witkowski 1996, tafel 76, fig. 9), not domed internally (Figs 14–16). Externally, there are two lateral sunken recesses in the hymenes of the marginal areolae (Fig. 17, arrow). Axial area narrow and internally raised (Fig. 16). Central area almost absent. Raphe filiform and straight, central raphe endings small and rounded, relatively close externally and very slightly bent to the primary side, coaxial internally (Fig. 15). Terminal raphe fissures double–hooked and deflected to the same side (Figs 12, 13, 17), opposite to that of the central endings. Relatively poorly developed helictoglossae (Fig. 15). Girdle is composed of several non–perforated bands (Figs 11, 12, 16), with a wavy valvocopula to the RV (Fig. 16, arrow).

Etymology: the generic name makes reference to ladder–like (scalar) appearance of the almost parallel, regularly spaced, SV striae.

Remarks: similitude to other achnanthoid diatoms, but with several distinctive features: 1) central raphe endings internally coaxial, 2) terminal raphe fissures strongly double–hooked, 3) hymen occluding the macroareolae without apparent slits, but with marginal recesses, 4) no central area, 5) presence of a hyaline, lunate–shaped, lateral area on each side of the RV (Table 1), dividing the individual areola of each stria into two (never more than two).

***Scalariella pseudofallacia* (Witkowski, Metzeltin et Lange–Bertalot) Riaux–Gobin et Witkowski comb. nov. [Figs 7–9 (LM), Figs 1–6; 10–17 (SEM)]**

Basionym: *Naviculadicta pseudofallacia* Witkowski, Metzeltin et Lange–Bertalot, in Metzeltin & Witkowski 1996, Iconographia Diatomologica 4, p. 23, figs 50/20–21, 76/9–12

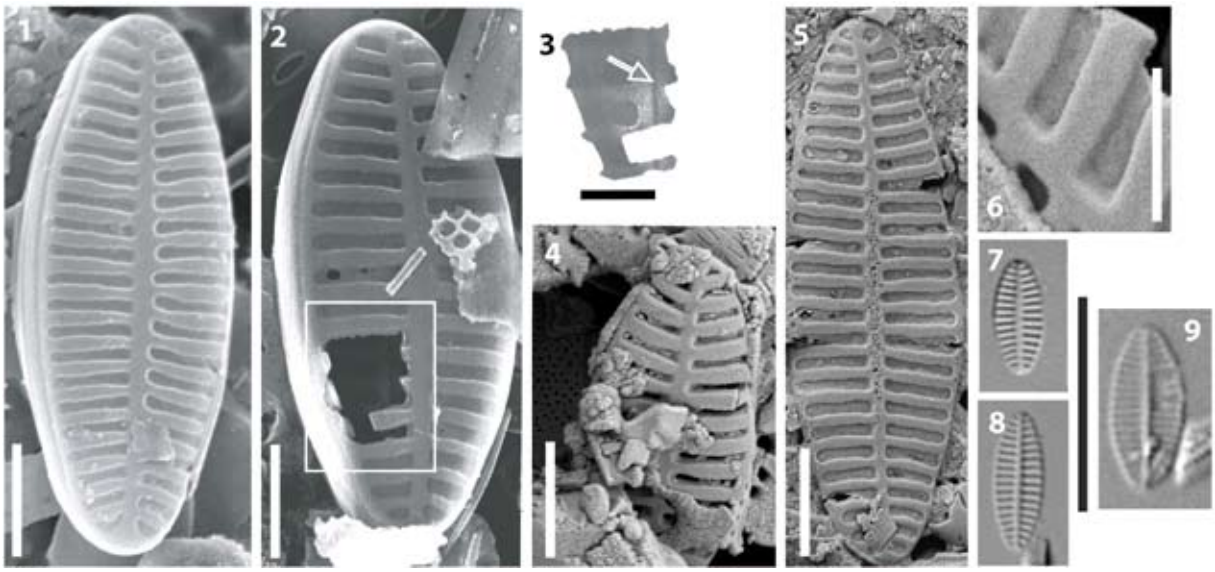
See p. 23, figs 50/20–21, 76/9–12, 79/4, 85/8 in Metzeltin & Witkowski 1996, for the RV. Also illustrated in pl 69/19 in Witkowski et al. 2000.

Holotype: praep. Bären–Insel No. 40–1, *in* FRA, Coll. Lange–Bertalot, Senckenberg Museum, Frankfurt am Main, Germany.

Description: See genus diagnosis for the general description of the frustule. Small–celled taxon, length: 5–10.5 µm; width: 2.5–5 µm. The SV striae are easily resolved in LM (Figs 7–9; specimens from Kerguelen). The SV is characterized by non–radiate, transapical, regular, wide, sub–parallel striae, open externally (Figs 1, 2, 5), with rounded ends near the border of the valve and the sternum. Narrow, linear axial area. The RV has radiate striae and a narrow axial area. Central raphe endings relatively close and slightly turned to primary side (e.g. Figs 10–17), internally coaxial (Fig. 15). Terminal raphe fissures strongly double–hooked on same side (Fig. 13). A TEM illustration (Metzeltin & Witkowski 1996, tafel 76, fig. 9) of a specimen from Bear Island confirms the doubly hooked terminal raphe fissure, the very thin internal hymenes with no apparent slits, and the undecorated area crossing each stria in the centre. Girdle composed of several (up to four)

Table 1. Comparative features and morphometry of *Scalariella pseudofallacia*, *S. oblongella* and *Achnanthes delicatissima*.

Taxon	*Scalariella pseudofallacia* (WITKOWSKI, METZELTIN et LANGE–BERTALOT) RIAUX–GOBIN et WITKOWSKI comb. nov.	*Scalariella oblongella* RIAUX–GOBIN, WITKOWSKI et RUPELL sp. nov.	*Achnanthes delicatissima* SIMONSEN ex HINZ, SIMONSEN et CRAWFORD
	present study	present study	HINZ et al. in press and present study
valve shape	elliptical to linear–elliptical	elongate–lanceolate	elliptical, round to flat apices
Length	5–10.5 µm	8–16 µm	8.9–9.8 µm
Width	2.5–5 µm	3.5–5 µm	4.5–5 µm
SV			
stria arrangement	non radiate, sub–parallel, equidistant	non radiate, sub–parallel, denser at apices	radiate, short, equidistant
stria density	20–25 (22.5) in 10 µm	13–20 to 18–25 on apices in 10 µm	35.5 in 10 µm
areola shape and arrangement	striae formed of a wide macroareola, opened externally	striae formed of a macroareola	marginal short striae formed of one transapically elongate foramina
Sternum	straight, narrow	straight, relatively narrow	large
Valvocopula	not observed	not observed	not observed
RV			
stria arrangement	radiate, equidistant	radiate, equidistant	radiate, equidistant
stria density	19–33 (26) in 10 µm	18–21 in 10 µm	32.6 in 10 µm
areola shape and arrangement	striae divided in two large foramina by a hyaline lateral lunate–shaped area	striae divided in two large foramina by a hyaline lateral lunate–shaped area	striae divided in two narrow foramina by a hyaline lateral lunate–shaped area
central area	absent	absent to small	relatively large
central raphe endings	Relatively close, slightly turned to primary side	well apart, slightly turned to primary side	well apart, slightly turned to primary side
terminal raphe endings	doubly hooked	doubly hooked	simply hooked
valvocopula	present, undulate margin	not observed	not observed
cingulum	several large unperforated bands	several unperforated bands	several unperforated bands



Figs 1–9. *Scalariella pseudofallacia* from Kerguelen Islands: (7–9) LM, Scale bar 10 µm ; SEM, Scale bars 2 µm (Figs 1–2, 4–5); 1 µm (Figs 3, 6). *Scalariella pseudofallacia* (1–2, 4–5) external views of sternum valve (SV) showing striation composed of an unique foramen or macroareola; (3) magnification of the square–detail of Fig. 2, showing the raphe valve (RV) with the raphe (framed arrow); (6) detail of macroareolae, with depressed hymen without slits; (7–9) SV in LM.

open bands (see Metzeltin & Witkowski 1996; tafel 76, fig. 10). A valvocopula with a wavy margin was observed on one RV specimen from Kerguelen (Fig. 16), confirming the previous observations from Bear Island (Metzeltin & Witkowski 1996; tafel 76, fig. 10). Approximately the same stria density on both valves (cf. Fig. 2 illustrating a broken specimen showing both valves, and Fig. 11 also showing both valves): SV with 20–25 (mean 22.5) striae in 10 µm; RV with 19–33 (mean 26) striae in 10 µm. Striae regularly spaced on each valve. Large range of stria density per specimen observed.
Distribution: unfrequent but not rare.
LM and SEM material: Specimens from marine sediments off Kerguelen.
Habitat: found in intertidal marine sediments from the main Kerguelen island
Ecology/ethology: *Scalariella pseudofallacia* was observed as solitary cells, never in chains. Found on marine sediments, but never attached to sand grains. Previously reported as *N. pseudofallacia* in Bear Island and the Norwegian Sea, near Narvik (Metzeltin & Witkowski 1996; Witkowski et al. 2000).

***Scalariella oblongella* Riaux–Gobin, Witkowski et Ruppel sp. nov. [Figs 18–20 (SEM)]**

Diagnosis: Valvae oblongae–lanceolatae, 8–16 longae, 3.5–5 µm latae, apicibus obtuse rotundis.
Sternumvalva : Area axialis recta et moderate angusta. Striae transapicales parallelae in medio valvae (13–20 in 10 µm), densiores ad polos (18–25 in 10 µm), ex areolis magnis factae, hymeno delicato clausis.
Raphevalva : valva plana ad leniter concava. Raphe directa filiformis, extremis centralibus distincte deflectis ad primarium latus. Fissurae terminales duplo curvatae. Area axialis anguste linearis, area centralis leniter inflata. Striae modice radiantes (18–21 in 10 µm), in media parte interruptae cum areis lateralibus. Habitat sedimentum marinum Kerguelense.

Description: Valve elongate–lanceolate with obtusely round apices
Sternum valve (Figs 18, arrow; Fig. 20, internal view): striae parallel (13–20 in 10 µm) at centre of valve, denser towards the apices (18–25 in 10 µm). Each stria, in SV and RV, is composed of a unique large areola/foramen occluded by a thin hymen. Sternum regular and straight, slightly raised internally (Fig. 20).
Raphe valve: raphe filiform. Axial area narrow, very slightly enlarged in median part. Central raphe endings small and externally deflected towards the primary side (Fig. 19). Striae regularly spaced on the whole valve (18–21 in 10 µm), interrupted by a lateral regular hyaline space. Terminal raphe fissures double–hooked (Fig. 19). Transapical striae parallel in the middle of the valve and slightly radiate on apices. Cingular bands present but not observed precisely.
Note: only three specimens were observed in SEM.
Distribution: rare, Bossière intertidal (see map in Riaux–Gobin & Romero 2003; site n° 5 in Fig. A)

Table 2. Morphological distinguishing features for the genera *Planothidium*, *Psammothidium*, *Achnanthes*, *Achnanthidium*, *Rossithidium, Karayevia*, *Nupela* and *Scalariella.*

	Scalariella this study	*Psammothidium* after BUKHTIYAROVA & ROUND 1996	*Planothidium* after ROUND & BUKHTIYAROVA 1996	*Achnanthidium* after ROUND & BUKHTIYAROVA 1996 and POTAPOVA & PONADER 2004	*Achnanthes* after ROUND et al. 1990	*Karayevia* sensu lato after BUKHTIYAROVA 2006	*Astartiella* after MOSER et al. 1998	*Rossithidium* after ROUND & BUKHTIYAROVA 1996	*Nupela* after VYVERMAN & COMPÈRE, 1991
curvature of the RV	flat	flat to convex	flat	concave, bent with various degree	convex, bent	flat	flat	flat	flat
central raphe endings coaxial internally	+	–	–	–	±	+	+	?	+
external central raphe endings	rounded, depressed slightly bent on primary side	coaxial	slightly bent on primary side	opposed, coaxial	slightly bent on primary side, or coaxial	coaxial	coaxial	slightly expanded	slightly expanded, distant from each other
terminal raphe endings	double–hooked in same side	simple or hooked in opposite directions	hooked in same side	simple or slightly hooked in same side, or in opposite side	hooked in the same side	double–hooked on one side or variable	double–hooked bent in opposite side	simple or slightly hooked in one side	often double–hooked on one side
striae	RV: two areolae SV: a single elongated foramen or macroareola	uniseriate	multiseriate	uniseriate denser on the valve apices	uni– to multiseriate	RV: uniseriate Presence of macroareolae on some taxa SV: uniseriate	RV: uniseriate with elongate areolae along the sternum and valve margin, SV: uniseriate, slit–like apically elongate	uniseriate	uniseriate composed of rather large areolae
occlusions	slightly depressed, plain hymen	slightly depressed	valve surface	slightly depressed	slightly depressed, poroids with complex cribra and volae	slightly depressed	slightly depressed, plain hymen	?	slightly depressed, hymen centrally perforated

Table 2 Cont.

specific features	RV: hyaline lunate–shaped area	SV often bearing extended central area, row(s) of pores on the mantle	absence of several striae on one side of the SV, some internally bearing a tunnel–like (capped) structure	SV often bearing a fascia, one row of pores on the mantle	predominantly marine species	mostly fresh–water taxa	valve margin of SV slightly elevated above the valve face one to a few stigmata present on the SV	linear valve outline, areolae on the mantle, often a central stauros on the RV	exclusively fresh–water species, some taxa are heterovlavar, one valve with long raphe slits, the other with short ones
girdle	up to 4 cingular bands, unperforated valvocopula with wavy margin	several	several	Several bands, non porous	3–7 open bands with 1–2 rows of transverse poroids	several bands (?) non porous	unknown	unknown	a few open cingular bands, unperforated
helictoglossae	Very low	low	+	+	+ low	low almost absent	?	low	low

Holotype: SEM stub B8, in Collection Horst Lange–Bertalot (Frankfurt am Main, Germany at the J.W–Goethe University, FRA), illustrated by the SEM Fig. 19.

Isotype: Slide 7356/10 housed at A. Witkowski Collection at the Institute of Marine Sciences, University of Szczecin (SZCZ).

Holotype locality: "Port Raymond subtidal" (see map in Riaux–Gobin & Romero 2003; site n° 3 in Fig. A). Sample "Port Raymond subtidal" in Collection Riaux–Gobin (USR 3278 CNRS–EPHE, CRIOBE–Perpignan University, France).

Etymology: the epithet refers to the shape of the valve.

Habitat: found in intertidal marine sediments from the main Kerguelen island

Remarks: shows all distinctive features of *Scalariella*. LM and more SEM illustrations are needed before a more complete description can be given (external view of the SV, internal view of the RV, and copulae).

Discussion

Comparison of *Scalariella* with other monoraphid genera, particularly *Karayevia* and *Nupela*

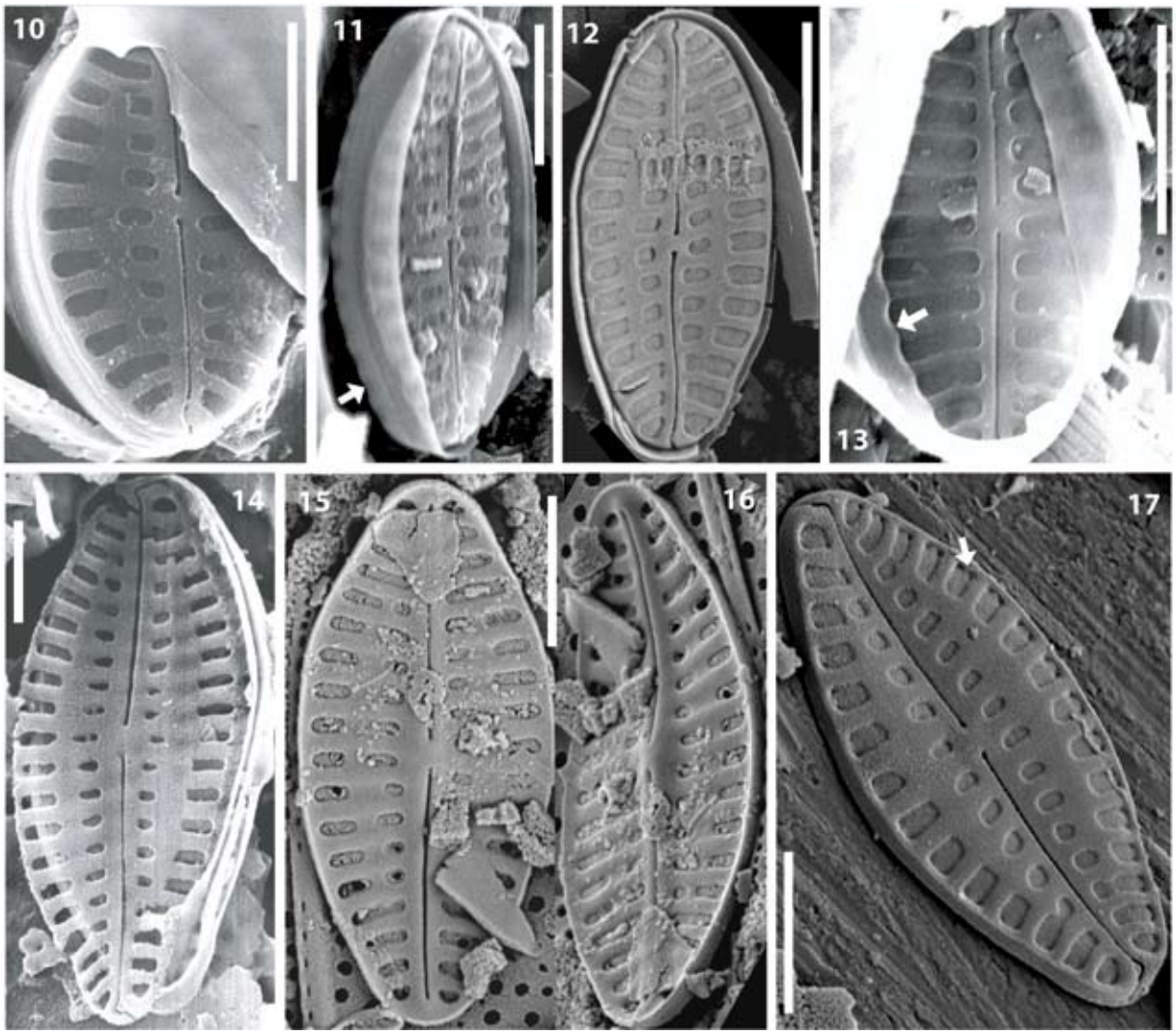
The morphological characteristics of the new genus *Scalariella* and other genera established after *Achnanthes* Bory sensu lato was first subdivided, are compared in Table 2. Several of these characteristics are not constant or may vary within a genus, such as the terminal raphe fissures, which may be either simple or hooked (i.e. in *Achnanthidium* and *Psammothidium*), or the structure of the striae, i.e. uni– to multiseriate. None of these new genera can be defined simply, using only a few criteria, except for *Nupela* whose areola pattern (with a round central hole on the hymen) seems unique (Vyverman & Compère 1991). Nevertheless, these recently established genera allow numerous taxa to be classified, although the position of several others remains uncertain, pending study with SEM, as proposed by Bukhtiyarova & Round (1996) and Round & Bukhtiyarova (1996).

When observed with LM, *Scalariella* most closely resembles *Planothidium* or *Psammothidium* (e.g. Buktiyarova & Round 1996; Witkowski et al. 2000; Krammer & Lange–Bertalot 2004). The general valve outline and the pattern of striae in both valves are relatively similar in

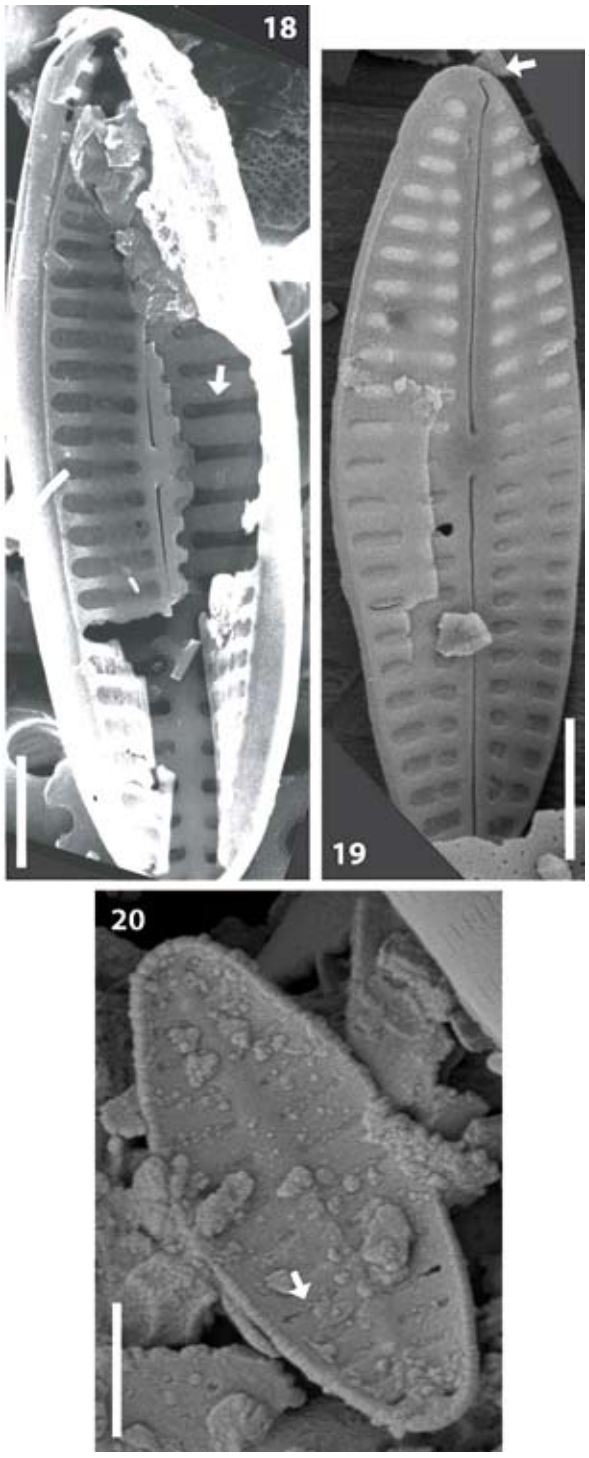
these genera. The most striking LM feature that differentiates *Scalariella* from *Planothidium* and *Psammothidium* is the lack of a central area in the RV of the first genus.

However, SEM and TEM images reveal that the ultrastructure of *Scalariella* is completely different from that of the other genera (Table 2), particularly with respect to stria and raphe ultrastructure. The SV transapical striae comprise one scalar elongated areola/foramen, or macroareola (BUKHTIYAROVA 2006), per stria opening externally (Figs 4–5, 7–9), and internally closed by a flat (or very slightly domed) thin hymen. A major difference is also observed around the RV areolae: our study shows that only two large and regular areolae, covered by a thin flat hymen, occur in *Scalariella*, and that both raphe endings are double–hooked in the same direction. The combination of these features is unique and it is difficult to classify our taxon under the genera cited in Table 2.

It should be noted that striae composed of one, slightly depressed, macroareola on the valve face, is a characteristic shared by several biraphid genera, such as *Diadesmis*, *Chamaepinnularia* [e.g. *C. mediocroformis* (COSTE et RICARD) LANGE–BERTALOT; in MOSER et al. 1998, tafel 32, fig. 11], *Gomphosphenia* [e.g. *G. oahuensis* (HUSTEDT) LANGE–BERTALOT; in MOSER et al. 1998, tafel 53, fig. 2], *Navicula(dicta) schmassmanii* HUSTEDT (WERUM & LANGE–BERTALOT 2004, plate 34) and the recently created *Microfissurata* (CANTONATI



Figs 10–17. *Scalariella pseudofallacia* from Kerguelen Islands: Scale bars 2 µm. SEM specimens from Kerguelen (Figs 10–17). *Scalariella pseudofallacia* (10–13, 17) external views of the RV showing the hyaline lunate–shaped interruption of the striae, the raphe endings and the copulae. The arrow in Fig. 11 shows the striation of the slightly convex SV; (14–16) internal views of the RV showing the central raphe endings and the poorly developed helictoglossae; (16) internal view of the RV showing the wavy valvocopula (arrow); (13, 17) apical raphe ending doubly hooked.



Figs 18–20. *Scalariella oblongella* from Kerguelen Islands: (18–20) SEM. Scale bars 2 µm. SEM specimens from Kerguelen. *Scalariella oblongella* (18–20) SEM, external views of the RV showing the hyaline lunate–shaped interruption of the striae, the raphe doubly hooked ending (19, arrow). The arrow in Fig. 18 shows the striation of the SV, denser on apices. (20) SEM, internal view of the SV with striation denser on apices and a slightly raised sternum. Note that the macroareolae (arrow) are not reaching the margin of the valve.

et al. 2009; fig. 1, j). But for most of these taxa, a row of oblong foramina is also present on the mantle, which is lacking in *Scalariella*.

Within the Achnanthales, several taxa have striae composed of a macroareola (shown in SEM) on both valves. For example: *A. carissima* Lange–Bertalot (Lange–Bertalot & Krammer 1989, tafel 38, figs 1–4). This taxon has a row of short foramina on the RV mantle, simple terminal raphe endings and several apical slits on each valve. *A. dornii* Lange–Bertalot (Lange–Bertalot & Krammer 1989, tafel 38, figs 5–7) has simply deflected terminal raphe endings. The two taxa have been transferred to the genus *Karayevia* (Bukhtiyarova 2006).

Several other taxa show the characteristic stria pattern only on their RV: e.g. *Karayevia kolbei* (Hustedt) Bukhtiyarova, previously named *Kolbesia kolbei* (Hustedt) Round et Bukhtiyarova, has more than two foramina on the SV and one on the mantle (Round & Bukhtiyarova 1996, figs 20–21), and hooked terminal raphe endings (ibid, fig. 22). *Achnanthes laterostrata* Hustedt transferred to *Karayevia* (Lange–Bertalot & Krammer 1989, tafel 44, figs 6, 7; Bukhtiyarova 2006, figs 9–12). *Karayevia suchlandtii* (Hustedt) Bukhtiyarova [Bukhtiyarova 2006, figs 13, 14, 16; previously named *Kolbesia suchlandtii* (Hustedt) J.C. Kingston].

The term of macroareola (for stria formed of a single foramen) and postmacroareola (stria formed of several "short macroareolae"), established by Bukhtiyarova (1996), permits her to define the genus *Karayevia* as containing "primitive features" (macroareolae on both valves, i.e. in *K. carissima*) and "progressive features" (postmacroareolae on both valves, i.e. in *K. clevei*). However, the *Karayevia* group appears highly heterogeneous, concerning: 1) the presence or absence of foramina on the SV mantle, 2) the raphe ending path (simple in *K. carissima* while the primitive feature would be hooked endings, Bukhtiyarova 2006), and 3) the great range of variation in complexity of the SV areolae (simple elongated foramina in *Karayevia kolbei*, to complex areolae with rota–type pore occlusions in *Karayevia clevei*).

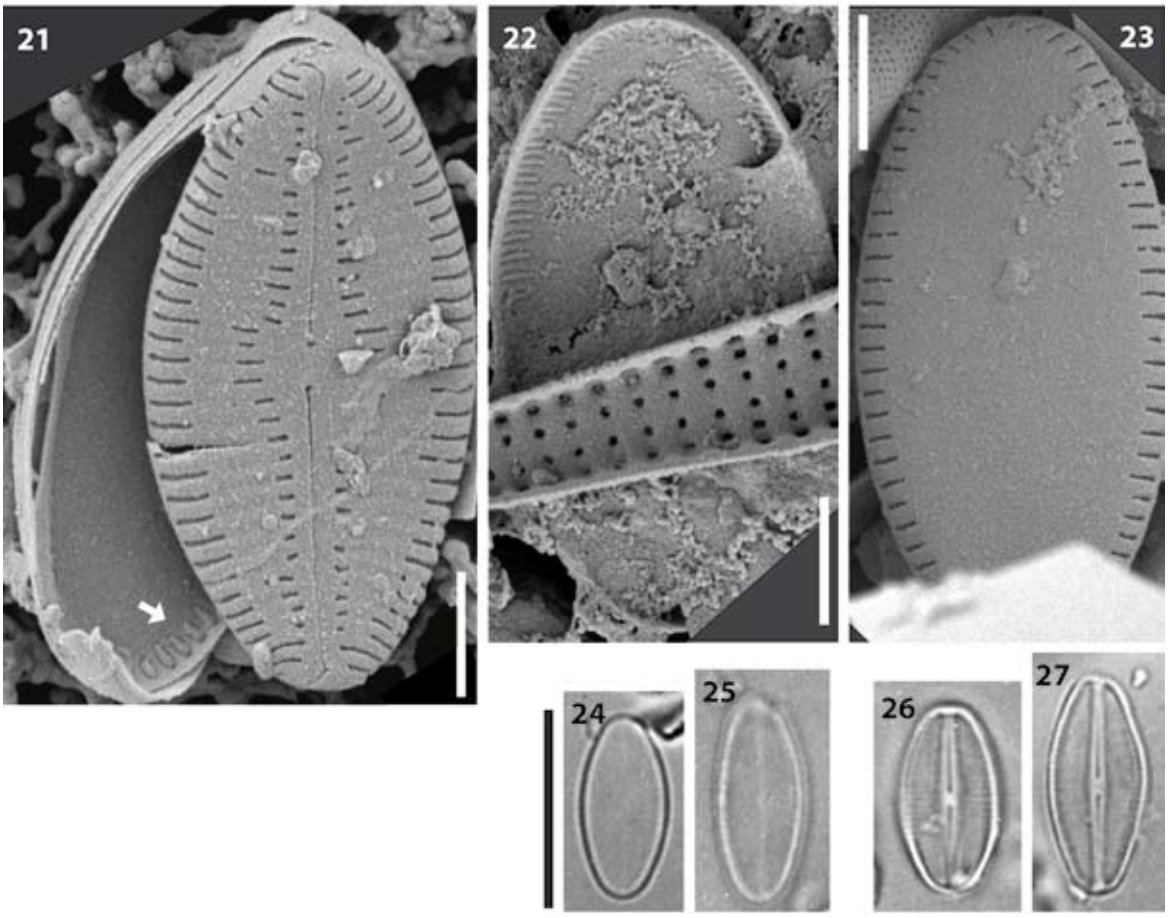
The stria pattern of *K. kolbei* SV, as illustrated in Bukhtiyarova (2006) [fig. 20, very different from previous illustrations in Round & Bukhtiyarova (1996, figs 20–21, with several elongate foramina)] could match that of

Scalariella pseudofallacia, except for the row of elongate foramina on the mantle, which is lacking in *Scalariella*. However, the RV of *Scalariella* is completely different from that of *K. kolbei* and does not match any *Karayevia* sp.

Some similarities can also be seen between *Scalariella* and *Nupela* VYVERMAN et COMPÈRE. *Nupela* is a biraphid diatom (VYVERMAN & COMPÈRE 1991), although hetereovalvy was recently demonstrated for some of its species (POTAPOVA et al. 2003; SIVER et al. 2007). We note that the *Scalariella* RV shows great similarity with respect to the raphe system of several *Nupela* spp. [e.g. *N. neglecta* PONADER, LOWE et POTAPOVA and *N. carolina* POTAPOVA et CLASON (POTAPOVA et al. 2003), *N. silvahercynia* (LANGE–BERTALOT) LANGE–BERTALOT, *N. lapidosa* (KRASSKE) LANGE–BERTALOT (WERUM & LANGE–BERTALOT 2004)].

Some similarities with *Achnanthes delicatissima* SIMONSEN ex HINZ, SIMONSEN et CRAWFORD

A previous observation by A.W. of unmounted material of *Achnanthes delicatissima* SIMONSEN (ex HINZ, SIMONSEN et CRAWFORD; see HINZ et al., in press) [sampled on 20.07.1955 (SIMONSEN 1959) from Sahrensdorfer Binnensee, Burgstacken (0.8 m), the type locality], and observation of the holotype slide Di–208, gave the opportunity to establish some similarities between the latter taxon and *Scalariella*. Features and morphometry of *A. delicatissima* are reported and compared to those of *Scalariella* species in Table 1. The LM and particularly the SEM illustrations of *A. delicatissima* (Figs 21–27) show some similitude within the RV of this taxon and that of *Scalariella*: the striae are split in two parts by a hyaline lunate–shaped area that does not reach the apices, each stria part being an oblong depressed foramina. That morphology is quite similar to that in *Scalariella*, except for the thickness of the striae (thinner in



Figs 21–27. *Achnanthes delicatissima* [unmounted type material from Sahrensdorfer Binensee, Burgstacken (0.8 m), sampled on 20.07.1955 (SIMONSEN 1959), and holotype slide Di–208]: (21–23) SEM. Scale bars 2 µm. (24–27) LM. Scale bar 10 µm. *Achnanthes delicatissima* (21) external view of the raphe valve (RV) showing striation interrupted by a hyaline area and elongated areolae; (21–22) showing the internal view of the SV, with short marginal striae; (23) external view of the SV; (24–27) LM images of entire frustules (24–25) and of RV (26–27).

A. delicatissima). However, *A. delicatissima* has a slightly expanded, rounded central area on the RV and the terminal raphe endings are simply deflected and not double–hooked. Furthermore the SV of *A. delicatissima* is very dissimilar to that of *Scalariella*, with an extremely wide sternum and very short, strongly radiate, marginal striae, also around the apices, with internally domed hymenes (Figs 21–22). The later remarks permit to state that *A. delicatissima* cannot pertain to *Scalariella*.

On the other hand, it can be noticed that a species of *Achnanthidium* sensu lato (Round et al. 1990), recently found in coral sediments off Mascarenes (Riaux–Gobin et al., in press), has features very similar to that of *Achnanthes delicatissima*, except a higher stria density on both valves (33–57 on the SV and 46–80 on the RV). Another tropical taxon, *Achnanthidium pseudochamaepinnularia* Riaux–Gobin et al. (2010), has also some similarities with *Achnanthes delicatissima* but *A. pseudochamaepinnularia* has a denser striation and dissimilar stria density on both valves (30–41 on the SV and 40–50 on the RV). The design of the SV striae is also different (much longer and irregular in *A. pseudochamaepinnularia*).

Following Hinz et al. (in press), *A. delicatissima* is now a valid species of *Achnanthes* sensu lato. Nevertheless, the latter taxon, as well as several species found on coral reefs off Mascarenes (e.g. *Achnanthidium pseudochamaepinnularia* and *Achnanthidium* sp., Riaux–Gobin et al., in press), with their very specific features (Table 1), may be transferred later on to an other genus.

It can also be remarked that *A. fogedii* Håkansson is a later synonym of *A. delicatissima* (see Håkansson 1978, e.g. figs D–F). *A. delicatissima* occurs in the Adriatic and Baltic Seas (Simonsen 1959) as *A. fogedii* (Håkansson 1978; Wunsam et al. 1999; Witkowski et al. 2000), and in Holocene saline lake sediments (Salziger See, Central Germany; Szylkiewicz 2006).

Biogeography

Naviculadicta pseudofallacia was described from Bear Island (74°30'–74°20'N; half way between northern Norway and south of Spitsbergen) (Metzeltin & Witkowski 1996). Two LM illustrations (Metzeltin & Witkowski 1996, pl. 76/11–12) come from examination of the slide N° 1669 of the Østrup Collection (Copenhagen) collected from the coast of Greenland. In Witkowski et al. (2000), the locality of Narvik is indicated for the same taxon (Norwegian Sea; 68°26'00N; 17°25'00E, north of the Polar circle). Recently Seidler (2004) and Nagumo et al. (2008) found *S. pseudofallacia* in subfossil sediments of Benicia State Park (San Francisco Bay) salt marshes and (as *Achnanthes* sp. 1, LM and SEM figures) in water pumped from 218 m deep in Shiretoko Rausu, Okhotsk Sea, respectively. Nagumo et al. (2008) also found *S. pseudofallacia* as an epiphyte among the attached diatom flora.

The new finding of *S. pseudofallacia* in the Southern hemisphere may indicate that this genus was misidentified in the past, and may be a rather widespread taxon on the sub–polar (cold water) environments of both hemispheres. Further investigation is needed to describe the exact biogeography of this small–celled taxon and that of *S. oblongella*, second species of this genus, for which more specimens need to be studied to understand its features better.

Our knowledge on the distribution of marine littoral diatom species suggests that bipolar distribution is not very common. There are a few other examples. e.g. *Fragilariopsis cylindrus* (Grunow ex Cleve) Frenguelli, *F. nana* (Steemann Nielsen) Paasche (e.g. Lundholm & Hasle 2008; Pike et al. 2008). Otherwise, littoral marine diatoms more commonly have a very broad geographic distribution, e.g. *Odontella aurita* (Lyngbye) C. A. Agardh, *Planothidium delicatulum* (Kützing) Round et Bukhtiyarova, *Catenula adhaerens* Mereschkowsky, *Navicula gregaria* Donkin, *Paralia sulcata* (Ehrenberg) Cleve, and *Nitzschia ligowskii* Witkowski, Lange–Bertalot, Kociolek et Brzezinska (Witkowski et al. 2000; Witkowski et al. 2004).

The new genus *Scalariella*, now comprises two small–sized species from the Kerguelen material, but *S. pseudofallacia* is known from other localities (see above), and valves with a lunate hyaline area on each side of the RV, and scalar striae composed of macroareolae on the SV, may have been misidentified in the past, and will probably be found in other environments, polar or otherwise.

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