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## European Journal of Phycology

Publication details, including instructions for authors and subscription information:  
<http://www.tandfonline.com/loi/tejp20>

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Available online: 15 Aug 2007

To cite this article: Regine Jahn & Anna-Maria M. Schmid (2007): Revision of the brackish-freshwater diatom genus *Bacillaria* Gmelin (Bacillariophyta) with the description of a new variety and two new species, *European Journal of Phycology*, 42:3, 295-312

To link to this article: <http://dx.doi.org/10.1080/09670260701428864>

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# Revision of the brackish-freshwater diatom genus *Bacillaria* Gmelin (Bacillariophyta) with the description of a new variety and two new species

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(Received 31 January 2006; accepted 9 January 2007)

*Bacillaria paxillifera* – perhaps better known by its synonym *B. paradoxa* – is epi-typified with material from close to the type locality. Its morphology – from the living cell and intact colony to the fine structure of the valve and girdle bands – is established using light microscopy, transmission electron microscopy and scanning electron microscopy. Since *B. paxillifera* is also the generitype, *Bacillaria* is here revised and emended to include only brackish-freshwater taxa showing the unique fibulate raphe system and construction type of this genus. Three new taxa are described within the re-defined genus: *B. paxillifera* var. *czarneckii*, *B. kuseliae* and *B. urve-millerae*, differing mainly in their raphe flanges, cell-outline and shape and number of plastids. The first taxon was found in both the Mississippi River, USA, and the River Weser, Germany, the second in the Avon River, Australia, and the third at a freshwater influx into the Atlantic in The Gambia, West Africa. Historical taxa, such as Grunow's *B. paxillifera* var. *tumidula*, var. *tropica*, and var. *pacifica* were also studied and lectotypified.

**Key words:** *Bacillaria*, biogeography, cell-wall; habitat; morphology; motile colonies, nomenclature, taxonomy

## Introduction

One of the first diatoms ever named was described by O.F. Müller, first mentioned in a talk given in 1781 at the Danish Academy of Sciences. Müller (1782) published and illustrated this taxon as 'Stäbgenthier' (in German), subsequently (Müller, 1783) as 'Pinddyret' (in Danish), finally naming it *Vibrio paxillifer* (Müller, 1786). Shortly afterwards, Gmelin (1788) established the genus *Bacillaria* and referred to Müller's Stäbgenthier when naming it *B. paradoxa*, apparently unaware that Müller had already given it a formal name. Since this is a homotypic synonym, Hendey (1951) was correct (rules of priority) in recombining it as *Bacillaria paxillifer[a]* (O.F. Müller) Hendey. An 'a' is added to the ending of the epitheton to improve the Latin (Hasle & Syvertsen, 1997, P. Compère, pers. comm.).

In a recent paper, Schmid (2007) showed that our concept of *B. paxillifera* has been incorrect for two centuries. For the first 50 years after its description every rod-like diatom was called *Bacillaria*; 100 years later the genus *Bacillaria* had become a subgenus of *Nitzschia*

(Cleve & Grunow, 1880). Roughly 200 years after its description it reappeared, but only as a monospecific genus; attempts to establish new species or varieties were unsuccessful. Researchers were probably so intrigued by the 'paradoxical' movement of the colonies that they were blind to details of, and differences between, populations and colonies from different habitats. By taking into account all available characters – living cells and colonies, specific habitats, ultrastructural investigations of the cell as revealed by transmission electron microscopy (TEM), and valve morphology as detected by scanning electron microscopy (SEM) – it is clear that the organisms subsumed under the generic name *Bacillaria* must be differentiated into several taxa. Three new taxa that are closely related to *B. paxillifera* and have the construction type of brackish-freshwater bacillarioid taxa as defined by Schmid (2007) will be described in this paper.

Before new taxa are described and named, the identity of *B. paxillifera* must be established. Since O.F. Müller's specimen is no longer available, his drawings must serve as the lectotype. However, a taxon cannot be understood by

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Table 1. Materials used in this study

	Name	Collection site	Collector	Date	Herbarium/Slide	Status
1	<i>Bacillaria paxillifera</i> (O.F.Müller) Hendeby var. <i>paxillifera</i>	Avedøre Holme, Copenhagen, Denmark	T. Christensen	20 Sept 1964	<b>C AT-2387</b> <b>B</b> 400 040 244	Epitype isoeotype
2	<i>Bacillaria paradoxa</i> Gmelin	Salzbach an der Naumburg bei Sondershausen, Germany. In: Exsiccatae Rabenhorst (1854): Algen Sachsens, Nr. 361.	O. Bulnheim	Sept 1853	<b>BRM</b> Rab 1/31	Voucher
3	<i>Bacillaria paxillifera</i> var. <i>czarnecki</i> R. Jahn & A.M. Schmid	Neusiedler See, Austria Peosta Channel, Mississippi River, Dubuque, Iowa, USA	A.M. Schmid D. Czarnecki	1969 onwards (Schmid 1995) 15 Sept 2003	<b>B</b> 40 0140 245 <b>B</b>	Voucher SEM
4b		Peosta Channel, Mississippi River, Dubuque, Iowa, USA	D. Czarnecki Culture L1875	Isolated on 18 Dec 2003	<b>B</b> 40 0140 246	Holotype
5	<i>Bacillaria paxillifera</i> var. <i>czarnecki</i> R. Jahn & A.M. Schmid	Close to the estuary of River Weser, Germany	E. Kusel	3 Sept 1998	<b>B</b> 40 0140 247	Voucher
6	<i>Bacillaria kuseliae</i> A.M. Schmid & R. Jahn	Avon River, York/Perth, West-Australia	E. Kusel	Sept 1998	<b>B</b> 40 0140 248	Holotype
7	<i>Bacillaria urve-milleriae</i> A.M. Schmid & R. Jahn	Bijilo Beach, Atlantic coast, Southwest of Serecunda, The Gambia, West-Africa Honduras, South America	A.M. Schmid	13 Dec 1997	<b>B</b> 40 0140 249	Holotype
8	<i>Bacillaria (paradoxa</i> var.?) <i>tropica</i> Grunow	Bangladesh, East Indies	Lindig		<b>W</b> 839R	Lectotype
9	<i>Nitzschia paradoxa</i> var. <i>tumidula</i> Grunow				<b>W</b> Diat 78	Lectotype
10	<i>Nitzschia paradoxa</i> var. <i>pacifica</i> Grunow	Samoa Islands, Pacific			<b>W</b> 1512	Lectotype

drawings alone; information on habitat and morphology using modern light microscopy (LM) and electron microscopy (EM) is essential. In addition, the genus *Bacillaria* is defined by its unique colonial movement (Müller, 1782, 1783; Smith, 1856; Drum & Pankratz, 1966; Drum *et al.*, 1966; Drebes, 1968; Round *et al.*, 1990; Pickett-Heaps & Pickett-Heaps, 2003; Skibbe, 2004). We therefore chose an epitype from a natural population at a site close to the type locality in Copenhagen. In addition, we have checked historical material from Rabenhorst and type slides from Grunow, on which he based new bacillarioid taxa.

### Materials and methods

Material from 10 different sites was investigated (see Table 1). Samples containing different motile morphotypes of *Bacillaria* were fixed immediately at the collection site or transported alive to Salzburg, or obtained as gifts. *Bacillaria* colonies were isolated from these samples and brought into culture. Osmolality of the media was adjusted for the respective habitat (50–200 mOsmol.kg<sup>-1</sup> for Neusiedler See and Avon River, 1100 mOsmol.kg<sup>-1</sup> for The Gambia). Details of media and culture conditions are given in Franz & Schmid (1994).

Permanent slides (by AMS) were deposited at the Botanic Garden and Botanical Museum Berlin-Dahlem (B), the Grunow Collection at the Museum of Natural History, Vienna (W), and the Botanical Museum in Copenhagen (C). For permanent slides, the material was cleaned with KMnO<sub>4</sub> and HCl, rinsed in distilled water and dried on cover slips, embedded in Naphrax. Photographs were taken on a Reichert Polyvar or Zetopan using Nomarski optics and a SPL100/130 objective (oil immersion), plus green filter, and Kodak T-Max 100 film, developed in T-Max developer. Photographs were also taken on a Zeiss Axioplan with a digital camera (AxioCam MRc).

Stubs for SEM (made by AMS) were prepared. For herbarium material, aluminium stubs with double-sided adhesive tape were stamped onto the uncleaned herbarium material. For cultured material intact colonies were transferred with a mouth-pipette from aqueous solution onto a glass slide glued to the aluminium stub and air dried. The West African material was a strewn preparation. Stubs were coated with Au/Pd in a Polaron sputter coater (Kontron, Austria). SEM-micrographs were taken on a Philips 515 (Eindhoven, The Netherlands). Figure 21 was taken on a Cambridge IIa (after gold-coating) by AMS while staying at Prof. Urve Miller's laboratory in December 1972. TEM methods are described in Schmid (2007).

### Observations

#### *O.F. Müller's original material*

Müller (1782) found this organism on 6–7 October 1781, on dark green *Ulva latissima* (in the

German version: breites Meergras, in the Danish version: brede Tang) on the Danish shore, at the timberyards outside Vester Port. Vester Port was the western gate in the wall and a water body that once surrounded the city of Copenhagen. It lay close to Tivoli and thus the type locality as such has disappeared (Helle Nielsen, pers. comm.).

Müller's drawings (Müller 1782, Figs 1–8) are presented here (Fig. 1). Since there is no type material from O.F. Müller in the Copenhagen Herbarium (C) (Ruth Nielsen, pers. comm.), we chose Müller's illustration as the lectotype. However, the Copenhagen Herbarium holds a sample of *B. paxillifera* collected by Tyge Christensen from a similar site in the Sound close to Copenhagen, probably close to O.F. Müller's collecting site. We have chosen this modern material as epitype based on proximity to the original locus typicus.

***Bacillaria paxillifera* (O.F. Müller) Hendeby**  
*J. Roy. Micr. Soc. Ser. 3* 1951; 71: 74.

BASIONYM: *Vibrio paxillifer* O.F. Müller, *Animal Infus.*: 54, pl. VII, figs 3–7. 1786.

SYNONYMS: *Bacillaria paradoxa* J.F. Gmelin, *Syst. nat.*, ed. 13, vol. 1 (6): 3903. 1788.

*Nitzschia paxillifer* (O.F. Müller) Heiberg, *Conspect. Diatom Dan.*: 113. 1863.

*Nitzschia paradoxa* (J.F. Gmelin) Grunow in Cleve & Grunow, *Kongl. Svenska Vetensk. Akad. Handl.* 17 (2): 85. 1880.

*Homoeocladia paxillifer* (O.F. Müller) Elmore, *Diatoms of Nebraska*: 143. 1921.

LECTOTYPE (designated here): O.F. Müller's original drawing in 1782, his figs 2, 3. They are the same as pl. VII, figs 3, 4 in his 1786 publication (Fig. 1).

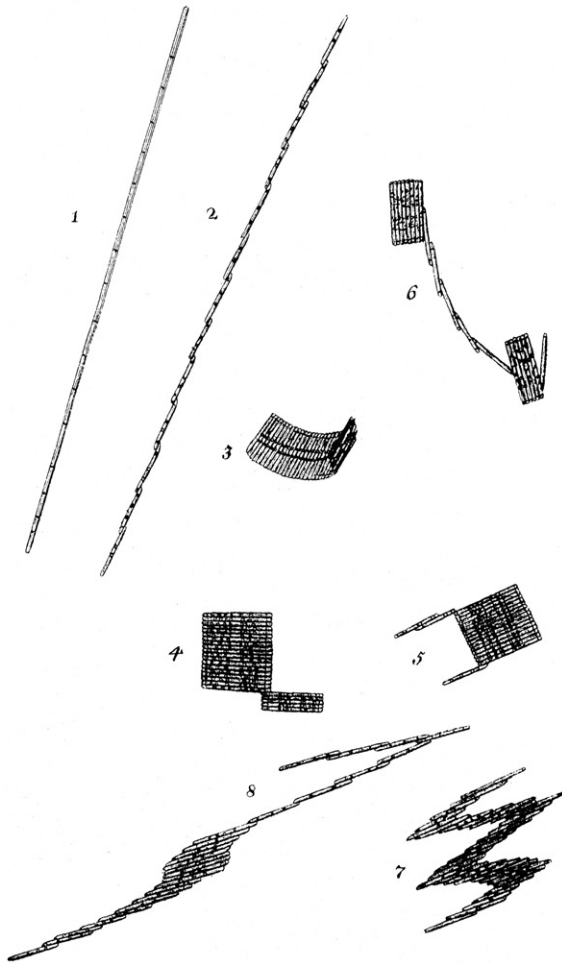
LOCUS TYPICUS: Vester Port at the timberyards, København, the western gate in the wall and waterbody once surrounding the city of Copenhagen close to Tivoli.

HABITAT: as described by Müller (1782): "lives on the dark green, broad seaweed, *Ulva latissima*, at the seashore".

EPITYPE (designated here): epitype slide C AT-2387 (Fig. 2); isoepitype slide B 400040244. Original material from which this slide was made was collected by Tyge Christensen on 20 September 1964 and deposited at C under No. 9554.

LOCUS TYPICUS: Avedøre Holme, Distr. 45a [a salt marsh just south of Copenhagen in 1964; now an industrialized area].

HABITAT: Natural population together with *Melosira nummuloides* C. Agardh. Tyge Christensen noted (translated) "being the main



**Fig. 1.** Müller's published drawing of 1782; his figs 2 & 3 are different images of the same colony and the designated lectotype of *Bacillaria paxillifera*. His legends are: "(1) Das Stäbgenthier gerade ausgestreckt, dem Faden einer Conferve nicht unähnlich, von oben gesehen. (2) Dasselbe in gleicher Streckung, von der Seite gesehen. (3) Dasselbe in einem länglichen Viereck zusammengezogen mit aufrechten stehenden Stäbgen und eingebogenen Enden, gleich einem Hobelspan. (4) In einem rechtwinkligen Viereck, davon sich das unterste Stück zu entfernen scheint. (5) Wie die äussersten Stäbgen das Fortschreiten nach einer Seite angefangen haben, und ein wenig auszuruhen scheinen. (6) Zwei kleinere durch eine Communications Linie verbundene Vierecke; an der einen ist das äusserste Stäbgen schräg gestellt. (7) Das Stäbgenthier im Zickzack. (8) Dasselbe in der Gestalt eines Wetterstrahls." (For a translation see Ussing *et al.*, 2005: 43).

part of woolly brown lumps the size of peas on the bottom of a small lowered area with open water near the beach". Because of the presence of the marine diatom *M. nummuloides*, conductivity must have been more than  $10,000 \mu\text{S cm}^{-1} = \text{ca } 200 \text{ mOsmol. kg}^{-1}$ .

#### Description (Figs 1, 2, 12–17)

According to Müller's drawing and legend (Müller 1786, fig. 3), the cells of a colony retract into

a rectangle with curved ends (like a wood shaving) with the individual cells parallel and perpendicular to the curved colony. Based on the habitat references (Müller, 1786; Christensen, herbarium annotation) *Bacillaria* was an epipellic/periphytic taxon, probably in a brackish habitat with great fluctuations in salinity (Schmid, 2007). *Ulva* indicates a high nutrient regime, and the habitat could also have been influenced by waste-water outflow from the town.

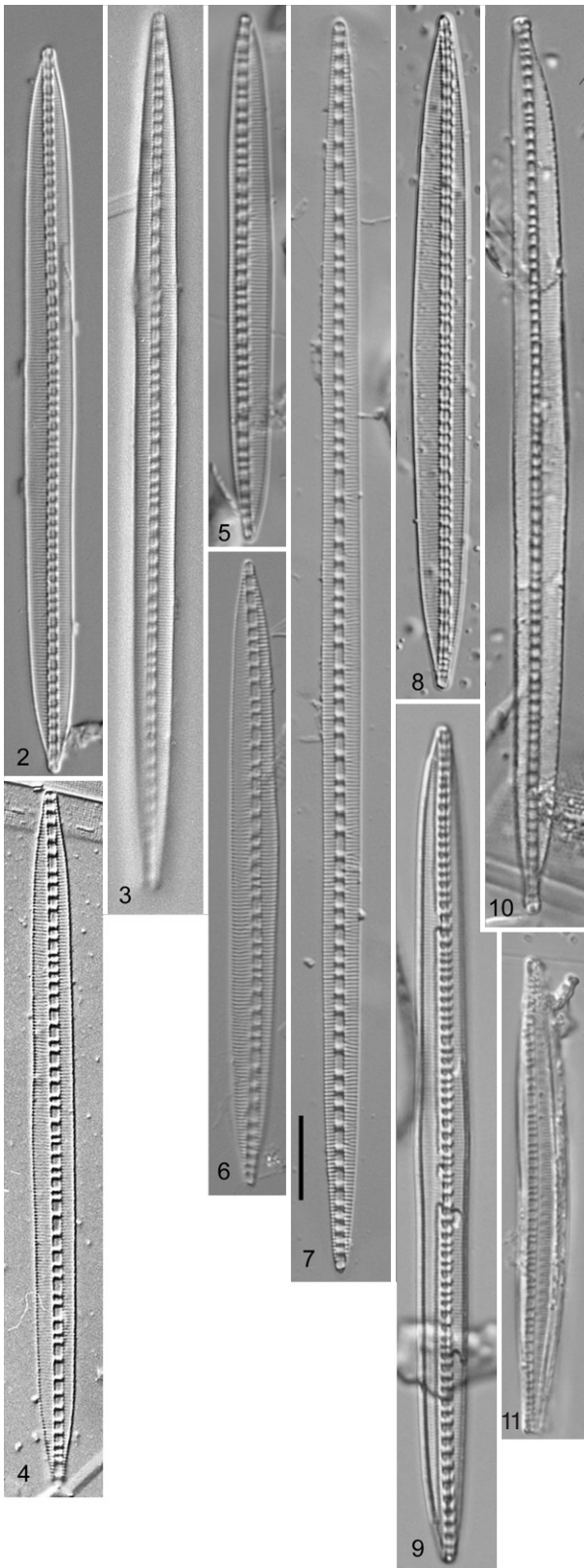
Since the herbarium material of the epitype has been air-dried on paper, the original shape of the colonies cannot be completely reconstructed, but even on the paper some colonies have remained slightly bent. The dead material does not allow us to say anything about the cells themselves although there are quite a number of intact colonies. Cell displacement in these (Fig. 12) indicates that they were actively moving at the time of sampling.

Individual valves are linear in outline with tapered ends (Fig. 2),  $65\text{--}170 \mu\text{m}$  long,  $6\text{--}7 \mu\text{m}$  wide, with 6–9 fibulae and 20–22 striae in  $10 \mu\text{m}$ . In LM the valve margin is highly refractive because of the deep valve mantle (revealed by EM) (Figs 12–14, 16).

With SEM the following features can be seen: the raphe fissure runs uninterrupted from pole to pole where it ends externally in a T-shape (Fig. 12); it is a tongue-in-groove structure (Figs 15–17, 35), with mirror symmetry in sibling valves. The raphe flange is on one side only, irregular (Fig. 14) or completely lacking (Fig. 35); it ends subapically (Fig. 12). Solid transapical ribs (interstriae) originate at right angles to the raphe ribs, are parallel and of a definite length, curving sharply into a deep valve mantle; they alternate with uniseriate striae (Figs 14–17). Deep pore channels (= canals, Schmid 2007) are covered by external vela (Figs 14, 17). Rudiments of marginal spines are sometimes visible (Fig. 14). In addition, and parallel to the raphe ribs, *Bacillaria* has an extra pair of axial ribs (= fibular ribs) where the fibulae are inserted (Figs 16, 17). There are four open girdle bands per epitheca (Fig. 13) with external vela; the first two (closest to the valve) are broader, and the third and fourth are narrow bands. This taxon expresses all the features typical for the construction type of bacillarioid brackish-freshwater taxa (Schmid, 2007).

#### Additional material of *B. paxillifera* var. *paxillifera*

**Rabenhorst's slide (Fig. 3).** This historical material from a creek influenced by saltwater influx was available only as a LM slide. It resembles the Copenhagen and Neusiedler See material, but has more pointed apices. EM-investigation was



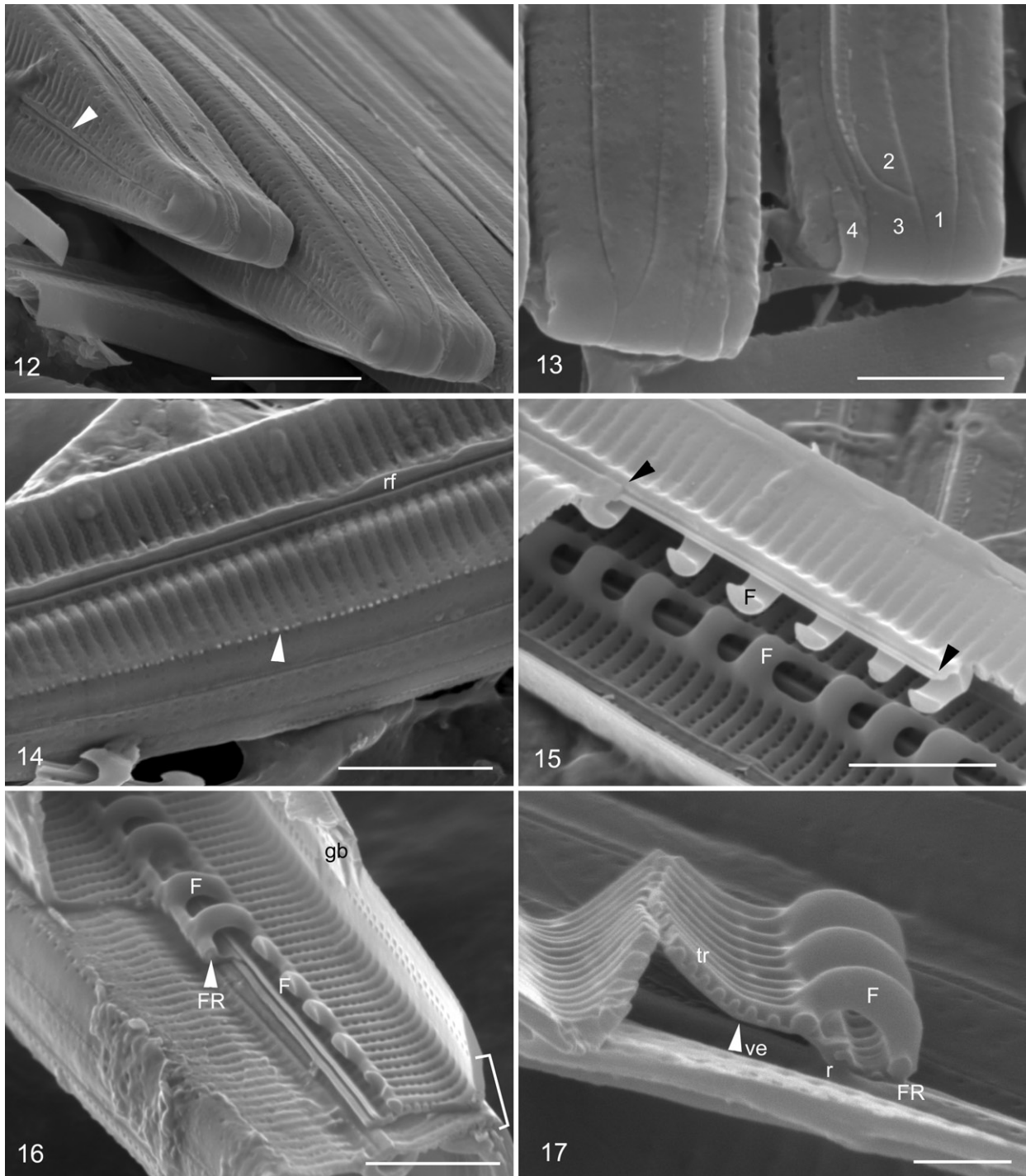
**Figs 2–11.** LM valve views of different *Bacillaria* and *Bacillaria*-like taxa. Figs 2–9. Note distinct circumferential rim visible in LM, varying positions of the raphe-system and branched transapical ribs on the broader valve side, typical of *Bacillaria* taxa. Fig. 2. *B. paxillifera* var. *paxillifera* from Copenhagen Sound, Denmark; epitype (C). Fig. 3. *B. paxillifera* var. *paxillifera* from Salzbach, Sondershausen, Germany (Rabenhorst exsiccatae in BRM). Fig. 4. *B. paxillifera* var. *paxillifera* from Neusiedler See, Austria (B). Fig. 5. *B. paxillifera* var. *czarneckii* from

not possible. We think it is *B. paxillifera* var. *paxillifera*, 100–120  $\mu\text{m}$  long, 6  $\mu\text{m}$  wide, with 5–7 fibulae and 20–25 striae in 10  $\mu\text{m}$ .

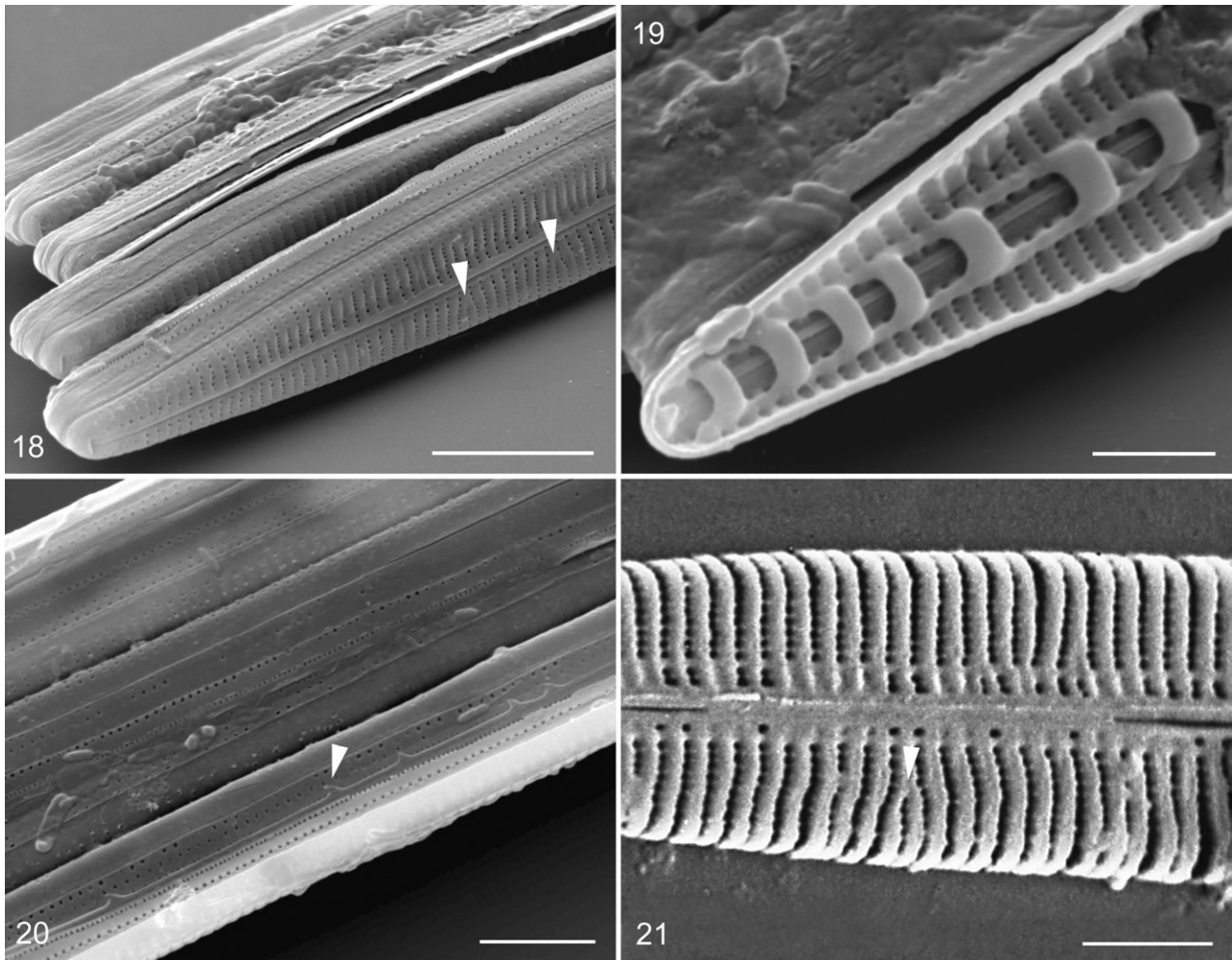
**Neusiedler See (Figs 4, 18–21, 38, 39).** In contrast to the historical samples, this material was studied alive and had been collected for many decades. The specimens resemble the Copenhagen material in outline and morphology, and the colonies are also slightly bent. However, cells are often shorter, 60–110  $\mu\text{m}$  long. Valves are 5–6  $\mu\text{m}$  wide with 6–9 fibulae and 20 striae in 10  $\mu\text{m}$ . During interphase the transapical axis is wider than the perivalvar axis. The structure of the girdle bands can be readily determined (Figs 20, 38, 39): The first band is wide and has two rows of roundish pores, the second and third bands are narrow and have only one row of pores, the second roundish, the third oval. In addition, the third band has a thick silicified ridge towards the interior. The fourth band is very narrow, has no pores but ‘thorns’ pointing from a central, plain zone towards each pole (Fig. 20). All bands are open bands with a ligula at their mid-point, an arrangement found in many pennate diatoms (e.g., Round *et al.*, 1990, fig. 5b), each opening supported by the ligula of the next band. Cells contain two elaborately folded chloroplasts, each extending from the nucleus to the poles (Schmid, 2007).

**ECOLOGY & HABITAT:** Epipelagic/periphytic; living in the reed-root-zone and surviving great fluctuations in salinity depending on wind-exposure. *Bacillaria paxillifera* is a possible immigrant from the marine littoral of the Baltic and North Seas (the Neusiedler See area is a sanctuary [World Wildlife Fund] for migratory birds). Conductivity-fluctuates between 1,800 and 10,000  $\mu\text{S cm}^{-1}$  (= ca 40–200 mOsmol.  $\text{kg}^{-1}$ ). *Bacillaria paxillifera* from this site seems to be pre-adapted to fluctuations in salinity and is most resistant to NaCl, contributing the major ions in the sea, but also tolerant to sulphates and sodium carbonate. It tolerates, and remains fully active, over a wide pH-range at low buffer strength (Schmid, 1973, 1995). The maximum tolerances towards mono-salt solutions and their mixtures, where *B. paxillifera* was still motile, are given in Table 2.

Mississippi River, Iowa, USA; holotype (B). Fig. 6. *B. paxillifera* var. *czarneckii* from River Weser estuary, Germany (B). Fig. 7. *B. kuseliae* from Avon River, York/Perth, West-Australia, holotype (B). Fig. 8. *B. urve-millerae* from Atlantic coast, The Gambia, West-Africa; holotype (B). Fig. 9. *B. paxillifera* var. *tumidula*; lectotype of *Nitzschia paradoxa* var. *tumidula*, East Indies (W). Fig. 10. *B. (paradoxa* var.?) *tropica*; Honduras; lectotype (W). Fig. 11. *N. paradoxa* var. *pacifica*; Samoa Island; lectotype (W). Scale bar: 10  $\mu\text{m}$ .



**Figs 12–17.** SEMs of *Bacillaria paxillifera* var. *paxillifera*; air-dried epitype material collected by Tyge Christensen in 1964 at a marine site close to Copenhagen, Denmark. Fig. 12. External view of intact colony viewed from the pole, T-shaped raphe endings; in the upper cell: subpolar ending of the asymmetric raphe flange (arrowhead); note the upper two cells in division, the hypotheca is complete (four girdle bands as in the epitheca); the position of the two uppermost cells relative to each other shows that the colony was motile prior to desiccation. Fig. 13. External view of the four girdle bands. Fig. 14. External valve view: asymmetrical (one side only), irregular flange (rf); rudiments of marginal spines (arrowhead); external vela; transapical ribs originating from the raphe ribs. Fig. 15. Fracture through a cell showing external and internal view simultaneously; upper valve broken along the fibulae (F) and raphe fissure (arrowheads); note tongue in groove; lower valve internal view: note solid transapical ribs separating uniseriate striae and the typical fibular-system (= ‘uniplanar ladder’ in LM, see Fig. 2). Fig. 16. Fracture through two cells of a colony; only the lower valve of the upper cell is visible; bracket: sibling valves: upper valve internal view, lower valve external view; note the deep valve mantle and girdle bands (gb); valve is broken along the raphe fissure and the fibular-system (F); note the fibular ribs (FR) and tongue in groove slit. Fig. 17. Fracture (pole view) through a mature valve, showing the characteristic *Bacillaria*: solid (see apical fracture, left) transapical ribs (tr) alternating with single rows of pores: raphe fissure (r) deep tongue in groove. Fracture through raphe and fibular ribs, and striae; vela exterior (ve); inverse funnel shaped pore channels (canals, Schmid, 2007); fibulae (F) connected to the fibular ribs (FR). Scale bars: 5  $\mu\text{m}$  (in Figs 12, 13), 4  $\mu\text{m}$  (Fig. 14), 3  $\mu\text{m}$  (Figs 15, 16), 1  $\mu\text{m}$  (Fig. 17).



**Figs 18–21.** SEMs of *Bacillaria paxillifera* var. *paxillifera* from the Neusiedler See, Austria. Fig. 18. External view of intact colony. Note two fault sites (branching transapical ribs) in the broader valve side (arrowheads). Fig. 19. Internal pole view. Fig. 20. External central region, girdle view. Note close attachment of the valves and deep mantle. Large perivalvar-axis indicates cell undergoing division; lower cell lost its sibling after sputter-coating, hence the bright new hypovalve, due to charging. Third and fourth bands of the mother epitheca (left), the fourth girdle band with thorn-like structures pointing toward the poles (arrowhead). Fig. 21. External view of developing valve; internal fibular ribs parallel to the raphe ribs visible because frets (cross-connections between transapical ribs) have just started to form; lower valve side with a ‘fault-site’ (arrowhead), i.e., forking of a transapical-rib; raphe slit partially coated with organic debris. Scale bars: 6  $\mu\text{m}$  (Fig. 18), 2  $\mu\text{m}$  (Figs 19, 21), 4  $\mu\text{m}$  (Fig. 20).

#### New Bacillaria taxa

##### *Bacillaria paxillifera* var. *czarnecki* R. Jahn et A.M. Schmid, var. nov. (Figs 5, 6, 22–26, 37)

**DIAGNOSIS:** Differt a *Bacillaria paxillifera* var. *paxillifera* duabus regulis raphis asymmetricis, fissura exterior raphis ad polos forma T non perspicue; spinae nullae in valvae superficie marginae. Valvae 58–86  $\mu\text{m}$  longae, 5–6  $\mu\text{m}$  latae, 6–8 fibulae in 10  $\mu\text{m}$ , 21 striae in 10  $\mu\text{m}$ .

**HOLOTYPE:** slide B 40 0040246 (Fig. 5).

**LOCUS TYPICUS:** Mississippi River, Peosta Channel, Dubuque (Dubuque County), Iowa USA, collected by D. Czarnecki.

**CULTURE STRAIN:** L1875, isolated by Dave Czarnecki on 18 December 2003, as ‘iso 3’.

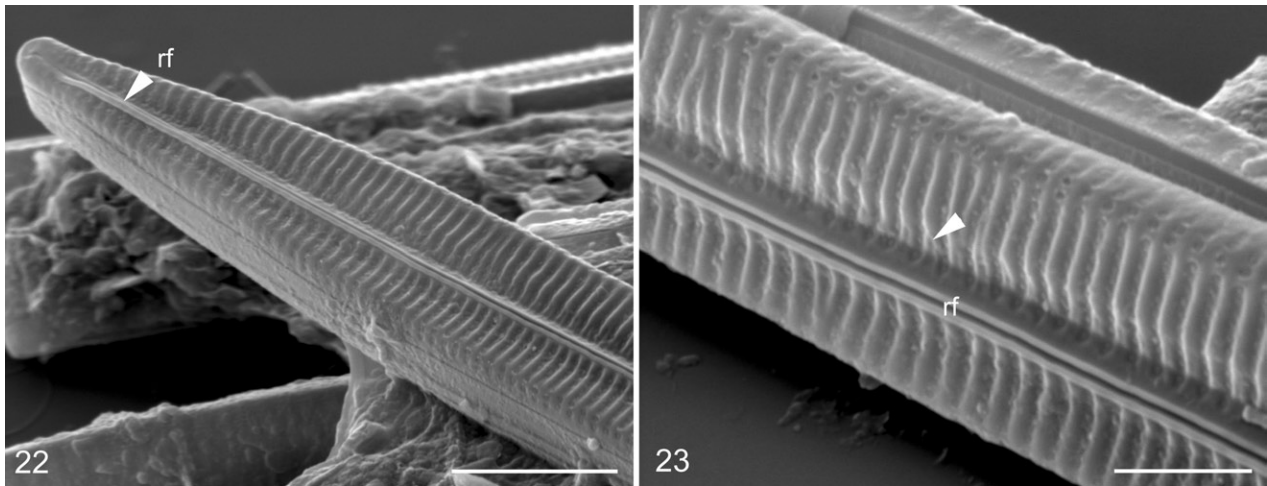
**HABITAT:** Epipellic, epi/periphytic. Conductivity rarely exceeding 1000  $\mu\text{S cm}^{-1}$ , between

400–2000  $\mu\text{S cm}^{-1}$ . In the natural sample (SEM-micrographs) it occurred together with *Pleurosira laevis* (Ehrenberg) Compère and *Achnanthes longipes* C.Agardh. Czarnecki writes of the type locality (pers. comm.), “about the only other diatom I encounter here that likes some salinity is *Nitzschia reversa*; but over the past 20 years, I’ve found *Bacillaria* here nearly every Fall thru early Winter.” Also found in the River Weser at Bremerhaven.

**ETYMOLOGY:** This taxon is dedicated to Dr Dave Czarnecki for his invaluable generosity in sending raw and cloned material from the Mississippi for our study and for his helpfulness with algal samples in general.

This variety differs from *B. paxillifera* var. *paxillifera* in having two, more or less





**Figs 22, 23.** SEMs of external valve views of *Bacillaria paxillifera* var. *czarneckii* from the Mississippi, Iowa, USA. Fig. 22. Two asymmetric flanges (rf) reaching almost to the poles; subpolar the flanges are more prominent, perhaps compensating for the decreasing perivalvar axis in this region; the polar fissure not T-shaped. Fig. 23. Externally, thickening ribs apparently composed of two, fusing, thinner ribs, as seen near the raphe (arrowhead). Due to sibling valve proximity during morphogenesis, a deep angular groove was caused by the two asymmetrical flanges (rf) of the other valve. Note deep valve mantle. Scale bars: 5  $\mu\text{m}$  (Fig. 22), 2  $\mu\text{m}$  (Fig. 23).

asymmetrical, raphe flanges that are rather inconspicuous over the major part of the valve but become a little more prominent closer to the poles. As in most *Bacillaria* taxa the flanges end before reaching the poles. At the poles the external raphe fissure is not clearly T-shaped and marginal spines were never found on the valve face. The longitudinal depression of the broader valve face (see Schmid, 2007) is more angular than in other members of this genus (see Figs 36, 22). Externally the transapical ribs often appeared as two parallel thickenings on top of the transapical ribs (Fig. 25). We interpret this topography as the result of premature valve release due to environmental elicitors, such as silica-limitation. In the natural samples (Figs 22, 23) valves were 58–86  $\mu\text{m}$  long, 5–6  $\mu\text{m}$  wide, with 6–8 fibulae and 21 striae in 10  $\mu\text{m}$ . Lengths and widths of valves in cultured material were more homogeneous: 62–66  $\mu\text{m}$  long and 5–5.5  $\mu\text{m}$  wide.

As in the Mississippi river, *B. paxillifera* var. *czarneckii* from the River Weser (Figs 6, 24, 26, 37) was accompanied by *P. laevis* and *A. longipes*. Conductivity must be periodically more than 10,000  $\mu\text{S cm}^{-1}$  (= 200 mOsmol.  $\text{kg}^{-1}$ ). The shape of its colony was slightly bent with many epiphytes, e.g. species of *Amphora* Kützing. The two raphe flanges are again very simple,  $\pm$  asymmetrical (see also Kapinga & Gordon, 1992, fig. 5), reduced at the poles. The transapical ribs are solid and the simple pores are as deep as the ribs. There are no marginal spines. Two plastids present per cell.

***Bacillaria kuseliae* A.M. Schmid et R. Jahn, spec. nov. (Figs 7, 27–30)**

**DIAGNOSIS:** *Differt a Bacillaria paxillifera* var. *paxillifera* et *B. paxillifera* var. *czarneckii* *valva tenui maxime polisque rotundatis, et colonia uniplana quasi. Epi/periphytica cellulaque affixa una colonia. Plasti duo cellula lobos proprios affixos ad polos valvae unicos (ad fibulas probabiliter). Regula raphis asymmetrica una similis valvae Bacillaria paxillifera* var. *paxillifera*. *Depressio longitudinalis delineatus acute usque at 8 costas furcatis transapicales non nisi lata parte valvae. Valva maxima 160  $\mu\text{m}$  longa, 5–5.5  $\mu\text{m}$  latae, 6–7 fibulae in 10  $\mu\text{m}$ , 22–24 striae in 10  $\mu\text{m}$ .*

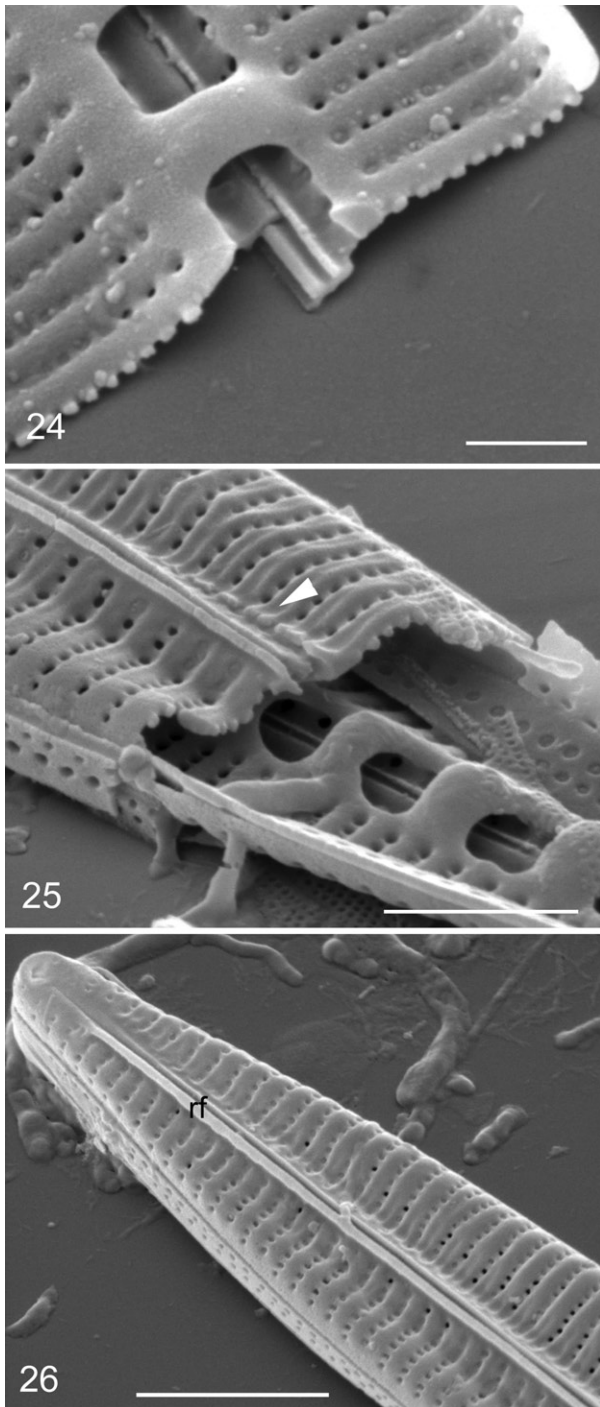
**HOLOTYPE:** slide B 40 0040248 (Fig. 7).

**LOCUS TYPICUS:** Avon River, York/Perth, West-Australia, collected by E. Kusel, 1998.

**HABITAT:** Epi/periphytic. In the natural population it occurred together with *Pleurosigma amara* Stidolph at a conductivity of ca 10,000  $\mu\text{S cm}^{-1}$ . The material was cultured at the same concentration, i.e., ca 200 mOsmol.  $\text{kg}^{-1}$ .

**ETYMOLOGY:** This diatom is named in honour of Prof Dr Elsa-Lore Kusel-Fetzmann, PhD supervisor of AMS, to acknowledge her continuous encouragement as well as her countless gifts of algal samples.

This taxon differs in outline from *B. paxillifera* var. *paxillifera* and *B. paxillifera* var. *czarneckii* as it is extremely long and slender with rounded poles. The colony is only slightly bent, almost uniplanar. It lives epi/periphytically and has, like all epiphytic colonies, one anchor cell per colony, which divides out of phase with the other cells. It has two plastids with characteristic lobes, each elaborately folded backwards, and is the only species of this group in which the plastids are anchored at the poles



**Figs 24–26.** SEMs of *Bacillaria paxillifera* var. *czarneckii* from the Weser estuary, Germany. Fig. 24. Internal view: raphe tongue-in-groove. Fig. 25. External view of an immature valve: externally ribs seem composed of two thinner ribs; arrowhead points to a fracture of the ribs along the raphe rib. Angular depression on the lower valve side; vela not yet formed. Fig. 26. External view including the pole; two asymmetrical raphe flanges (rf) reaching almost to the end; the external polar fissure not T-shaped. Scale bars: 1  $\mu\text{m}$  (Fig. 24), 2  $\mu\text{m}$  (Fig. 25), 3  $\mu\text{m}$  (Fig. 26).

(probably at the fibulae) during interphase. The pyrenoids point in one direction in each cell, and thus in the entire colony (see Schmid, 2007). Like *B. paxillifera* var. *paxillifera* it has one asymmetric

irregular raphe flange. There is a sharply delineated, longitudinal depression, and up to eight (sometimes more) irregularities in the transapical ribs on the broader half of the valve (Schmid, 2007). The pores are arranged in uniseriate rows with external vela. Valves are up to 160  $\mu\text{m}$  long, 5–5.5  $\mu\text{m}$  wide, with 6–7 fibulae and 22–24 striae in 10  $\mu\text{m}$ .

***Bacillaria urve-millerae* A.M. Schmid et R. Jahn, spec. nov. (Figs 8, 31–34, 36)**

**DIAGNOSIS:** Differt a *Bacillaria paxillifera* var. *paxillifera* *duabus regulis raphis prominentibus valvae* *Bacillaria paxillifera* var. *czarneckii*. *Valvae lanceolatae leviter latis valvas* *Bacillaria paxillifera* var. *paxillifera*. *Costas furcatas transapicales, in parte lata valvae, atque per Bacillaria generem typica*. *Plasti quatuor cellula*. *Vela exterior ut in taxis geni hujus sed attenuatis distale propriis canalium poriorum*. *Diatotepum crassum maxime*. *Valvae 65–130  $\mu\text{m}$  longae, 6–7  $\mu\text{m}$  latae, 8–9 fibulae in 10  $\mu\text{m}$ , 24 striae in 10  $\mu\text{m}$ .*

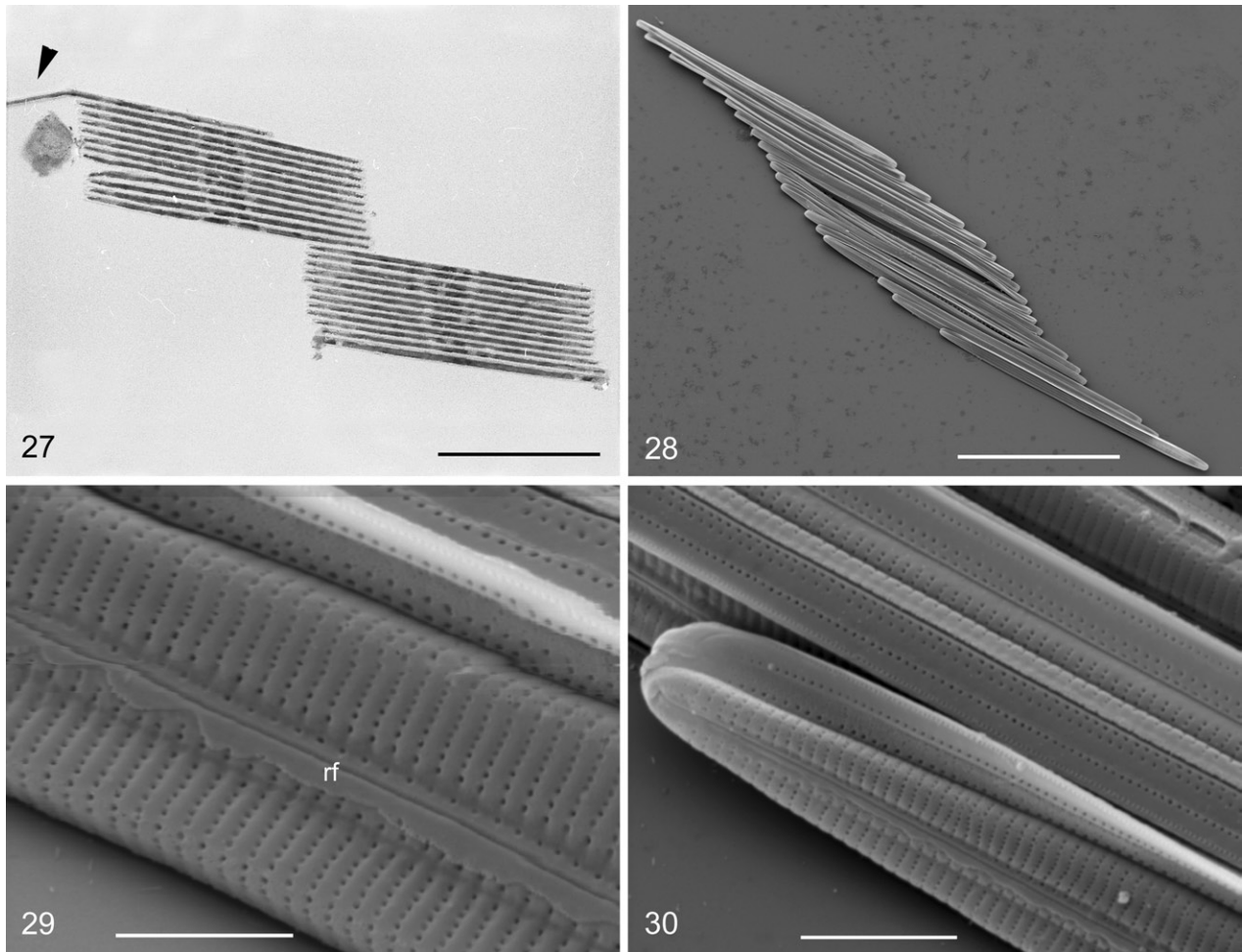
**HOLOTYPE:** slide B 40 0040249 (Fig. 8).

**LOCUS TYPICUS:** Bijilo Beach, Southwest of Serecunda, The Gambia, Atlantic coast, West Africa. Collected by A.M. Schmid on 13 December 1997.

**HABITAT:** Epipellic, epipsammic. The natural population is from the intertidal mangrove- and reed-root-zone with fresh/wastewater inflow from the village probably causing great fluctuations in salinity. *Melosira nummuloides* is also present attached to the *Bacillaria* colonies.

**ETYMOLOGY:** This diatom is named in honour of Prof Dr Urve Miller, Stockholm University. Without her generosity enabling AMS, as a young scientist, to delve into the three-dimensional SEM world of diatoms, the latter would never have become a diatomist: Note: SEM in Fig. 21 was taken on Prof Urve Miller's SEM on 1 December 1972.

Differs from *B. paxillifera* var. *paxillifera* in having two raphe flanges which are more pronounced than in *B. paxillifera* var. *czarneckii*, with one flange thicker than the other (Figs 31, 33, 34, see also Schmid, 2007, fig. 3). Valves have protracted apices, are lanceolate, and wider than *B. paxillifera* var. *paxillifera*. The transapical ribs have irregularities on the broader side of the valve, a typical feature of the genus *Bacillaria*, facilitating discrimination of this species from lanceolate marine forms, even in LM. This taxon has four plastids per cell. Vela are external and the pores are characteristically narrowed towards the valve exterior, as is visible in cross-sections (Fig. 36). In this taxon, the diatotepum (*sensu* von Stosch, 1981) is extremely thick, almost as thick as in the marine taxa. The shape of the colony is only



**Figs 27–30.** *Bacillaria kuseliae*; original material from Avon River, York/Perth, West-Australia. Fig. 27. LM; colony of 24 cells. Note the upper anchor cell (arrow). Figs 28–30. SEMs, external views. Fig. 28. Colony of 18 cells. Fig. 29. Valve centre; one irregular raphe flange (rf). Note the dark lines parallel to the raphe indicating the position of the internal fibular ribs. Fig. 30. Valve pole; irregular raphe flange becoming smaller and ending subpolarly; note the relatively rounded apices and deep valve mantles. Scale bars: 8  $\mu$ m (Figs 27, 28), 3  $\mu$ m (Fig. 29), 5  $\mu$ m (Fig. 30).

slightly bent, like *B. kuseliae*. No marginal spines are present. The valves are 65–130  $\mu$ m long, 6–7  $\mu$ m wide, and have 8–9 fibulae and 24 striae in 10  $\mu$ m.

#### *Grunow's three 'Bacillaria' taxa*

#### *Bacillaria (paradoxa var.?) tropica* Grunow, *Hedwigia* 1867; 6: 19.

SYNONYM: *B. paradoxa* var. *tropica* (Grunow) DeToni, *Sylloge Algarum*: 494. 1892.

LECTOTYPE (designated here): slide 839 R at W (see valve in Fig. 10).

LOCUS TYPICUS: Honduras, on *Sargassum*. Leg. Lindig.

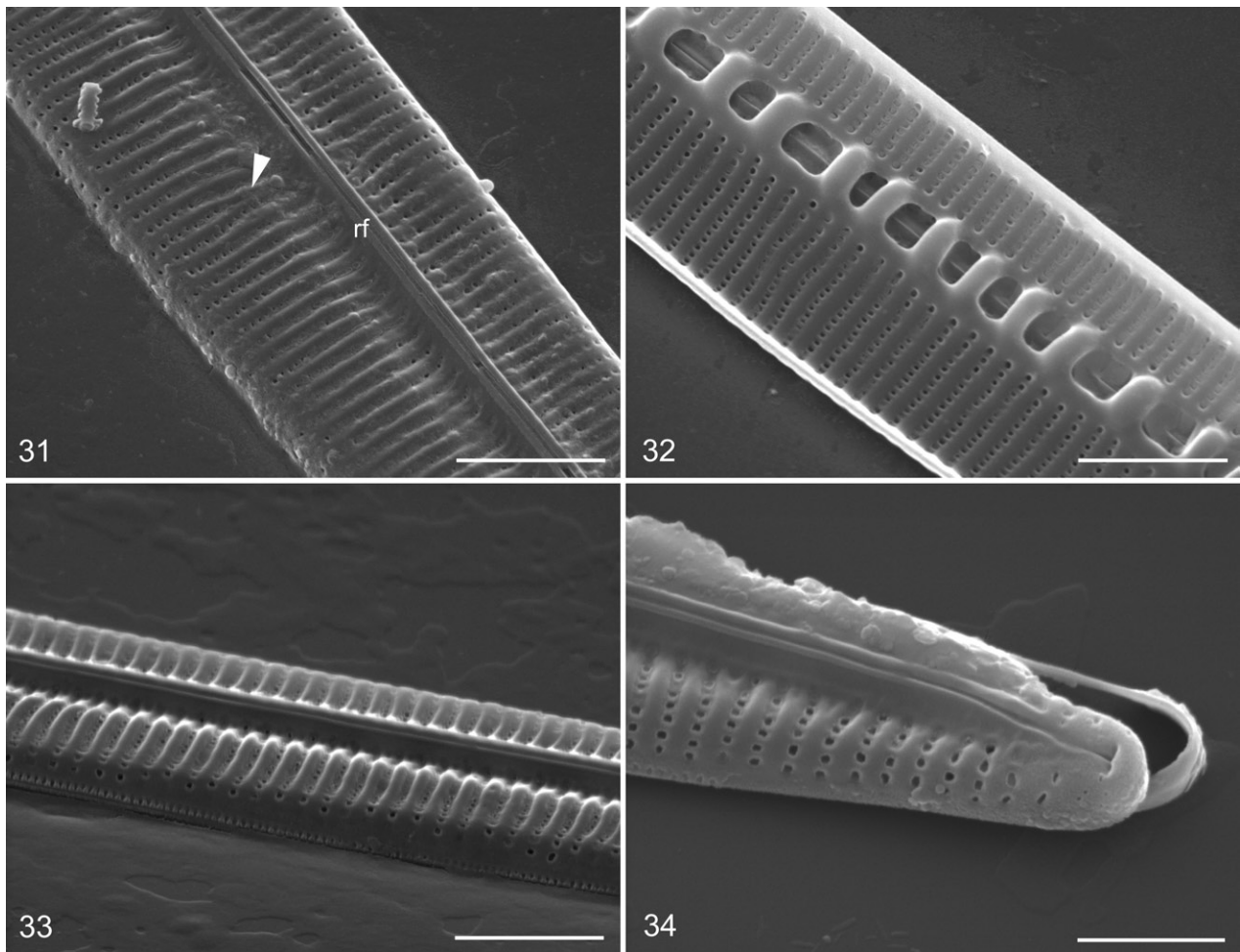
HABITAT: Brackish-marine based on the presence of *Grammatophora* Ehrenberg, *Triceratum tessela* (A.I. Krotov) N.I. Strelnikova and *Asterionellopsis* Round in this sample.

Grunow (1867) described this taxon as very similar to *B. paradoxa* but with slightly more produced apices and 24 striae in 10  $\mu$ m. Grunow (in Cleve & Grunow 1880) stated that it does

not only occur in Honduras but everywhere in Europe. Based on the two drawings in the Grunow Collection, there were two different valve outlines. One is produced, capitate and very long: 110–155  $\mu$ m long, 6  $\mu$ m wide, with 9 fibulae and 28 striae in 1  $\mu$ m. The other is shorter, slimmer, with fewer striae in 1  $\mu$ m: 92  $\mu$ m long, 5–5.5  $\mu$ m wide, 7–8 fibulae and 18 striae in 10  $\mu$ m. We chose the first, longer example with denser striae, as the lectotype.

This diatom has the fibular system of *Bacillaria sensu lato* but the taxon cannot be unequivocally identified since colony shape and EM-details are lacking. In addition, no branched transapical ribs were seen, which would be typical for *Bacillaria sensu stricto*. On the other hand, the valve outline is refractive in LM, indicating the deep valve mantle typical of *Bacillaria sensu stricto*.

#### *Bacillaria paxillifer[a] var. tumidula* (Grunow) Witkowski, Lange-Bertalot et Metzeltin, *Iconogr. Diatomol.* 2000; 7: 357.



**Figs 31–34.** SEMs of *Bacillaria urve-millerae* original material from The Gambia, West Africa. Fig. 31. External view of valve centre; eccentrically located raphe system, with two rather symmetric raphe flanges (rf); note the forked transapical rib (arrowhead) on the broader valve side. Fig. 32. Internal view of valve centre; note the displaced, typical fibular system and raphe. Fig. 33. External view of valve centre showing valve topography. Fig. 34. External valve poles; note the T-shaped raphe endings and the reduction of the raphe flanges. Scale bars: 3  $\mu\text{m}$  (Figs 31–33), 2  $\mu\text{m}$  (Fig. 34).

**BASIONYM:** *Nitzschia paradoxa* var. *tumidula* Grunow in Cleve & Grunow, *Kongl. Svenska Vetensks. Akad. Handl.*, ser. 4, 17(2): 86. 1880.

**SYNONYM:** *B. paradoxa* var. *tumidula* (Grunow) DeToni, *Sylloge Algarum*: 494. 1892.

**LECTOTYPE** (designated here): Cleve & Möller, *Diat. 78*, *Nitzschia Kurzii* Rabh., East Indies at W (Fig. 9).

**LOCUS TYPICUS:** Bengal [Bangladesh], East Indies.

**HABITAT:** Presumed freshwater/brackish since, in addition to the dominant *Nitzschia* species, *Surirella* Ehrenberg, *Cymatopleura* W. Smith, *Hantzschia* Grunow, *Rhopalodia* O. Müller and *Cymbella* C. Agardh are present.

Grunow (in Cleve & Grunow, 1880) wrote that it was similar to the previous taxon, i.e. *B. (paradoxa* var.?) *tropica*, with valves that were slightly swollen in the middle with 24–25 striae in 10  $\mu\text{m}$ . *Bacillaria paxillifera* var. *tumidula* was supposed to occur intermingled with *B. paxillifera* but we did not find any specimens of the latter on this slide. Valves (ten specimens) were 95–108  $\mu\text{m}$

long, 5.5–6  $\mu\text{m}$  wide, with 7–8 fibulae and 24–28 striae in 10  $\mu\text{m}$ .

This diatom has a fibular system typical of *Bacillaria sensu lato*. In addition, it has branched transapical ribs on the broader valve side and a refractive valve outline, typical for *Bacillaria sensu stricto*. Grunow's taxon (but not the one shown by Witkowski *et al.*, 2000) probably belongs in *Bacillaria*, but whether it is a discrete species or a variety of *B. paxillifera* cannot be established since the shape of the colony and EM-details are lacking.

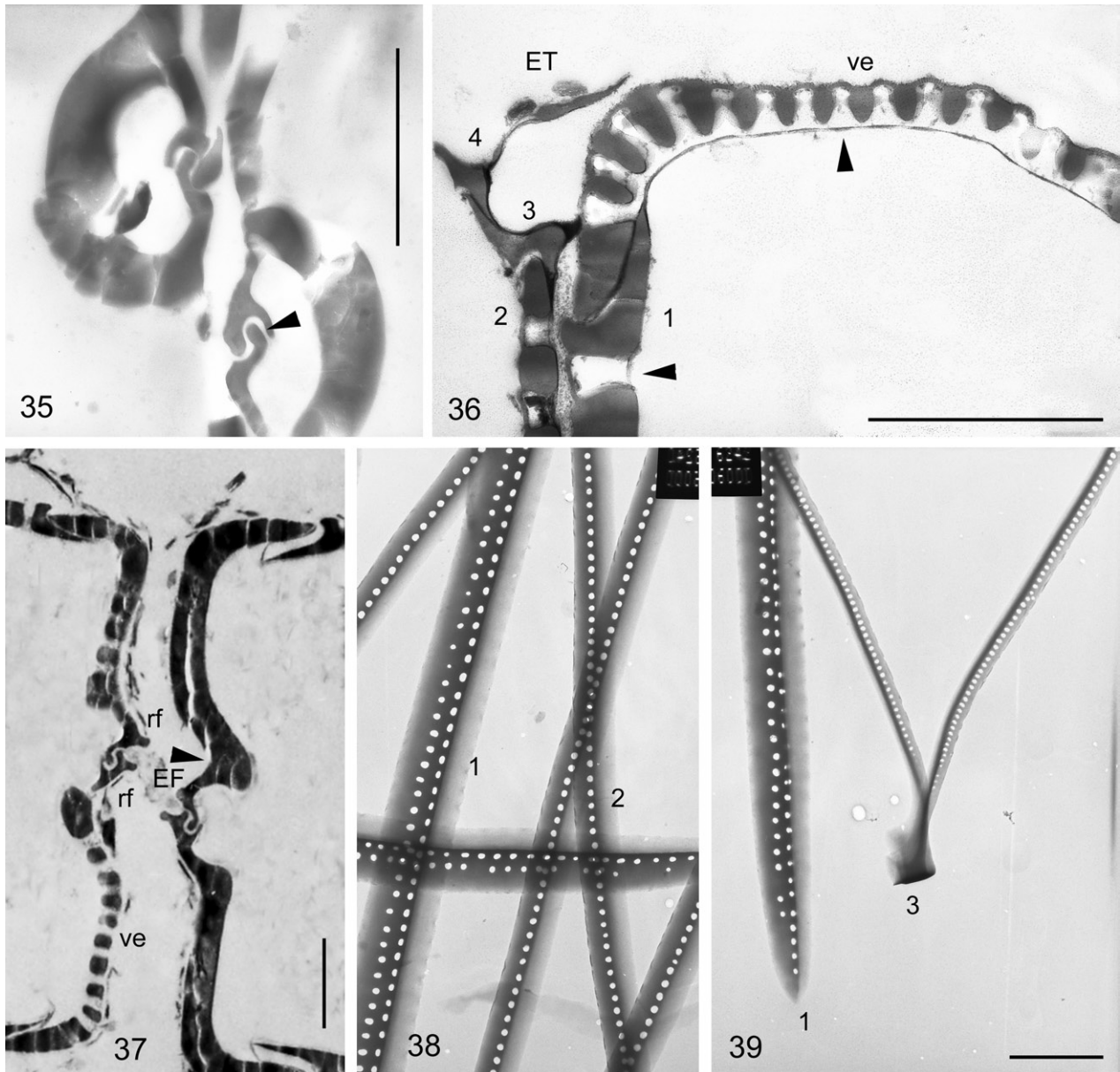
***Nitzschia paradoxa* var. *pacifica* Grunow in Cleve & Grunow, *Kongl. Svenska Vetensks. Acad. Handl.*, ser. 4, 1880; 17(2): 86.**

**SYNONYM:** *B. paradoxa* var. *pacifica* (Grunow) DeToni, *Sylloge Algarum*: 494. 1892.

**LECTOTYPE** (designated here): 1512 at W (Fig. 11).

**LOCUS TYPICUS:** Samoa Island.

**HABITAT:** Upola, on algae in sandy soft water. Since the slide also contains marine



**Figs 35–39.** TEMs of different *Bacillaria* taxa. Fig. 35. *Bacillaria paxillifera* var. *paxillifera* from original epitype material, Copenhagen. Cross-section of two sibling valves through the raphe and fibulae showing typical tongue-in-groove fissure (arrowhead). Fractures in the silica are sectioning artefacts (the herbarium material was very difficult to embed). Left hand valve: fibula-bow and (striae lost during sectioning). Fig. 36. *B. urve-millerae* from original material, The Gambia; transapical-section (pole view) through stria (between transapical ribs), showing the deep mantle and some girdle bands (raphe system not visible); note the uniseriate pores, constricted towards the exterior, and covered with external vela (ve), ornamented frets; internal dark line = diatotepum (arrowhead). First hypothecal band (1), internally attached to the valve, with pore canal, external velum and internal diatotepum (arrow). Epithecal girdle bands (ET) from top to bottom: the pre-stressed fourth band with external ridge to the left (4); the third band with internal siliceous (grey) and additional organic (black) ridge to the right (3); concave side of the third band like a hinge on the abvalvar edge of the second girdle band; the latter with pores, external vela and internal diatotepum (2). Fig. 37. *B. paxillifera* var. *czarneckii* from Weser estuary. Cross section of two sibling valves showing the two small flanges, one a little bigger (rf) than the other, which function as gliding rails for the elastic fibrils (EF) secreted for adhesion. The angular groove (arrow) created during morphogenesis: one valve shows the solid transapical rib, the other the uniseriate pores covered with external vela (ve). The tongue in groove fissures as mirror images in sibling valves. Figs 38, 39. Girdle bands of *B. paxillifera* var. *paxillifera* from the Neusiedler See. First band (1) with two rows of roundish pores, second band (2) with a single row of round pores, third band (3) with one row of elliptical pores and a thick silicified ridge on one side (reference line for cell division), and a ligula at one pole where the second bands have tapered ends (see Fig.13); undulated *pars interior*; lacking pores in the fourth girdle band but bearing thorn-like lateral extensions (see Fig. 20). Scale bars: 1  $\mu\text{m}$  (Figs 35–37), 2  $\mu\text{m}$  (Figs 38, 39).

**Table 2.** Motile *B. paxillifera* colonies and maximum values of mono-salt solutions and their mixtures tolerated (data from Schmid, 1973, 1995)

Mono-salt/salt mix	Primary = ion stress	Secondary = water stress
NaCl:	up to 500 mval	i.e. ca 1000 mOsmol. kg <sup>-1</sup>
Mg <sup>2+</sup> Cl <sup>-</sup> SO <sub>4</sub> <sup>2-</sup> :	up to 150 mval	i.e. ca 200 mOsmol. kg <sup>-1</sup>
Na <sup>+</sup> Cl <sup>-</sup> SO <sub>4</sub> <sup>2-</sup> :	up to 400 mval	i.e. ca 800 mOsmol. kg <sup>-1</sup>
SO <sub>4</sub> <sup>2-</sup> Na <sup>+</sup> Mg <sup>2+</sup> :	up to 600 mval	i.e. ca 550 mOsmol. kg <sup>-1</sup>
Cl <sup>-</sup> Na <sup>+</sup> Mg <sup>2+</sup> :	up to 500 mval	i.e. ca 1000 mOsmol. kg <sup>-1</sup>
MgSO <sub>4</sub> :	up to 800 mval	i.e. ca 200 mOsmol. kg <sup>-1</sup>
Mg Cl <sub>2</sub> :	up to 200 mval	i.e. ca 150 mOsmol. kg <sup>-1</sup>
Na <sub>2</sub> SO <sub>4</sub> :	up to 200 mval	i.e. ca 300 mOsmol. kg <sup>-1</sup>
Na <sub>2</sub> CO <sub>3</sub> :	up to 200 mval	i.e. ca 300 mOsmol. kg <sup>-1</sup>

Notes: The total salt concentration of the Mediterranean Sea is approximately 1,100 mOsmol. kg<sup>-1</sup>. Although a brackish/fresh-water taxon, *B. paxillifera* from the Neusiedler See can tolerate the concentration of the ocean water when the major ions are sodium and chloride. No other diatom living together with *B. paxillifera* in the same microhabitat was able to tolerate such a high osmotic stress.

*Mastogloia* (Thwaites) W. Smith species, it is presumed to be a brackish-marine habitat.

Grunow (in Cleve & Grunow, 1880) wrote that the valves are short with long-drawn-out apices. Valves are 60–70 µm long, 5–6 µm wide, with 8 fibulae und 24 striae in 10 µm.

This diatom has the fibular system of *Bacillaria sensu lato*, but its identity cannot be determined since colony shape and EM details are lacking. No branched ribs, typical for *Bacillaria sensu stricto*, were seen.

## Discussion

### History of *Bacillaria* and its names

Since the name *Bacillaria* had been applied to many different taxa, which are now placed in completely different genera, there are numerous literature references. After its establishment in 1788 (by Gmelin), almost all rod-like diatoms were called ‘*Bacillaria*’ (i.e. *B. sigmoidea* Nitzsch ≡ *Nitzschia sigmoidea* (Nitzsch) W. Smith, *B. ulna* Nitzsch ≡ *Ulnaria ulna* (Nitzsch) Compère; etc.), in a similar way to the use of the name ‘*Navicula*’, a ‘Sammelbecken’ for ship-like diatoms.

As was recently documented for the genus *Ceratoneis* Ehrenberg (Jahn & Kusber, 2005), with the establishment of the genus *Nitzschia* by Hassall (1845) and of other genera incorporating rod-like and/or moving diatoms, a major nomenclatural reshuffle took place in the systematics of the diatoms in the mid-19th century, (Kützing, 1844; Smith, 1853, 1856; Grunow, 1862; Rabenhorst, 1864; Cleve & Grunow, 1880).

In 1862 and 1867 Grunow described two *Bacillaria* spp., *B. frauenfeldii* (1862: 584,

pl. 12, fig. 1), recently recombined as *Nitzschia amphibia* var. *frauenfeldii* (Grunow) Lange-Bertalot, and *B. (paradoxa* var.?) *tropica*. We checked Grunow’s slide of the latter taxon and found a fibular-system typical for *Bacillaria sensu lato* (Fig. 11). At that time Grunow (1867) was uncertain about the rank of this entity, whereas in 1877 he referred to it as *B. paradoxa* var. *tropica*. Later (Cleve & Grunow, 1880), he placed it in *Nitzschia* subgenus *Bacillaria*, and described two more varieties of *Nitzschia paradoxa* (Gmelin) Grunow: *N. paradoxa* var. *tumidula* and *N. paradoxa* var. *pacifica* (Figs 9, 11). Due to the lack of cytoplasmic and EM information their identity remains uncertain, but we think that Grunow’s var. *tumidula* might belong to *Bacillaria sensu stricto*.

In the 20th century, two more infraspecific taxa, *N. (Bacillaria) paradoxa* var. *paucistriata* Frenguelli (1923) and *N. paradoxa* var. *perpusilla* Playfair (see data from INA by Silva, 1997), were described, but the original material needs to be checked to be sure of their identity. Whereas Hustedt (1930) used the name *B. paradoxa*, also reinstating Grunow’s var. *tumidula*, Cleve-Euler (1952) continued to use *N. paradoxa*. Finally, Hendey (1951) was the first to combine Gmelin’s genus *Bacillaria* with the correct epithet, *paxillifer*, based on O.F. Müller’s *Vibrio paxillifer*, not on Gmelin’s later *B. paradoxa*; (see Table 3 for a summary of the data and nomenclatural history of *B. paxillifera*).

The latest reinstatement of names attached to *Bacillaria* was carried out by Witkowski *et al.* (2000): *B. paxillifer* var. *paxillifer* and var. *tumidula* (Grunow) Witkowski, Lange-Bertalot & Metzeltin as well as *B. socialis* (Gregory) Ralfs. However, var. *tumidula sensu* Witkowski *et al.* (2000) is unequivocally not Grunow’s taxon (compare the lectotype, Fig. 9, with Witkowski *et al.*, 2000, pl. 196, fig. 8); it must be placed in a different genus. The same holds true for the third taxon *B. socialis* described as *Nitzschia socialis* Gregory (1857).

### Habitat, ecology and biogeography

*B. paxillifera* was first found on European shores (Müller, 1782, 1786; Ehrenberg, 1838; Smith, 1856) and in inland salt-influenced creeks (Rabenhorst, 1854). In the second half of the 19th century this species and its varieties were reported from tropical America and Asia (Grunow, 1867; Cleve & Grunow, 1880; Table 3), and in the first half of the 20<sup>th</sup> century it was reported from the Southern Hemisphere (Frenguelli, 1923; Playfair in Silva, 1997; Cholnoky, 1968; Giffen, 1963). According to the bibliography on *B. paradoxa*

**Table 3.** Data and names of *B. paxillifera* taxa from main historical references (as published)

Name as published (with author if new name or new combination)	Reference	Length	Breadth	Striae	Fibulae	Ecology/habitat/biogeography (translated)
<i>Vibrio paxillifer</i> O.F. Müller	Müller (1786), p. 54, pl. VII, Figs 3–7.					Lives on the dark green, broad seaweed, <i>Ulva latissima</i> , at the seashore, Copenhagen Sound
<i>Bacillaria paradoxa</i> Gmelin	Gmelin (1788), p. 3903.					
<i>Bacillaria paradoxa</i>	Ehrenberg (1838), p. 196, pl. XV, Fig. 1.	15x longer than wide			9 in entire valve	At Wismar, Germany, and Göteborg, Sweden, in marine waters between <i>Ceramium</i> and <i>Callithamnium</i>
<i>Bacillaria paradoxa</i>	Kützing (1844), p. 63, pl. 21, Fig. XVIII	1/20''			1/100''	In the Baltic between other algae
<i>Bacillaria paradoxa</i>	Smith (1856), p. 10, pl. 32 Fig. 279.	0025–0042''				Brackish water, a native of ditches near the sea or in estuaries subject to marine influxes; not uncommon
<i>Nitzschia paxillifer</i> (O.F. Müller) Heiberg	Heiberg (1863), p. 113.					Brackish or marine waters near the coast. He found it at the same site as O.F. Müller
<i>Bacillaria paradoxa</i>	Rabenhorst (1864), p. 165.	1/45–1/20''' = 0.0019–0.0045''				In brackish waters and in salty lakes and rivers in boreal Europe, not in salt water from the Mediterranean and not seen in Eastern Europe
<i>Bacillaria (paradoxa</i> var.?) <i>tropica</i> Grunow	Grunow (1867), p. 19.	0.004–0.0063''	0.0003''	70 in 0.001''	18–22 in 0.001''	Honduras and Europe
<i>Bacillaria paradoxa</i> var. <i>tropica</i>	Grunow (1877), Fig. 11.	0.10–0.16 mm	0.0065 mm	24–25 in 0.01 mm	6–7 in 0.01 mm	Common in the Honduras gatherings, Bengal, Polynesian Islands
Subgenus <i>Bacillaria</i> : <i>Nitzschia paradoxa</i> (O.F. Müller) Grunow	Cleve & Grunow (1880), pp. 85–86.			21.5–22.5 in 10 µm	6–8 in 10 µm	Everywhere
Subgenus <i>Bacillaria</i> : <i>Nitzschia paradoxa</i> var. <i>tumidula</i> Grunow	Cleve & Grunow (1880), pp. 85–86.	Swollen center		24–25 in 10 µm		Together with the nominate variety in Bangladesh
Subgenus <i>Bacillaria</i> : <i>Nitzschia paradoxa</i> var. <i>pacifica</i> Grunow	Cleve & Grunow (1880), pp. 85–86.	60–70 µm	5–6 µm	24 in 10 µm	8 in 10 µm	Samoa and Bangladesh
Subgenus <i>Bacillaria</i> : <i>Nitzschia paradoxa</i>	van Heurck (1880–1881), pl. 61, Fig. 6. (1896), p. 392, Fig. 518.	60 µm		20.5–22.5 in 10 µm	6–8 in 10 µm	Brackish water ... almost everywhere. Sometimes found in water containing only a trace of salt
Subgenus <i>Bacillaria</i> : <i>Nitzschia paradoxa</i> var. <i>major</i> Grunow	van Heurck (1880–1881), pl. 61, Fig. 7. (1896), p. 392, Fig. 519.			20.5 in 10 µm		
Subgenus <i>Bacillaria</i> : <i>Nitzschia paradoxa</i>	Peragallo & Peragallo (1897–1908), pp. 278–282, pl. 72, Fig. 16.	60–120 µm		21.5–22.5 in 10 µm	6–8 in 10 µm	Wide occurrence in brackish and light salty waters

Subgenus <i>Bacillaria</i> : <i>Nitzschia paradoxoxa</i> var. <i>tropica</i>	Peragallo & Peragallo (1897–1908), pp. 272–282, pl. 72, Fig. 17.	24 in 10 µm				DeToni gives Grunow's data
<i>Bacillaria paradoxoxa</i> var. <i>tropica</i>	DeToni (1892), p. 494.					DeToni gives Grunow's data
<i>Bacillaria paradoxoxa</i> var. <i>tumidula</i> (Grunow)	DeToni (1892), p. 494.					DeToni gives Grunow's data
<i>Bacillaria paradoxoxa</i> var. <i>pacifica</i> (Grunow)	DeToni (1892), p. 494.					DeToni gives Grunow's data
<i>Bacillaria paradoxoxa</i> var. <i>pacifica</i> (Grunow)	DeToni (1892), p. 494.					DeToni gives Grunow's data
<i>Nitzschia</i> ( <i>Bacillaria</i> ) <i>paradoxoxa</i> var. <i>paucistriata</i> Frenguelli	Frenguelli (1923), p. 93, pl. 8, fig. 21.	15 in 10 µm	5–5.5 in 10 µm	8 µm	110–125 µm	Rio Primero, Córdoba. Not marine
<i>Bacillaria paradoxoxa</i>	Hustedt (1930), p. 396, fig. 755.	20–25 in 10 µm	6–8 in 10 µm	4–8 µm	60–150 µm	Euryhaline species in salty waters of different concentrations, sometimes also in fresh water Together with the nominate variety at Bremen
<i>Bacillaria paradoxoxa</i> var. <i>tumidula</i>	Hustedt (1930), p. 397, fig. 756.					
<i>Bacillaria paradoxoxa</i> var. <i>tumidula</i>	Hustedt (1930), p. 397, fig. 756.					
Subgenus <i>Bacillaria</i> : <i>Nitzschia paradoxoxa</i>	Cleve-Euler (1952), p. 69, fig. 1457a–d.	21.5–22.5 in 10 µm	6–8 in 10 µm	4–8 µm	60–150 µm	Brackish to almost freshwater, not seldom found in the Baltic Sea; also fossil
<i>Bacillaria paxillifer</i> (O.F. Müller) Hendey 1951	Hendey (1964), p. 274, pl. 21, fig. 5.	7–9 in 10 µm	7–9 in 10 µm	4–8 µm	70–100 µm	Marine and brackish, strongly euryhaline. Common on all coasts bordering the North Sea and English Channel. Sometimes in the plankton
<i>Bacillaria paradoxoxa</i>	Drebes (1974).	70–250 µm				Littoral in marine and brackish waters; in turbulences also in the plankton
<i>Bacillaria paradoxoxa</i>	Werff & Huls (1976), p. 136.	20–25 in 10 µm	6–8 in 10 µm	4–8 µm	60–150 µm	Euryhaline, eutraphentic in brackish, fresh and marine waters
<i>Bacillaria paradoxoxa</i>	Navarro (1983).	16–17 in 10 µm		4.5–7 µm	194–200 µm	Marine & brackish water, neritic, estuarine, cosmopolitan
<i>Bacillaria paxillifer</i>	Ricard (1987).	–	–	–	–	Marine or brackish, very euryhaline, often present in the littoral plankton of temperate waters
<i>Bacillaria paxillifera</i>	Hasle & Syvertsen (1997), pp. 290–293, pl. 66a,b.	20–21 in 10 µm	7–9 in 10 µm	5–6 µm	70–115 µm	Occasionally in plankton of shallow waters swept up from the bottom. Probably cosmopolitan
<i>Bacillaria paradoxoxa</i> (≡ <i>Bacillaria paxillifer</i> )	Krammer & Lange-Bertalot (1997), pp. 8, 587; pl. 87: figs 4–7.	20–25 in 10 µm	5–9 in 10 µm	4–8 µm	(38) 60–150 µm	Cosmopolitan, commonly at marine coasts and in very electrolyte rich inland waters
<i>Bacillaria paxillifer</i>	Witkowski <i>et al.</i> (2000), p. 357, pl. 212: figs 10–12.	20–25 in 10 µm	5–9 in 10 µm	4–8 µm	60–150 µm	Brackish-water species commonly inhabiting marine coasts and very electrolyte rich inland waters
<i>Bacillaria paxillifer</i> var. <i>tumidula</i> (Grunow)	Witkowski <i>et al.</i> (2000), p. 357 (non pl. 196, Fig. 8).	30 in 10 µm	10–13 in 10 µm	6 µm	66 µm	Witkowski <i>et al.</i> give Hustedt's data (1930)
Witkowski, Lange-Bertalot & Metzeltin						



(Ussing *et al.*, 2005), *B. paxillifera* seems to occur throughout the world, in freshwater, brackish and marine habitats, on sea shores as well as in inland water bodies, implying that *B. paxillifera* is ubiquitous and cosmopolitan. However, this assumption of cosmopolitanism is based on a broad concept of this taxon, with the result that several taxa have been subsumed under this name.

Based on our data, *B. paxillifera* var. *paxillifera* is found in different habitats in Europe including the shore of the Danish Copenhagen Sound between the Baltic and the North Seas (Figs 2, 12–17, 35–39), the Neusiedler See in Austria and Hungary (Figs 4, 18–21), and historically (Rabenhorst, 1854) in the tiny German Salzbach ('saltcreek') (Fig. 3). *Bacillaria paxillifera* var. *czarneckii* has been recorded from the Mississippi (North America) (Figs 5, 22, 23) and the River Weser, Germany (Figs 6, 24–26). *B. kuseliae* has only been found in a river in Western Australia (Figs 7, 27–30), and *B. urve-millerae* on the African West Coast in The Gambia (Figs 8, 31–34). With respect to historical records, only Grunow's var. *tumidula* (Grunow in Cleve & Grunow, 1880; fig. 9) from the East Indies belongs to *Bacillaria sensu stricto*; the other records, from Samoa and Honduras, probably belong to marine bacillarioid taxa. Records of *B. paxillifera*-related taxa from an inland river in Argentina (Frenguelli, 1923) and Eastern Australia (Silva, 1997) indicate additional occurrences, but their true identity needs checking. As indicated above, *Bacillaria* taxa are habitat-specific and may show a more restricted biogeographical distribution than previously assumed, once they have been more carefully differentiated and recorded (as shown for *Surirella* taxa in African lakes by Cocquyt & Jahn, 2005).

Summarizing the above, it is clear that members of *Bacillaria sensu stricto* are benthic, epipelagic or epi- and periphytic in freshwater to brackish habitats with great fluctuations in salinity, such as sea-shores under the influence of fresh- and/or wastewater inlets (Copenhagen Sound, The Gambia). They are also quite frequent in rivers with higher salt content, either due to estuarine impacts (e.g. River Weser, this study; River Elbe, Geissler & Kies, 2003) or the influx of salt from salt-mines (e.g. River Werra, Jahn & Wendker, 1987). They also occur in still-water zones of large inland rivers, such as the Mississippi (USA), or the Danube (from Austria to its delta in the Black Sea) (Kusel-Fetzmann, 1998), and on the shores of slow-running rivers in semi-arid zones, such as the Avon River, Australia. But *Bacillaria sensu stricto* have also been occasionally found in smaller water bodies in Berlin (Geissler & Kies, 2003; Skibbe, 2004). Their seasonal peak seems to occur

in the autumn (Müller, 1782; Schmid, 1995; Czarnecki, pers. comm.).

Concerning the autecology of *B. paxillifera* var. *paxillifera*, one of its best studied populations are those of the Neusiedler See (Schmid, 1973, 1995; see Table 2). Fluctuations in salinity due to the Pannonian climate as well as fluctuations in nutrient supply due to the seasonal movements of migratory birds make this large shallow inland lake (WWF bird sanctuary) an ideal habitat for *Bacillaria*. Already in 1957, Hustedt had linked the increasing occurrence of *Bacillaria* in the River Weser to increasing pollution and salinization. The view that eutrophication would favour growth of *Bacillaria* in the Neusiedler See was first put forward by Hustedt (1959), because he had found mass development of *Bacillaria* in the River Havel after flocks of birds had passed through the area. This was in contrast to Cholnoky (1968) who was convinced that *Bacillaria* was not heterotrophic for nitrogen but dependent on higher concentrations of inorganic salts and had a high pH-optimum. Interestingly, Grunow did not find it in the Neusiedler See in the 19th century, while Hustedt (1959) reported that its occurrence in the lake was rare at the beginning of the 20th century. This probably initiated the suggestion that it might have been introduced into the lake by sailboats. In today's Neusiedler See, *B. paxillifera* var. *paxillifera* forms macroscopic aggregates of entangled colonies, forming brown, pea-sized lumps in the reed-root zone, similar to what Tyge Christensen (see his herbarium sheet at C) had described for the epitype material in the Copenhagen Sound.

#### Comparison with published EM information on *Bacillaria*

Because *Bacillaria* taxa are unequivocally recognized from their EM-features (Schmid, 2007), we examined published EM information on *Bacillaria* taxa. One of the earliest EM pictures is in Geissler *et al.* (1961); unfortunately, the specimen named *B. paradoxa* (pl. 296 and text) is not a true *Bacillaria* but a diatom similar to that on plates 710 and 711, identified as *N. angularis* W. Smith. Ricard (1987, fig. 1127) also shows an SEM interior labelled *B. paradoxa*, but again unrelated to *Bacillaria*.

Drum & Pankratz (1966) and Drum *et al.* (1966, plate 533a, b) presented the first cross-sections of a true *B. paxillifera*. They studied a natural population, probably epipelagic/periphytic, from the Des Moines River at Windom (Minnesota, USA). The colonies were reported to be a 'loose spiral', with two plastids per cell. Dimensions were not

given but the transapical axis was ca. 5 µm. The raphe fissure is a tongue in groove structure and the authors wrote that “a single siliceous flange extends from opposite sides of both adjacent raphes”. The raphe is in a ‘median depression’ and valve structure deduced from the apical sections conforms to the construction type of *Bacillaria* (Schmid, 2007).

Specimens of *B. paxillifera* shown by Kapinga & Gordon (1992) are heterogeneous; figs 2, 3 and 5 show clones from D. Czarnecki, clearly *Bacillaria*. Their Fig. 4 is from a natural population from Delta Marsh (Manitoba, Canada). This specimen has radial ribs and a central interruption to the raphe, features lacking from our investigated taxa in *Bacillaria sensu lato*.

Paddock & Sims (1977) presented a *Bacillaria* sp. with a valve outline matching the type, but with prominent marginal spines, uni to biseriate striae over the valve and two raphe flanges, one larger than the other. This specimen belongs to *Bacillaria sensu lato* but probably not to the genus *Bacillaria sensu stricto*. Similarly Figs c–j, in Round *et al.* (1990, 608–609), are specimens of *Bacillaria sensu lato*, but not *Bacillaria sensu stricto*.

#### Nomenclatural and taxonomical conclusions

Schmid (2007) demonstrated that three different morphological construction types (Baupläne), designated A, B and C are found in *Bacillaria*-like colonies. Group A comprises brackish-freshwater taxa, B marine littoral, and C marine planktonic species. In this paper we have discussed the brackish-freshwater taxa of Bauplan A, belonging to *Bacillaria sensu stricto* because they include the type, *B. paxillifera*. This study necessitates an emendment of the genus *Bacillaria*, laying the foundation for the description of new genera (Schmid *et al.*, in prep.).

***Bacillaria* J.F. Gmelin, *Syst. nat.*, ed. 13, 1788; 1 (6): 3903. emend. A.M. Schmid et R. Jahn**

TYPE: *Bacillaria paxillifera* (O.F. Müller) Hendey, *J. Roy. Micr. Soc. Ser. 3*, 71: 74. 1951. [Basionym: *Vibrio paxillifer* O.F. Müller, *Animal Infus.*: 54, pl. VII, figs 3–7. 1786].

Valves usually linear, vela exterior; solid transapical ribs with several branching (fault) sites at the broader side of all valves visible in LM; valve formation sequence rather from the outside to the inside or from a middle basis to both sides (as in *Navicula*, or *Synedra*), raphe fissure tongue-in-groove. Last girdle band pre-stressed (sprung) with curved spines pointing to the poles. Two, rarely four (*B. urve-millerae*), narrow and sometimes branched, chloroplasts, with membrane-bound pyrenoids (Schmid, 2001, 2007) pointing

in the same direction in all cells of a colony. Living in brackish to freshwater habitats.

#### Acknowledgements

We are grateful for algal samples to Prof Elsa Kusel (Neusiedler See, Perth, Bremen) and to Dr Dave Czarnecki for a natural sample and clones. Dr Ruth Nielsen kindly provided herbarium-material collected by Dr T. Christensen, and Dr Helle Nielsen provided a xerox-copy of the O.F. Müller 1782-paper. Dr Christine Cocquyt kindly translated the diagnoses into Latin, and Dr Eileen Cox polished our English. Dr A. Sommer helped with sectioning, and Jeanette Ueckert with the SEM.

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