Typification of Colletonema viridulum with the correct name for Frustulia erifuga and the description of a new Frustulia species (Amphipleuraceae, Bacillariophyta)

Typification of *Colletonema viridulum* with the correct name for *Frustulia erifuga* and the description of a new *Frustulia* species (Amphipleuraceae, Bacillariophyta)

Bart Van de Vijver[1,2], Ingrid Jüttner[3] and Wolf-Henning Kusber[4]

[1]Botanic Garden Meise, Research Department, Nieuwelaan 38, 1860 Meise, Belgium (correspondence: bart.vandevijver@plantentuinmeise.be)

[2]University of Antwerp, Department of Biologie – ECOSPHERE, Universiteitsplein 1, B-2610 Wilrijk, Belgium

[3]Amgueddfa Cymru - Museum Wales, Department of Natural Sciences, Cathays Park, Cardiff, CF10 3NP, United Kingdom

[4]Botanischer Garten und Botanisches Museum Berlin, Freie Universität Berlin, Königin-Luise-Straße 6-8, 14195 Berlin, Germany

ORCID

Bart Van de Vijver: https://orcid.org/0000-0002-6244-1886

Ingrid Jüttner: https://orcid.org/0000-0003-0841-6206

Wolf-Henning Kusber: https://orcid.org/0000-0003-4543-5764

Abstract

The historic material of *Colletonema viridulum* from Falaise, France, has been investigated and compared with samples containing *Frustulia erifuga* and *F. torfacea*. *Colletonema viridulum* is considered to be the original material for *F. erifuga* and comparison of both populations showed that *C. viridulum* is conspecific with the larger morphotype I of *F. erifuga*. Moreover, a morphological analysis using both LM and SEM observations showed that *F. torfacea*, described in 1853, does also not show any morphological differences and hence should be accepted, following the priority rule of ICN, as the legitimate name for *C. viridulum* and *F. erifuga*. The second, smaller morphotype II of *F. erifuga* shows sufficient morphological differences to be separated as a separated species, described here as new: *Frustulia subtorfacea* Van de Vijver, Jüttner & Kusber, sp. nov. All populations are illustrated with LM and SEM images and their morphology is discussed.

Keywords: *Frustulia*, Europe, new species, type material analysis, morphology

Introduction

The genus *Frustulia* Rabenhorst (1853) comprises a group of usually relatively large-sized biraphid diatoms characterized by a very fine, uniseriate striation, internally two clearly thickened longitudinal ribs bordering the raphe branches, characteristic porte-crayon helictoglossa, and two plate-like plastids (Round et al. 1990; Taylor and Cocquyt 2016). Most species in the genus *Frustulia* are typically found in acidic, oligo- to mesotrophic waters with low mineralisation. Cells can be solitary or forming large colonies living in mucilage tubes. The genus has a worldwide distribution although species often exhibit restricted biogeographical distributions (e.g. Lange-Bertalot 2001; Van de Vijver et al. 2002; Beier and Lange-Bertalot 2007; Graeff et al. 2012; Urbánková et al. 2015; Casa et al. 2018). According to Algaebase (Guiry and Guiry 2023) there are 234 accepted taxon names with an additional 45 names currently of uncertain status along with 26 names that have not been verified so far. It should be noted that some of these taxa might be transferred to other genera such as the genus *Berkella* R.Ross & P.A.Sims (Jüttner et al. in press).

The taxonomic and nomenclatural history of the genus *Frustulia* is rather complex as discussed in Fourtanier and Kociolek (1999) and Lange-Bertalot and Jahn (2000). The name *Frustulia* was finally conserved in 1961 in the Montreal Code with *F. saxonica* Rabenhorst as typus generis (Lanjouw et al. 1961).

The European diatom flora comprises almost 20 different *Frustulia* taxa, among them several widely reported in European literature such as *F. amphipleuroides* (Grunow) A.Cleve, *F. crassinervia* (Brébisson ex W.Smith) Lange-Bertalot & Krammer, and *F. saxonica* (Lange-Bertalot et al. 2017). Another often reported species in European oligotrophic waters, is *Frustulia erifuga* Lange-Bertalot & Krammer (in Lange-Bertalot and Metzeltin 1996). The name *Frustulia erifuga* was introduced in 1996 to replace the name *Frustulia rhomboides* var. *viridula* (Brébisson ex Kützing) Cleve, originally described in 1849 as *Colletonema*

viridulum Brébisson ex Kützing, the typus generis of the genus *Colletonema* Brébisson ex Kützing (Kützing 1849). Kützing (1849) published the scientific names but attributed them to Brébisson because he received the relevant information 'in litt.' from the latter. This might be the reason why some authors who recombined the epithet interpreted the authorship as 'Brébisson in Kützing' instead of 'Brébisson ex Kützing'. The genus *Colletonema* was described for exclusively freshwater diatom species with a "filiform algal body composed of boat-shaped, tightly connected valves, arranged in rows and inwards rolled in an amorphous jelly-like mucus, lacking an external jelly tube ('*Phycoma filiforme ex naviculis seriatis connatis et muco gelineo amorpho involutis compositum, tubo exteriori gelineo nullo'*) (Kützing 1849, p. 105). Originally, only two taxa were placed in the new genus: *C. viridulum* and *C. lacustre* (C.Agardh) Kützing, currently regarded as a synonym of *Encyonema lacustre* (C.Agardh) Pantocsek (Krammer 1997), whereas two other taxa, *C.* (?) *amphioxys* (Ehrenberg) Kützing and *C.* (?) *americanum* (Ehrenberg) Kützing were added as '*species dubiae*', doubtful species.

Colletonema viridulum was transferred to the genera *Schizonema* [as *S. viridulum* (Brébisson) Rabenhorst] and *Vanheurckia* [as *V. viridula* (Brébisson) Brébisson] to end up finally in the genus *Frustulia* as *F. viridula* (Brébisson) Schaarschmidt (Schaarschmidt 1881). The latter unfortunately proved to be a younger homonym of *F. viridula* Kützing described 1833, now transferred to the genus *Navicula* as *N. viridula* (Kützing) Ehrenberg. Cleve (1894, p. 123) recombined the species as a variety of *Frustulia rhomboides* [*F. rhomboides* var. *viridula* (Brébisson) Cleve]. Lange-Bertalot and Metzeltin (1996) doubted whether *Frustulia rhomboides* conformed to the original concept of *Navicula rhomboides* Ehrenberg (1843) and brought some of the former *F. rhomboides* varieties (back) to species level such as *Frustulia crassinervia* (Brébisson) Lange-Bertalot & Krammer and *Frustulia saxonica* Rabenhorst. Four years later, Lange-Bertalot and Jahn (2000) analysed *N. rhomboides* and concluded that

the transfer of the latter to the genus *Frustulia* by De Toni (1891) was not correct as the species did not show the typical features of the genus *Frustulia* (without, however, specifying to what genus it might belong: "*So far it can only be attributed to the traditional concept of the genus* Navicula *sensu lato; it is unlikely that it belongs to* Navicula *sensu stricto on account of the central raphe ends and the raphe sternum*.") (Lange-Bertalot and Jahn 2000, p. 256). As a consequence, they changed the taxonomic status of all other former *F. rhomboides* varieties.

One of the taxa, already raised to species level in 1996 by Lange-Bertalot and Metzeltin (1996), was *Frustulia erifuga*, the new name for *F. viridula* (Brébisson) Schaarschmidt. The new name was chosen because the old one was a younger homonym of *Frustulia viridula* Kützing as stated above. Two morphotypes were separated in the Julma Ölkky material based on valve width (14–19 µm for Morphotype I versus 13–14.5 µm for Morphotype II), and the areola pattern at the apices (interrupted in MT I, continuous in MT II) (Lange-Bertalot and Metzeltin 1996; Lange-Bertalot 2001).

In the present paper, the population of both *F. erifuga* morphotypes observed in the original 1996 Julma Ölkky slide, retrieved from the Lange-Bertalot collection in the Senckenberg Museum (Frankfurt, Germany) and recently (i.e. 2020) collected new material from Julma Ölkky have been studied using light (LM) and scanning electron (SEM) microscopy. The observations are compared to original de Brébisson material from Falaise (France), handwritten labelled as *C. viridulum* and kept in Meise Botanic Garden (BR, Belgium). Additionally, the original material of a presumed synonym of *F. erifuga*, *F. torfacea* A.Braun ex Rabenhorst, was retrieved from the Van Heurck collection (also kept in Meise Botanic Garden, Belgium). Since Cleve (1894, p. 123) had listed the latter taxon as one of the synonyms of *F. rhomboides* var. *viridula*, the species name was no longer reported in later European floras such as Hustedt (1930), Krammer and Lange-Bertalot (1986) or Lange-

Bertalot et al. (2017). The morphology and variation of each taxon is studied and compared. Based on this comparison, Morphotype II of *F. erifuga* is described as a new species: *Frustulia subtorfacea* Van de Vijver, Jüttner & Kusber, sp. nov., and compared with other *Frustulia* from the European realm and locations elsewhere.

Material & Methods

For this study several samples have been investigated.

1. SF-161: Finnland, Julma Öllkysee, N. Kussamo, L2024 13602, original slide from J. Öllky used in Lange-Bertalot and Metzeltin (1996)
2. BR-4812: *Colletonema viridulum*, Falaise (France), leg. A. de Brébisson (bar code : BR5010056427626)
3. BR-4815 : *Frustulia torfacea*, Rabenhorst sample n° 761, Im Torfmoor am Titisee im badischen Schwarzwalde, leg. Schnurmann (bar code: AWH10072554).
4. BR-4814: *Frustulia erifuga*, Julma Ölkky, Finland, Sample JO-01, coll. date 15.X.2020, leg. Raino-Lars Albert

Subsamples of latter three samples were prepared for LM and SEM observations following the method described in van der Werff (1955). Small amounts of each sample were cleaned by adding 37% H_2O_2 and heating to 80°C for about 1 h, after which the reaction was completed by addition of saturated $KMnO_4$. Following digestion and centrifugation (three times for 10 minutes at 3700 × rpm), the resulting cleaned material was diluted with distilled water to avoid excessive concentrations of diatom valves on the slides. Cleaned diatom material was mounted in Naphrax (refraction index 1.73) and analysed using an Olympus BX53 microscope at 1000x magnification (N.A. 1.30), equipped with Differential Interference Contrast (Nomarski) optics and the Olympus UC30 Imaging System, connected to the Cell Sense Standard program. For each taxon, the number of specimens, measured at

random on the slide, is indicated (n=X). For SEM analysis, part of the suspension was filtered through 5-µm Isopore™polycarbonate membrane filters (Merck Millipore), pieces of which were affixed with conductive double-sided adhesive carbon-tabs to aluminum stubs after air–drying. Stubs were coated with a platinum layer of 15 nm, and studied using a JEOL-JSM-7100F field emission scanning electron microscope at 2 kV and a working distance of 4 mm. Slides and stubs are stored at the BR-collection (Meise Botanic Garden, Belgium). Plates were prepared using Photoshop CS5.

Terminology used in the description of the various structures of the siliceous cell wall is based on Ross et al. (1979, areola structure), Cox and Ross (1981, stria structure), Round et al. (1990, raphe structure), Lange-Bertalot (2001, genus features for *Frustulia*), and Sawai et al. (2016, genus features for *Frustulia*). The new species was compared with different *Frustulia* taxa described from several geographical regions (Lange-Bertalot 2001; Van de Vijver et al. 2002; Beier and Lange-Bertalot 2007; Graeff et al. 2012; Urbánková et al. 2015; Casa et al. 2018).

The length and width of 30 specimens of each taxon have been measured in every sample except for *F. erifuga* MT1 in the original Julma Ölkky 1996 slide where only 7 specimens could be observed. Measurements were performed using the Cell Sense Standard program. For typification of the species, we chose to use the entire slide as the type, following article 8.2 of the International Code for Botanical Nomenclature (Turland et al. 2018). Diatoms vary in shape during their cell cycle, hence selecting the slide with a population as the type allows us to show the variability of the new species. To avoid the risk of confusion with similar species in the same samples, one specimen was selected that illustrates a typical valve. All novelties are registered proactively according to Art. 42.3 (Turland et al. 2018).

Results

The light and scanning electron microscopy observations of the different populations showed that there are hardly any morphological and morphometric differences between *Colletonema viridulum*, *Frustulia erifuga* MT I and *Frustulia torfacea*. The results of the morphometric analysis are represented in Figure 1. Two clusters can be observed. Table 1 shows the measurements for each slide individually. A first cluster groups all measured specimens identified as *F. erifuga* morphotype II in both the original 1996 and the recently collected Julma Öllky slide. The length for all specimens ranges between 70.5 and 84 µm in the original Julma Ölkky slide and 75.0–81.7 µm in the recently collected J. Öllky material. The second cluster is composed of all measured specimens of *F. erifuga* morphotype I in both the 1996 and the recently collected J. Ölkky material, of all specimens in the *Colletonema viridula* type slide, and all specimens in the *F. torfacea* type slide.

These results show that the first cluster has shorter and typically much narrower valves (average 13 µm in MT2 versus 17 µm in MT1). An overlap in valve length can be noted between both clusters but there is no overlap in valve width.

Given the very similar morphometric results for the three (combined data for Julma Ölkky 1996 and 2020 slide) larger populations, we conclude that there is no difference in length nor width between them as Figure 1 clearly demonstrated. Additionally, Table 2 presents the morphological comparison of the three taxa, based on the morphological observations of *Colletonema viridulum* (Figs 3 & 4), *Frustulia erifuga* (Figs 2a,b, 6 & 6) and *F. torfacea* (Figs 7 & 8). Therefore, all three taxa should be considered conspecific following art. 11.4. of the International Code of Nomenclature for algae, fungi, and plants (Turland et al. 2018) stating that the ‘correct name is the combination of the final epithet of the earliest legitimate name of the taxon at the same rank, with the correct name of the genus or species to which it is assigned’, the name *Frustulia torfacea* is the legitimate name for this taxon. An emended

description for *F. torfacea* is proposed and sample Rabenhorst 761 is officially designated as lectotype for the species. A lectotype is also designated for *Colletonema viridulum*.

The second taxon in the Julma Ölkky sample, *F. erifuga* MT II, differs in morphology and morphometry from the other three taxa. Since this taxon could not be identified based on the currently available literature, it is described hereby as a new species: *Frustulia subtorfacea* Van de Vijver, Jüttner & Kusber, sp. nov. (Figs 9, 10).

***Frustulia torfacea* A.Braun ex Rabenhorst, emend. Van de Vijver, Jüttner & Kusber**

(Figs 2a,b, 3–8)

Original description

Rabenhorst, L. (1853). *Die Süsswasser-Diatomaceen (Bacillarien) für Freunde der Mikroskopie*, p. 50, pl. 7, fig. 2.

= *Colletonema viridulum* Brébisson ex Kützing 1849

≡ *Schizonema viridulum* (Brébisson ex Kützing) Rabenhorst 1864

≡ *Vanheurckia viridula* (Brébisson ex Kützing) Brébisson 1869

≡ *Frustulia viridula* (Brébisson ex Kützing) Schaarschmidt 1881, nom. illeg. non Kützing 1834

≡ *Frustulia rhomboides* var. *viridula* (Brébisson ex Kützing) Cleve 1894

≡ *Navicula rhomboides* var. *viridula* (Brébisson) F.W. Mills 1934, nom. inval.

≡ *Vanheurckia rhomboides* var. *viridula* (Brébisson) F.W.Mills 1935, nom. inval.

= *Frustulia rhomboides* [var. *viridula*] f. *hustedtii* H.Germain 1981

≡ *Frustulia hustedtii* (H.Germain) Lange-Bertalot in Wydrzycka & Lange-Bertalot 2001

- *Frustulia erifuga* Morphotype I Lange-Bertalot & Krammer in Lange-Bertalot and Metzeltin 1996

To be excluded from synonymy: *Frustulia viridula* Kützing 1834 [syn. *Navicula viridula* (Kützing) Kützing 1844] and *Frustulia erifuga* Morphotype II in Lange-Bertalot & Metzeltin 1996 (see *Frustulia subtorfacea*)

Lectotype for* Frustulia torfacea *(here designated)

BR-4815, Rabenhorst sample n° 761, Im Torfmoor am Titisee im badischen Schwarzwalde, leg. Schnurmann (bar code: AWH10072554)

Lectotype for* Colletonema viridulum *(here designated)

BR-4812, Falaise, France, leg. A. de Brébisson (bar code : BR5010056427626)

Registration

Lectotypification *F. torfacea* http://phycobank.org/104017

Lectotypification *C. viridulum* http://phycobank.org/104018

Emended description

Light microscopy (Figs 2,a,b, 3,5 & 7). Valves strictly lanceolate with convex margins and slightly protracted, very weakly subrostrate broadly rounded apices. Valve dimensions (n=97): length 81–124 (132) µm, width 16.0–19 (20) µm, length/width ratio 5.1–6.8. Initial valve length 132 µm, width 20 µm, l/w ratio 6.7. Axial area narrow, linear, weakly curved from the apices towards the central area. Two longitudinal parallel ribs bordering the raphe branches, slightly widening and curved at the central area before fusion with the central nodule. Central area formed by weakly widening of the axial area, apically elongated, elliptical in outline, not constricted. Ribs fused with the helictoglossa at the apices forming an elongated porte–crayon ending. Striae radiate throughout the entire valve, 27–31 in 10 µm, usually discontinuous at the apices, leaving a narrow or wider hyaline zone between both valve sides. Areolae well discernible in LM, ca 27–28 in 10 µm.

Scanning electron microscopy (Fig. 4, 6, 8). Axial area narrow, linear, weakly widened towards the central area (Figs 4a, 4b, 6a, 6c, 8a & 8b). Raphe branches slight curved, especially towards the central area with crescent-moon-shaped external central endings (Figs 4b, 6c & 8b). Terminal raphe fissures very short with T-shaped, slightly recurved, central and terminal endings (Figs 4c, 6b & 8c). Striae uniseriate, composed of small, oval, apically elongated areolae throughout the entire valve, except beside the central area and near the apices where areola are round (Figs 4b–c, 6a–c & 8a–c). First row of areolae bordering the axial area slightly shorter than the other areolae. At the apices, a narrow but distinct hyaline zone present due to shortening or absence of circumpolar striae (Figs 4c, 6b & 8b), occasionally absent with circumpolar areolae (Fig. 4e). Internally, areolae rounded, covered by large round to quadrangular hymenes (Figs 4e, 6d & 8e). Central nodule not or very weakly constricted, often with convex margins, fused with expanded longitudinal ribs (Figs 4d, 6e & 8d). Long, well–developed porte–crayon endings present at the apices (Figs 4e, 6d & 8e).

Frustulia subtorfacea **Van de Vijver, Jüttner & Kusber sp. nov.** **(**Figs 9 & 10)

- *Frustulia erifuga* Morphotype II in Lange-Bertalot & Metzeltin 1996, non Morphotype I

Holotype

BR-4814 (Meise Botanic Garden, Belgium). Figure 7c illustrates the holotype.

Isotype

Slide 431 (University of Antwerp, Belgium)

Type material

Julma Ölkky, Finland, Sample JO-01, coll. date 15.X.2020, leg. Raino-Lars Albert

Etymology

The specific epithet refers to the similarity with *F. torfacea*.

Registration

http://phycobank.org/104013

Description

Light microscopy (Fig. 9). Valves lanceolate, occasionally weakly rhombic-lanceolate with convex margins and distinctly protracted, subrostrate to rostrate, broadly rounded apices. Valve dimensions (n=60): length 69–84 µm, width 12.5–15.0 µm, length/width ratio 5.4–6.1. Axial area narrow, linear, weakly curved from the apices towards the central area. Two longitudinal parallel ribs bordering the raphe branches, hardly widening at the central area before fusion with the central nodule. Central area hardly widened to narrow oval, formed by a very weakly widening of the axial area, apically elongated. Ribs fused with the helictoglossa at the apices forming a short porte–crayon ending. Striae more or less parallel at the valve centre, elsewhere convergent, 29–30 in 10 µm, usually continuing around the apices. Areolae well discernible in LM, ca. 30 in 10 µm.

Description – Scanning electron microscopy (Fig. 10). Axial area narrow, linear, only very weakly widened towards the central area (Figs 10a & c). Raphe branches slight curved, especially towards the central area (Fig. 10c). Terminal raphe fissures very short with T-shaped, slightly recurved, central endings and distal endings (Fig. 10b). Striae uniseriate, composed of strictly rounded, occasionally weakly elliptical areolae throughout the entire valve (Figs 10b–c). Vimines broader than virgae. Slit-like areolae not observed so far. At the apices, striae circumpolar, leaving only a very narrow gap between both sides (Fig. 10b). Internally, areolae covered by rounded, quadrangular or transapically elongated elliptical hymenes (Figs 10d–e). Central nodule constricted, fused with slightly expanded longitudinal ribs (Fig. 10e). Short porte–crayon endings present at the apices (Fig. 10d).

Ecology: *Frustulia torfacea* and *F. subtorfacea* are sympatrically observed, almost in equal abundances, in the Julma Ölkky sample, both in the historic slide discussed in Lange-Bertalot and Metzeltin (1996) and in the newly collected material in 2020. The Julma Ölkky lake is located near Kuusamo in northeastern Finland. According to Lange-Bertalot and Metzelin (1996, p. 9) this lake should be classified as oligo-dystrophic, extremely electrolyte poor, and humic acid rich. The diatom flora in both the historic and the recently collected samples did not show significant differences (Van de Vijver, pers. Obs.) and is dominated species from the genera *Eunotia* (such as *E. faba* Ehrenberg, *E. incisa* W.Gregory, *E. serra* Ehrenberg), *Brachysira* (mainly *B. confusa* Van de Vijver et al., *B. elisabethiana* Van de Vijver et al., *B. microcephala* (Grunow) Compère, *B. follis* (Ehrenberg) R.Ross), *Frustulia* (e.g. *F. crassinervia* (Brébisson) Lange-Bertalot & Krammer, *F. saxonica* Rabenhorst, *F. quadrisinuata* Lange-Bertalot), and *Tabellaria flocculosa* s.l. (Roth) Kützing These genera are usually observed in acidic, oligotrophic and oligsaprobic environments (Lange-Bertalot et al. 2017). More information regarding the accompanying flora for both taxa can be found in Lange-Bertalot and Metzeltin (1996) who recorded more than 500 different diatom taxa in Julma Ölkky. The type sample of *F. torfacea*, collected from a peat bog near Lake Titi in Germany, has a similar, though less species-rich, diatom composition dominated by several *Frustulia* species (*F. torfacea*, *F. crassinervia*, *F. saxonica*), *Gomphonema coronatum* Ehrenb., *Brachysira confusa*, *Tabellaria flocculosa* s.l. and *Encyonema neogracile* Krammer, all known to prefer similar oligotrophic, acidic conditions (Lange-Bertalot et al. 2017). Finally, the type slide of *Colletonema viridulum* contained less species and was mainly characterized by several *Eunotia* species such as *E. incisa*, *E. pectinalis* (Kützing) Rabenhorst and *E. sphagnicola* Van de Vijver et al., reflecting nevertheless similar oligotrophic, acidic conditions with low mineralization (Lange-Bertalot et al. 2011, Van de Vijver et al. 2022).

Discussion

In his overview on the European *Frustulia* species, Lange-Bertalot (2001: 167–168) discussed the taxonomic identity of *F. erifuga* (without mentioning the name *F. torfacea*). According to this discussion, the "type" of *Colletonema viridulum* had already been seen by both Patrick and Reimer (1966: 309 as *F. rhomboides* var. *viridula*) and Germain (1981: 138 as *F. rhomboides* var. *viridula* f. *hustedtii* Germain). Patrick & Reimer (1966) used slide 88 in the exsiccata set *Diatomacearum Species Typicae*, put together by H.L.Smith (1876–1888). This slide, based according to H.L.Smith on original material sent to him by de Brébisson [*Species asterisco signatae speciminibus originalibus sunt representae. Specimina Gallica communicavit cl. de Brébisson*. (Species labelled with an asterisk are representative of the original specimens. The specimens from France were transmitted by the honorable de Brébisson)], was labelled *Colletonema viridulum* – La Tour (France). 'La Tour' could refer to Domaine de la Tour or Ruisseau de la Tour, two geographic names close to the city of Falaise (Normandy, France) where de Brébisson lived. However, the illustrated valve in Patrick and Reimer (1966, plate 21, fig. 21) was based on the analysis of slide 163 in the exsiccata set "Types du Synopsis des diatomées de Belgique, made by Van Heurck, that was collected from Ben Lomond, a mountain in Scotland, UK [as already stated in Lange-Bertalot (2001, p. 167)]. Germain (1981, p. 138), on the other hand stated that he had examined a large population from a pool in Normandy that was kept in the Museum in Paris (France), but did not specify a more exact locality. Kützing (1849, p. 105) mentioned "*Circa Falaise in aqua dulci legit clar. De Brebisson!*" as locality where the species was described from. This could in fact be La Tour. In the BR collection, two original de Brébisson samples (based on his handwriting) collected in Falaise could be found. Analysis of this material and of slide 88 of the H.L.Smith exsiccata set, showed that both samples contained a small population of

Colletonema viridulum, but differed slightly in the associated diatom flora. Moreover, Germain (1981, p. 138) actually did not illustrate *Colletonema viridulum*, but in fact a new form he described as *Frustulia rhomboides* [var. *viridula*] f. *hustedtii*, that he found to be identical to the taxon Hustedt described in the A. Schmidt Atlas (Hustedt 1930, plate 369, fig. 2) as *Frustulia rhomboides* (var. *saxonica*) f. *undulata* from the Titisee in Germany. The latter, however, was already described earlier as *Frustulia torfacea* based on Rabenhorst exsiccata sample 761. Analysis of the latter material, retrieved from the Van Heurck collection in BR, showed the presence of three *Frustulia* species (Van de Vijver, unpubl. res.). The largest population could be identified as *F. crassinervia* whereas one of the smaller populations most likely belonged to *F. saxonica*, based on the typically rhombical-lanceolate outline. A third, intermediately large, population was composed of valves with an elongated, strictly linear-lanceolate outline, that showed a resemblance to *F. erifuga* based on Lange-Bertalot (2001). Although the original drawing in Rabenhorst (1853, plate VII, fig. 2) does not show too many morphological details, the illustrated valves were quite elongated and narrowly lanceolate, a valve outline observed more in what was identified as *F. erifuga* than in *F. crassinervia* or *F. saxonica*.

As stated above, our analyses showed no distinct morphological differences between *F. torfacea*, *F. erifuga* and the original de Brébisson population of *Colletonema viridulum*. The areolae of all three taxa have the same apically elongated, oval outline. The apices present a distinct hyaline zone due to the absence or shortening of the apical (circumpolar) striae, a feature also clearly visible in LM. The central area presents a similar elliptical, thickened central nodule with straight to convex margins in all three taxa. There is a clear overlap in valve dimensions (Fig. 1, Table 1), although the stria density in *C. viridulum* is slightly higher (28–31 in 10 µm) than in the other taxa (27–29 in 10 µm). Based on this morphological comparison, it is obvious that all three are conspecific and our decision to put forward the

name *F. torfacea* for the taxon previously identified as *F. erifuga* in Lange-Bertalot and Metzeltin (1996) and originally described as *C. viridulum* by de Brébisson is therefore justified. Although the replacement name for *F. viridulum*, nom. Illeg., *F. erifuga* is a widely used name, often reported from acidic, oligotrophic habitats, the valid name *F. torfacea* is the earliest legitimate name for this taxon under *Frustulia* and therefore has priority according to the Botanical Code (Turland et al. 2018). The species is regularly misspelled as *F. torphacea* (for instance on the label for Rabenhorst sample 761) but the original description in Rabenhorst (1853, p. 50) clearly mentioned *F. torfacea*.

The conspecificity between *F. torfacea* and *F. erifuga* only includes the larger Morphotype I of the latter, as defined by Lange-Bertalot (2001, p. 167). The analysis of both the morphological ultrastructure and the valve dimensions of the two morphotypes, showed significant differences. The results of the morphometric analysis (Fig. 1, Table 1) showed no intermediate forms clearly separating two clusters representing each a different morphotype. Morphotype II is constantly smaller (70–84 µm versus 81–124 µm) and narrower (12.5–15.0 µm versus 16–19.0 µm) than Morphotype I, a feature already observed in Lange-Bertalot and Metzeltin (1996, p. 58) and Lange-Bertalot (2001, p. 168). The constantly lower width in Morphotype II and the slight overlap in valve length, also results in a lower minimum in length/width ratio for all measured populations of Morphotype I (Table 2), whereas the maximum remains similar. This means that for any given length, Morphotype I has always broader valves. Both morphotypes also differ in valve outline. Morphotype I possesses a strictly lanceolate valve outline with convex, rounded, gradually sloping valve margins. The other morphotype, on the other hand, has a weakly rhombic-lanceolate valve outline with a slight but distinct bend in the valve margin at the widest point of the valves. Moreover, the valve apices in Morphotype I are broadly rounded and only weakly protracted and rostrate. So far, all observed valves, identified as Morphotype II, have clearly protracted, rostrate

apices. Whereas both morphotypes were present in the slides from Julma Ölkky (both the 1996 and 2020 slides), only the larger Morphotype I was observed in the type samples of *Colletonema viridulum* and *F. torfacea*, while the narrower, rostrate Morphotype II was not recorded. The Julma Ölkky slides contain a very diverse *Frustulia* flora with at least nine species: *Frustulia crassinervia*, *F. gaertneriae* Lange-Bert. *F. krammeri* Lange-Bert., *F. quadrisinuata*, *F. saxonica*, *F. septentrionalis* Lange-Bert., *F. subtorfacea* (as *F. erifuga* MT2), *F. torfacea* (as *F. erifuga* MT1) and *F. vulgaris* (Thwait.) De Toni. All species can be easily separated using LM based on valve outline, valve dimensions and, often, the shape of the central area. In the other two investigated samples, the *Frustulia* diversity is much lower with only maximum three species present (*F. crassinervia*, *F. saxonica* and *F. torfacea*), despite the application of the same morphological criteria when analysing the *Frustulia* valves. The use of scanning electron microscopy observations adds several other morphological differences between the *Frustulia* species. A clear difference, remarkably not discussed by Lange-Bertalot and Metzeltin (1996, p. 58) and Lange-Bertalot (2001, p. 168) between both former *F. erifuga* morphotypes, is the shape of the external areola foramina. Morphotype I possesses apically elongated, slit-like areolae, typically observed in almost all *Frustulia* species (Lange-Bertalot 2001), whereas Morphotype II has clearly rounded external areola foramina throughout the entire valve face. As both Morphotypes were observed in the same sample, and thus both subject to the same possible valve erosion, the difference we observed is not the result of erosion but a distinct morphological feature. It is, however, unclear whether *Frustulia* species can exhibit different shapes of areola foramina within the same population. So far all valves identified in SEM as Morphotype II (based on valve outline) presented the rounded areolae whereas the valves in the *Colletonema viridulum*, *F. torfacea* and *F. erifuga* MT2 populations always possessed the elongated areolae.

A final, though least convincing difference between both morphotypes is the striation pattern at the apices. In Morphotype I, a clear hyaline zone can be seen at the valve apices in Morphotype I where the striae from both valve sides are separated due to the lack of circumpolar striae. In Morphotype II on the other hand, such a distinct gap between both sides is hardly visible. Often the striae are circumpolar (Fig. 10f–h) or a very narrow hyaline line (Fig. 10b) can be seen, and when present, this zone is never as broad as in Morphotype I. Following these differences in valve outline, valve dimensions and several, sometimes subtle, differences in the ultrastructure, Morphotype II should be separated from *F. torfacea* and since the name *erifuga* was chosen to replace *Colletonema viridulum*, it can no longer be used for the second Morphotype, necessitating the description of Morphotype II as a new species. Pinseel et al. (2019) discussed the cryptic diversity in *Pinnularia borealis* Ehrenb. concluding that a lot of diatom species complexes present pseudocryptic species, with species differentiated by only very subtle differences. Given the discussed differences, the separation of both *Frustulia* species is justified.

Frustulia subtorfacea shows some resemblance to previously described *Frustulia* species. Most described *Frustulia* usually have a more rhombic to broadly lanceolate outline such as *F. saxonica* and *F. krammeri* Lange-Bertalot & Metzeltin (more rhombic) or *F. crassinervia* and *F. pangaeopsis* Lange-Bertalot (more broadly rounded) (Lange-Bertalot 2001). Nevertheless, some species show a similar narrowly lanceolate valve outline as *F. subtorfacea*. *Frustulia amphipleuroides* can be separated by its elongated central area with the less developed central nodule, the presence of two conspicuous pores in the central area and a long porte-crayon at the apices (Lange-Bertalot 2001, plate 133, figs 1–4). *Frustulia cassieae* Lange-Bertalot & T.Beier, described from New Zealand, shows a similar narrowly lanceolate valve outline, but differs in having narrower valves (11–14 μm), and less protracted, acutely rounded apices (Beier and Lange-Bertalot 2007). The recently described

F. yaganiana Casa et al. (in Casa et al. 2018) has a clearly constricted central nodulea larger valve width (21–25.5 µm), no protracted apices and circumpolar striae (Casa et al. 2018). Finally, *F. subantarctica* Van de Vijver & Beyens, observed in the sub-Antarctic region, is smaller (width 11–13 µm) with more elliptical valve outline and circumpolar striae (Van de Vijver et al. 2002).

Acknowledgements

The authors want to thank sincerely Prof. dr Horst Lange-Bertalot (Senckenberg Institute, Frankfurt, Germany) for his help in retrieving the original 1996 Julma Ölkky slide. Mr. Reino-Lars Albert (Ecomonitor Oy, Joensuu, Finland) is thanked for providing us the new material of the Julma Ölkky lake.

Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

Funding for this research was provided by Meise Botanic Garden.

Author contributions

Bart Van de Vijver

Contribution: generation and analyses of LM and SEM materials, discussion of results, development, writing, revision and editing of the manuscript.

Ingrid Jüttner

Contribution: discussion of results, revision and editing of the manuscript.

Wolf-Henning Kusber

Contribution: discussion of results, taxonomic and nomenclatural analysis, revision and editing of the manuscript.

References

Beier, T, H Lange-Bertalot. 2007. A synopsis of cosmopolitan, rare and new *Frustulia* species (Bacillariophyceae) from ombrotrophic peat bogs and minerotrophic swamps in New Zealand. Nova Hedwigia 85(1/2): 73–91.

Brébisson A. de (1869). Extrait d'un essai monographique sur les *Vanheurckia*, nouveau genre appartenant à la tribu des Diatomacées Naviculées. Annls Soc Phytol Microgr Belg. 1: 201–206.

Casa, V, G Mataloni, B Van de Vijver. 2018. Six new *Frustulia* species (Bacillariophyta) in Tierra del Fuego peatbogs, Patagonia, Argentina. Fottea 18(1): 55–71.

Cleve, PT. 1894. Synopsis of the naviculoid diatoms. Part I. Kongl Svenska Vetenskapsakad Handl, Series 4. 26(2):1–194.

Cox, EJ, R Ross. 1981. The striae of pennate diatoms. In R Ross, editor. Proceedings of the Sixth Symposium on Recent and Fossil Diatoms. Budapest, September 1-5, 1980. Taxonomy · Morphology · Ecology · Biology. Koenigstein: Otto Koeltz; p. 267–278.

De Toni, GB. 1891. Sylloge algarum omnium hucusque cognitarum. Vol. II. Sylloge Bacillariearum. Sectio I. Rhaphideae. Patavii [Padua]: Sumptibus auctoris; p. [i–iii], [i]–cxxxii, 1–490.

Ehrenberg, CG. 1843. Verbreitung und Einfluss des mikroskopischen Lebens in Süd- und Nord-Amerika. Abh Königl Akad Wissensch Berlin 1841: 291–445.

Fourtanier, E, JP Kociolek. (1999. Catalogue of the diatom genera. Diatom Res 14(1): 1–190.

Germain, H. 1981. Flore des diatomées Diatomophycées eaux douces et saumâtres du Massif Armoricain et des contrées voisines d'Europe occidentale. pp. 1–444. Paris: Société Nouvelle des Éditions Boubée 11 place Saint-Michel, 75006, Paris.

Guiry, MD, GM Guiry. 2023. AlgaeBase. World-wide electronic publication. [Galway (Ireland)]: National University of Ireland; [accessed 2023 September 26]. https://www.algaebase.org.

Graeff, C, JP Kociolek, AL Burliga. 2012. Valve morphology of four species of *Frustulia* (Bacillariophyta), including two described as new. Phytotaxa 42: 62–76.

Hustedt, F. 1930. Bacillariophyta (Diatomeae). In A Pascher, editor. Die Süsswasser-Flora Mitteleuropas. Vol. 10. Jena: Gustav Fischer; p. 1–466.

Krammer, K. 1997. Die cymbelloiden Diatomeen. Eine Monographie der weltweit bekannten Taxa. Teil 1. Allgemeines und *Encyonema* Part. Bibl Diatomol 36: 1–382.

Krammer, K, H Lange-Bertalot. 1986. Bacillariophyceae 1. Teil: Naviculaceae. In H Ettl, J Gerloff, H Heynig, D Mollenhauer, editors. Süßwasserflora von Mitteleuropa. Vol. 2/1. Stuttgart – New York: Gustav Fischer Verlag; p. 1–876.

Kützing, FT. 1834 '1833'. *Synopsis diatomearum* oder Versuch einer systematischen Zusammenstellung der Diatomeen. Linnaea 8: 529–620.

Kützing, FT. 1844. Die kieselschaligen Bacillarien oder Diatomeen. Nordhausen: W. Köhne; p. 1–152, pls 1–30. doi:10.5962/bhl.title.64360

Kützing, FT. 1849. Species Algarum. Lipsiae. F.A. Brockhaus, 922 pp.

Lange-Bertalot, H. 2001. *Navicula* sensu stricto. 10 Genera separated from *Navicula* sensu lato. *Frustulia*. Diatoms of Europe 2: 1–526.

Lange-Bertalot, H, R Jahn. 2000. On the identity of *Navicula* (*Frustulia*) *rhomboides* and *Frustulia saxonica* (Bacillariophyceae). Syst Geogr Pl 70(2): 255–261.

Lange-Bertalot, H, D Metzeltin. 1996. Indicators of oligotrophy. 800 taxa representative of three ecologically distinct lake types. Carbonate buffered – oligodystrophic – weakly buffered soft water. Iconogr Diatomol. 2:1–390.

Lange-Bertalot, H, M Bąk, A Witkowski 2011. *Eunotia* and some related genera. Diatoms of Europe. 6: 1–747.

Lange-Bertalot, H, G Hofmann, M Werum, M Cantonati. 2017. Freshwater benthic diatoms of Central Europe: over 800 common species used in ecological assessment. English edition with updated taxonomy and added species. Schmitten-Oberreifenberg: Koeltz Botanical Books; p. 1–942.

Lanjouw J, C Baehni, W Robyns, R Ross, J Rousseau, JM Schopf, GM Schulze, AC Smith, R de Vilmorin, FA Stafleu. 1961. International Code of Botanical Nomenclature, "Montreal-Code". Utrecht, IAPT.

Mills, FW. 1934. An index to the genera and species of the Diatomaceae and their synonyms. 1816–1932. Part 15 (Na-Na). pp. 1081–1161.

Mills, FW. 1935. An index to the genera and species of the Diatomaceae and their synonyms. 1816–1932. Part 21 (Sy-Z, appendices, supplement). pp. 1571–1726.

Patrick, R, CW Reimer. 1966. The diatoms of the United States. Exclusive of Alaska and Hawaii. Volume 1. Fragilariaceae, Eunotiaceae, Achnanthaceae, Naviculaceae. Monogr Acad Nat Sci Philadelphia. 13:1–688.

Pinseel, E, J Kulichová, V Scharfen, P Urbánková, B Van de Vijver, W Vyverman. 2019. Extensive cryptic diversity in the terrestrial diatom *Pinnularia borealis* (Bacillariophyceae) Protist 170(2): 121–140.

Rabenhorst, L. 1853. *Die Süsswasser-Diatomaceen (Bacillarien.): für Freunde der* Mikroskopie, pp. 72, Leipzig: Eduard Kummer.

Rabenhorst, L (1864). Flora europaea algarum aquae dulcis et submarinae. Sectio I. Algas diatomaceas complectens, cum figuris generum omnium xylographice impressis. pp. 1-359. Lipsiae [Leipzig]: Apud Eduardum Kummerum.

Ross, R, EJ Cox, NI Karayeva, DG Mann, TBB Paddock, R Simonsen, PA Sims. 1979. An amended terminology for the siliceous components of the diatom cell. Nova Hedwigia Beiheft. 64:513–533.

Round, FE, RM Crawford, DG Mann. 1990. The diatoms: biology & morphology of the genera. Cambridge: Cambridge University Press; p. 1–747.

Sawai Y, T Nagumo, AR Nelson 2016. A brackish diatom, *Pseudofrustulia lancea* gen. et sp. nov. (Bacillariophyceae), from the Pacific coast of Oregon (USA). Phytotaxa 267(2): 103–112.

Schaarschmidt, J 1881. Algae. In: Kanitz, A. *Plantas Romaniae hucusque cognitas*. Magyar Novenytani Lapok 5: 151–165, 261–268.

Taylor, JC, C Cocquyt 2016. Diatoms from the Congo and Zambezi Basins – Methodologies and identification of the genera. ABC Taxa 16: 364 pp.

Turland, NJ, JH Wiersema, FR Barrie, W Greuter, DL Hawksworth, PS Herendeen, S Knapp, W-H Kusber, D-Z Li, K Marhold, TW May, J McNeill, AM Monro, J Prado, MJ Price, GF Smith, editors. 2018. International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017. Regnum Vegetabile 159:[i]–xxxviii, 1–253. Glashütten: Koeltz Botanical Books. doi:10.12705/Code.2018

Urbánková, P, J Kulichová, C Kilroy 2015. *Frustulia curvata* and *Frustulia paulii*, two diatom species new to science. Diatom Res 30(1):65–73.

Van de Vijver, B, Y Frenot, L Beyens. 2002. Freshwater diatoms from Île de la Possession (Crozet Archipelago, sub-Antarctica). Bibl Diatomol. 46:1–412.

Van de Vijver, B, H Lange-Bertalot, C Goeyers, A Mertens, TM Schuster, L Ector 2022. The identity of *Eunotia paludosa* Grunow 1862 (Eunotiaceae, Bacillariophyta), a revision, and the description of three new species of *Eunotia* Ehrenberg. Phytotaxa 545(3): 261–277.

van der Werff, A. 1955. A new method of concentrating and cleaning diatoms and other organisms. Verh Int Ver Theor Angew Limnol. 12:276–277. doi:10.1080/03680770.1950.11895297

Wydrzycka, Ú, H Lange-Bertalot. 2001. Las diatomeas (Bacillariophyceae) acidófilas del río Agrio y sitios vinculados con su cuenca, volcán Poás, Costa Rica. Brenesia 55/56: 1–68.

Table 1. Morphometric details (length & width) for all measured populations. Average and median are added for each population.

	length range (µm)	average length (µm)	median length (µm)	width range (µm)	average width (µm)	median width (µm)
Collectonema viridula	83.4–109.8	97.1 ± 6.2	98.7	15.8–18.5	17.2 ± 0,8	17.2
Frustulia torfacea	80.7–120.7	100 ± 9	99.1	15.9–18.9	17.4 ± 0.8	17.5
Frustulia erifuga MT1 -1996*	89.1–115.3	103 ± 8	103.5	16.4–18.0	17.0 ± 0.6	16.7
Frustulia erifuga MT1 -2020	83.3–124.0	100 ± 10	99.3	15.8–18.8	17.1 ± 0.8	16.9
Frustulia erifuga MT2 -1996	70.5–84.0	79.7 ± 2.9	80.7	12.3–14.7	13.9 ± 0.5	13.9
Frustulia erifuga MT2 - 2020	75.0–81.7	79.3 ± 1.7	79.8	12.7–14.4	13.6 ± 0.3	13.6

*only 7 specimens measured

Table 2. Comparison table of the four *Frustulia* populations discussed in the paper.

	Colletonema viridulum	*Frustulia erifuga* MT I*	*Frustulia torfacea*	*Frustulia subtorfacea* (=*F. erifuga* MT II)*
original author	de Brébisson ex Kützing	Lange-Bertalot & Krammer	A.Braun ex Rabenhorst	Van de Vijver, Jüttner & Kusber
year of publication	1849	1996	1853	this paper
valve length (µm)	84–110	83–124	81–121 (132)**	70–84
valve width (µm)	16.0–18.5	16.0–19.0	16.0–19.0 (20)**	12.5–15
valve/width ratio	5.1–6.3	5.1–6.6	5.0–6.8	5.4–6.1
number of striae (in 10 µm)	28–31	27–29	27–29	29–30
central area	enlarged central nodule, only weakly constricted, almost convex margins	enlarged central nodule, only weakly constricted, almost convex margins	enlarged central nodule, occasionally constricted, often almost convex margins	constricted central nodule with concave margins
apices	clear hyaline gap due to absence of circumpolar striae	clear hyaline gap due to absence of circumpolar striae	clear hyaline gap due to absence of circumpolar striae	absence of hyaline gap, clear circumpolar striae
areolae	slit-like, apically elongated	slit-like, apically elongated	slit-like, apically elongated	rounded, elongated areolae not observed

*combined measurements of Julma Ölkky 1996 and 2020 slide.

**possible initial valve

Figure Captions

Figure 1. Diagram representing the morphometric details (length versus width) of all 6 measured populations. Dark crosses represent *F. subtorfacea* specimens from the 1996 Julma Ölkky slide, grey crosses = *F. subtorfacea* specimens from the 2020 Julma Ölkky slide, grey triangles = *F. torfacea* specimens from the 1996 Julma Ölkky slide, dark diamonds = *F. torfacea* specimens from the 1996 Julma Ölkky slide, black squares = *F. torfacea* specimens from the *Colletonema viridulum* type slide, and grey circles = *F. torfacea* specimens from the Rabenhorst type slide. Length and width are expressed in µm.

Figure 2. *Frustulia erifuga* Lange-Bertalot & Krammer Morphotype I (=*Frustulia torfacea* A.Braun) and Morphotype II (= *F. subtorfacea* sp. nov.) . LM images taken from the 1996 Julma Ölkky sample (SF-161, Julma Ölkky, Kuursamo, Finland). Fig. 2a, b. *Frustulia erifuga* Lange-Bertalot & Krammer Morphotype I (=*Frustulia torfacea* A.Braun). Fig. 2c–f. *Frustulia erifuga* Lange-Bertalot & Krammer Morphotype II (=*F. subtorfacea* sp. nov.). Scale bar represents 10 µm.

Figure 3. *Colletonema viridulum* de Brébisson ex Kützing (=*Frustulia torfacea* A.Braun). LM images taken from the lectotype sample (BR-4812, Falaise, France, leg. A. de Brébisson). Figs 3a–3f. LM views of a size diminution series. Scale bar represents 10 µm.

Figure 4. *Colletonema viridulum* de Brébisson ex Kützing (=*Frustulia torfacea* A.Braun). SEM images taken from the lectotype sample (BR-4812, Falaise, France, leg. A. de Brébisson). Fig. 4a. SEM external view of an entire valve. Fig. 4b. SEM external detail of the central area with the weakly widened axial area near the central area. Fig. 4c. SEM external detail of the valve apex with the clear hyaline zone due to the gap in the striation. Fig. 4d.

SEM internal detail of the central area with the clearly thickened, convex central nodule. Fig. 4e. SEM internal detail of the valve apex with the porte-crayon structure. Scale bars represent 10 µm.

Figure 5. *Frustulia erifuga* Lange-Bertalot & Krammer (=*Frustulia torfacea* A.Braun). LM images taken from the 2020 Julma Ölkky sample (BR-4814, Julma Ölkky, Kuursamo, Finland, sample JO01, leg. R.L. Albert). Figs 5a–5e. LM views of a size diminution series. Scale bar represents 10 µm.

Figure 6. *Frustulia erifuga* Lange-Bertalot & Krammer (=*Frustulia torfacea* A.Braun). SEM images taken from the 2020 Julma Ölkky sample (BR-4814, Julma Ölkky, Kuursamo, Finland, sample JO01, leg. R.L. Albert). Fig. 6a. SEM external view of an entire valve. Fig. 6b. SEM external detail of the valve apex with the clear hyaline zone due to the gap in the striation. Fig. 6c. SEM external detail of the central area with the weakly widened axial area near the central area. Fig. 6d. SEM internal detail of the valve apex with the porte-crayon structure. Fig. 6e. SEM internal detail of the central area with the clearly thickened, convex central nodule. Scale bars represent 10 µm.

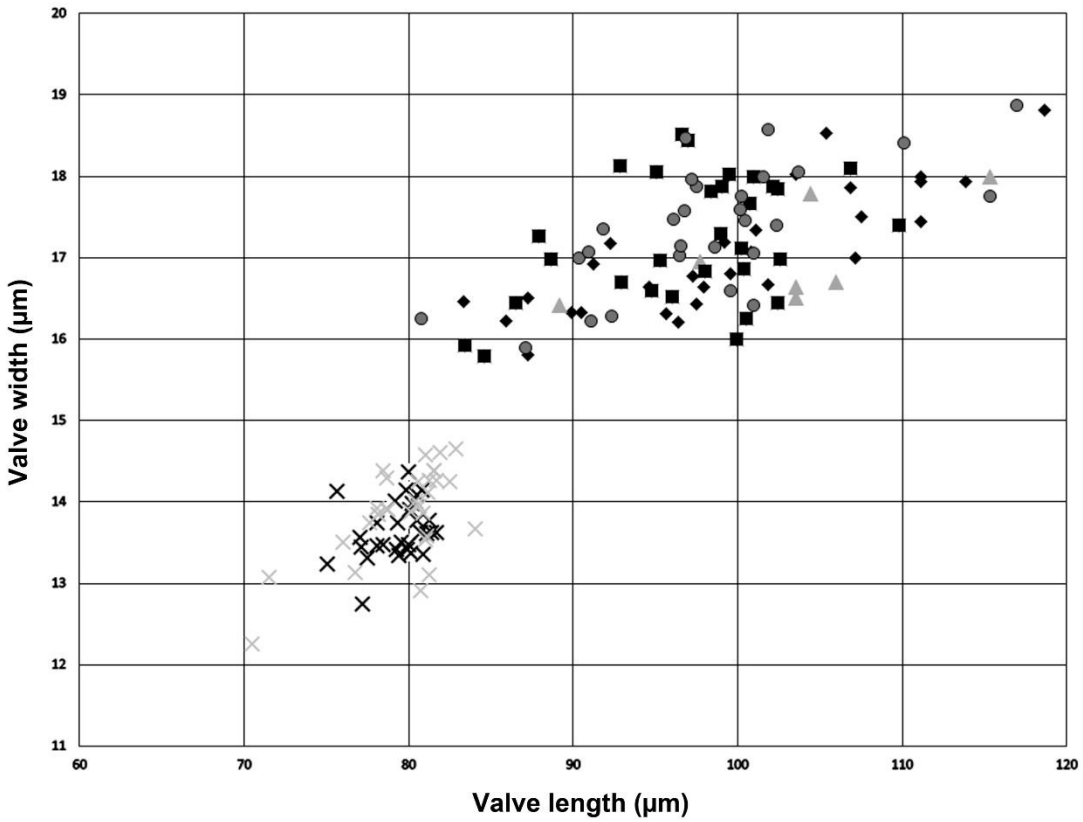
Figure 7. *Frustulia torfacea* A.Braun ex Rabenhorst. LM images taken from the lectotype sample (BR-4815, Im Torfmoor am Titisee im badischen Schwarzwalde, leg. Schnurmann). Figs 7a–7f. LM views of a size diminution series. Scale bar represents 10 µm.

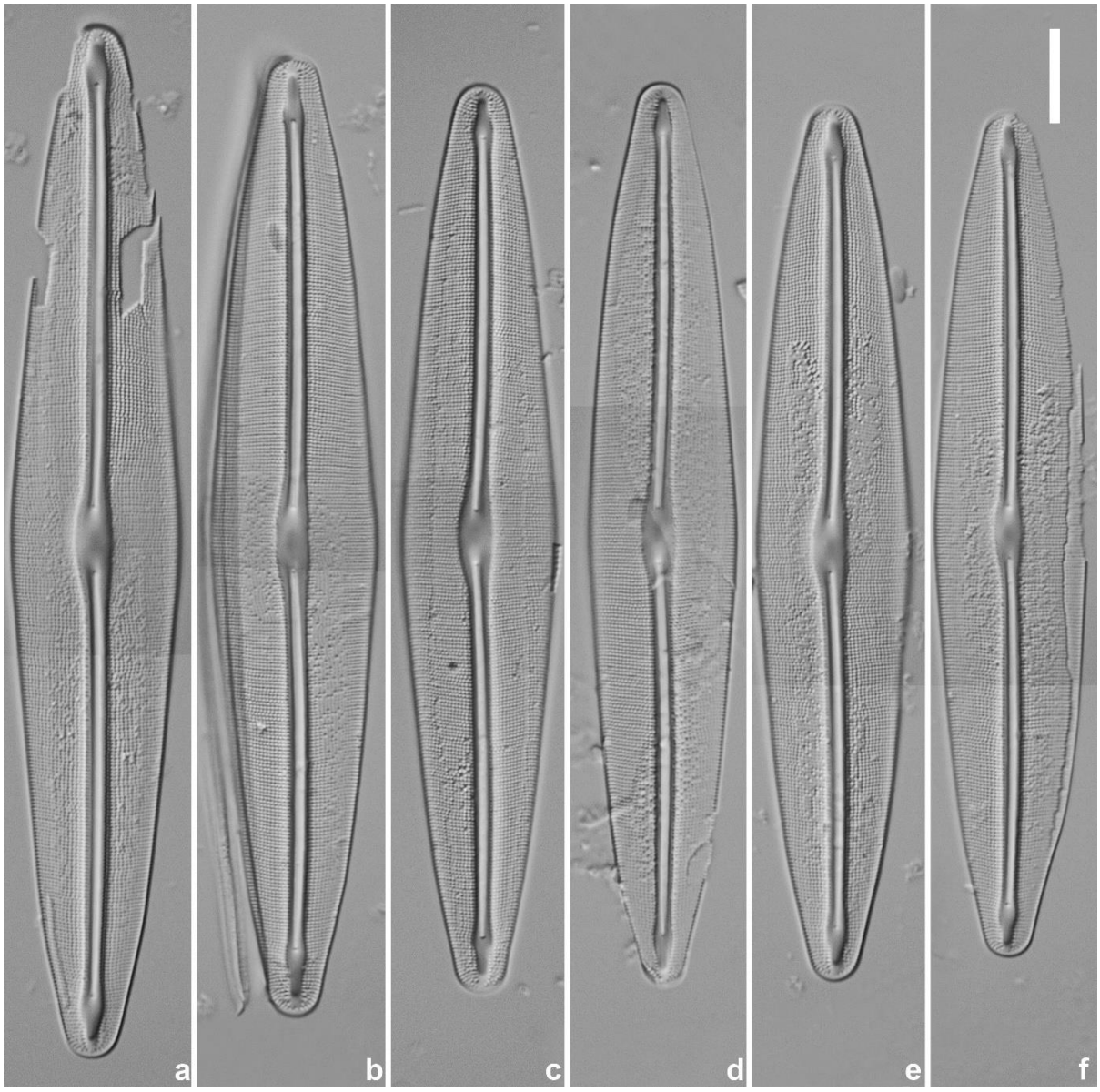
Figure 8. *Frustulia torfacea* A.Braun ex Rabenhorst. SEM images taken from the lectotype sample (BR-4815, Im Torfmoor am Titisee im badischen Schwarzwalde, leg. Schnurmann). Fig. 8a. SEM external view of an entire valve. Fig. 8b. SEM external detail of the central area

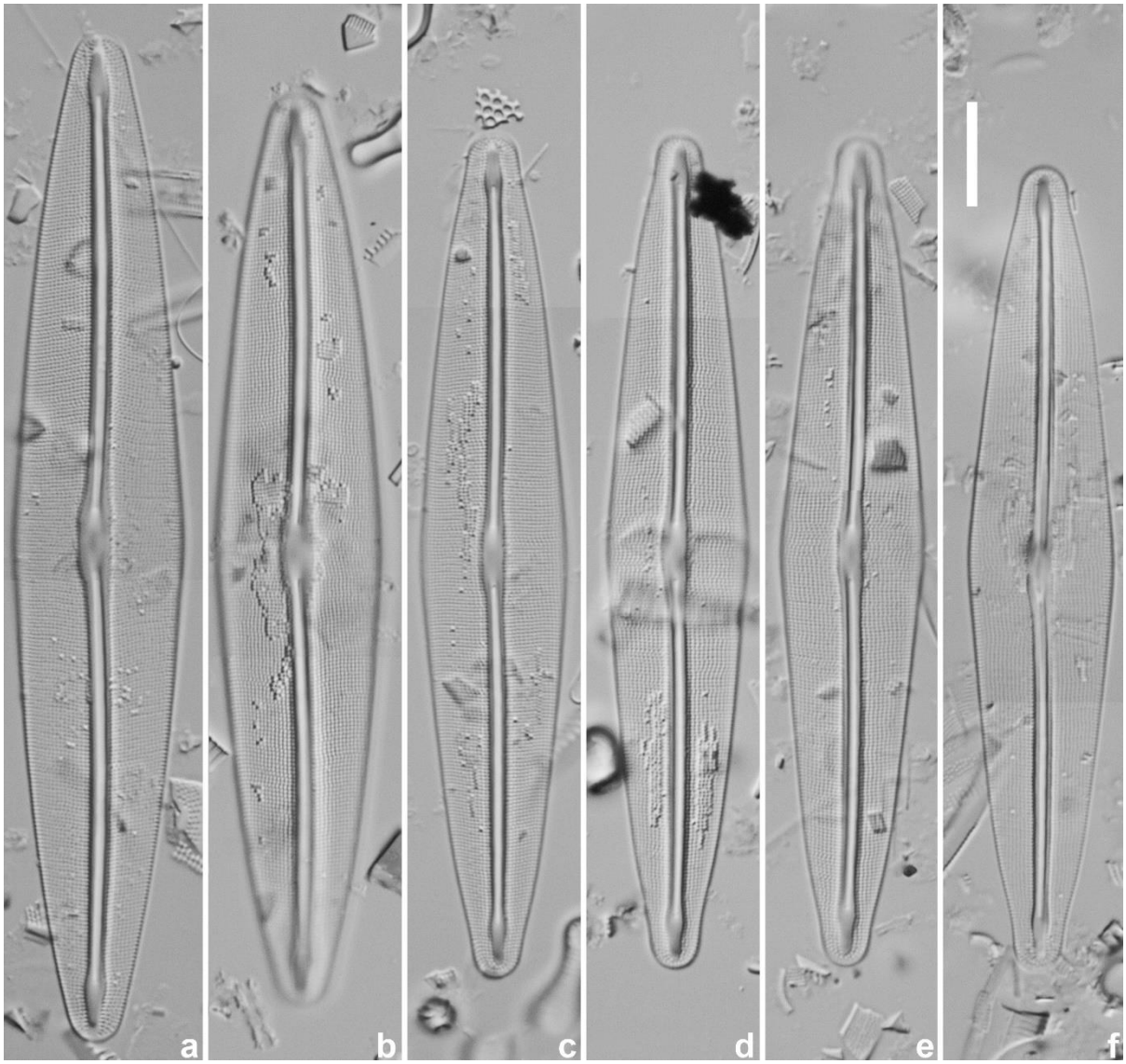
with the weakly widened axial area near the central area. Fig. 8c. SEM external detail of the valve apex with the clear hyaline zone due to the gap in the striation. Fig. 8d. SEM internal detail of the central area with the clearly thickened, convex central nodule. Fig. 8e. SEM internal detail of the valve apex with the porte-crayon structure. Scale bars represent 10 µm.

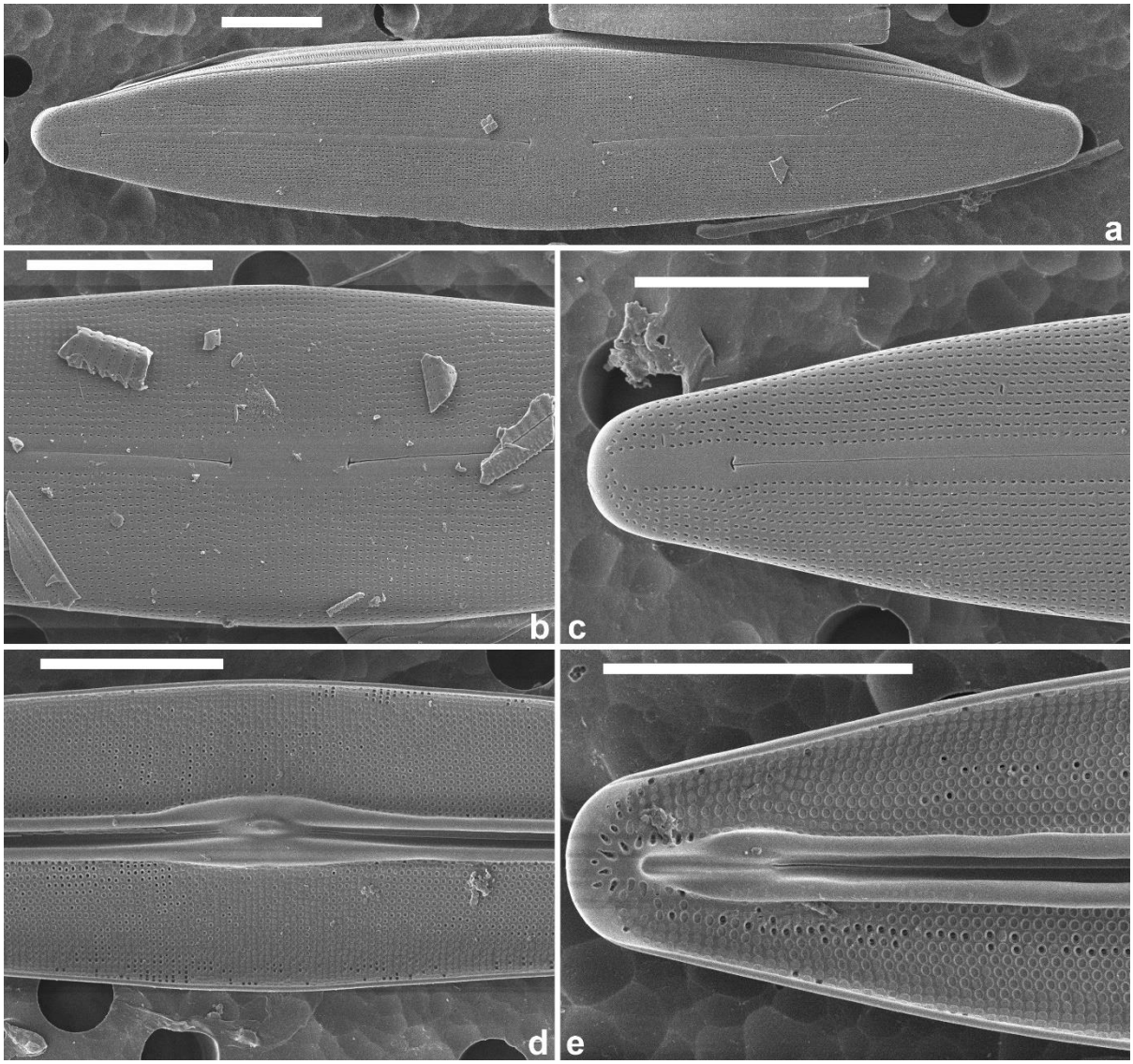
Figure 9. *Frustulia subtorfacea* Van de Vijver, Jüttner & Kusber, sp. nov. LM images taken from the holotype sample (BR-4814, Julma Ölkky, Kuursamo, Finland, sample JO01, leg. R.L. Albert). Figs 9a–9f. LM views of a size diminution series. Scale bar represents 10 µm.

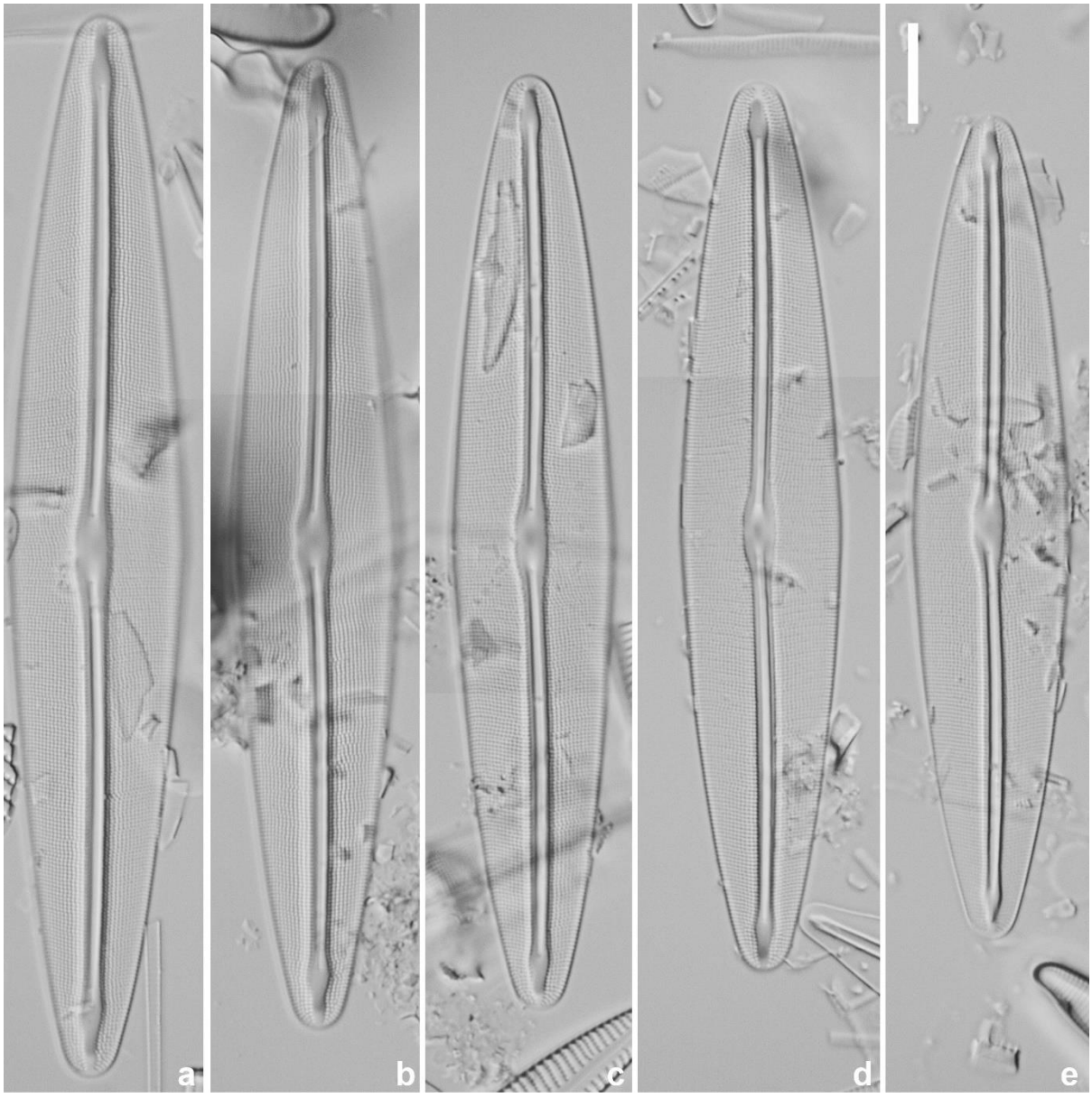
Figure 10. *Frustulia subtorfacea* Van de Vijver, Jüttner & Kusber, sp. nov. SEM images taken from the holotype sample (BR-4814, Julma Ölkky, Kuursamo, Finland, sample JO01, leg. R.L. Albert). Fig. 10a. SEM external view of an entire valve. Fig. 10b. SEM external detail of the central area. Note the rounded areolae and the almost widened axial area near the central area Fig. 10c. SEM external detail of the valve apex lacking a hyaline zone due to the circumpolar striae. Fig. 10d. SEM internal detail of the central area with the clearly thickened, convex central nodule. Fig. 10e. SEM internal detail of the valve apex with the porte-crayon structure. Fig. 10f–g. SEM external details of a valve apex showing the very narrow gap in both striation sides due to almost circumpolar areolae. Scale bars represent 10 µm.

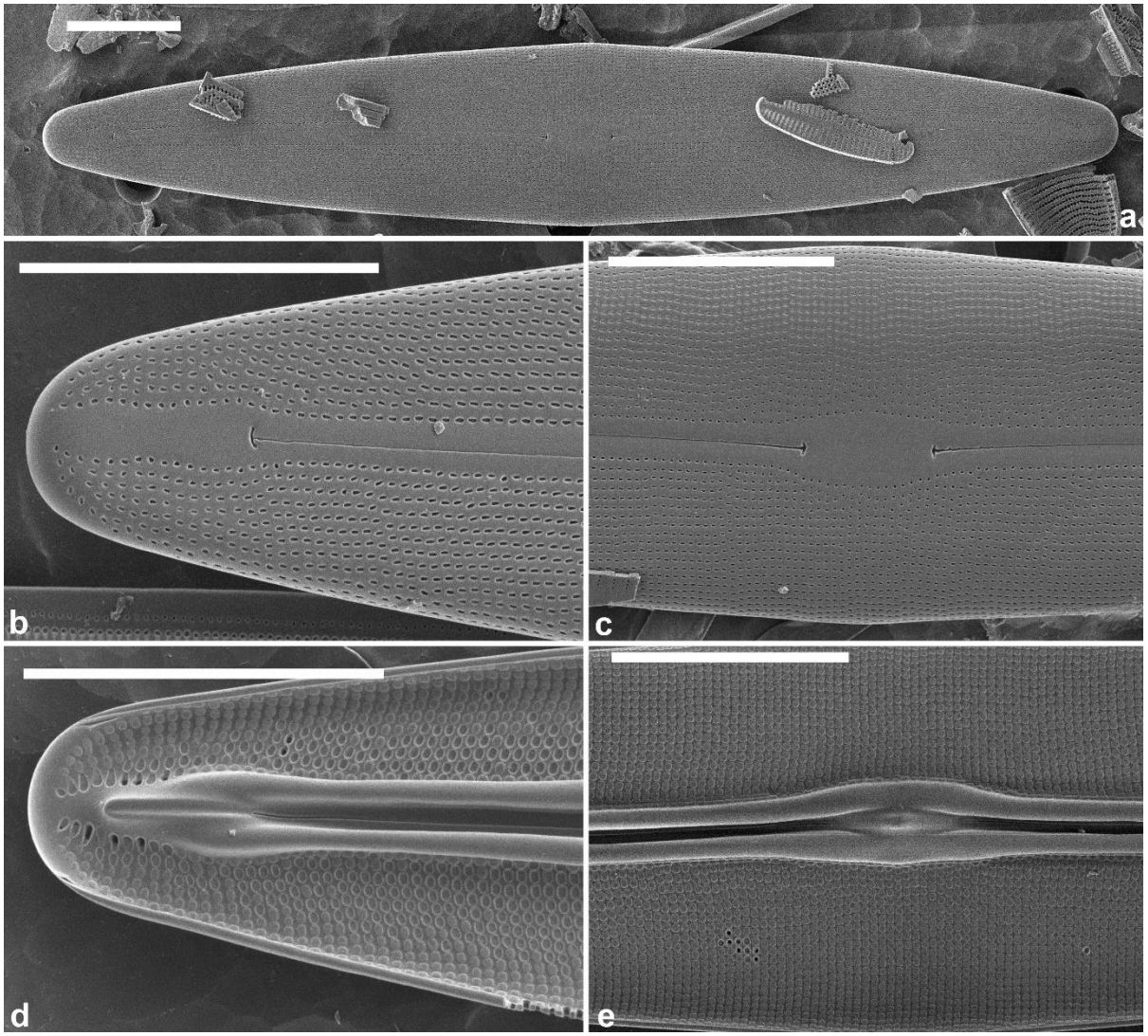

Valve width (µm)
Valve length (µm)
20
19
18
17
16
15
14
13
12
11
60
70
80
90
100
110
120

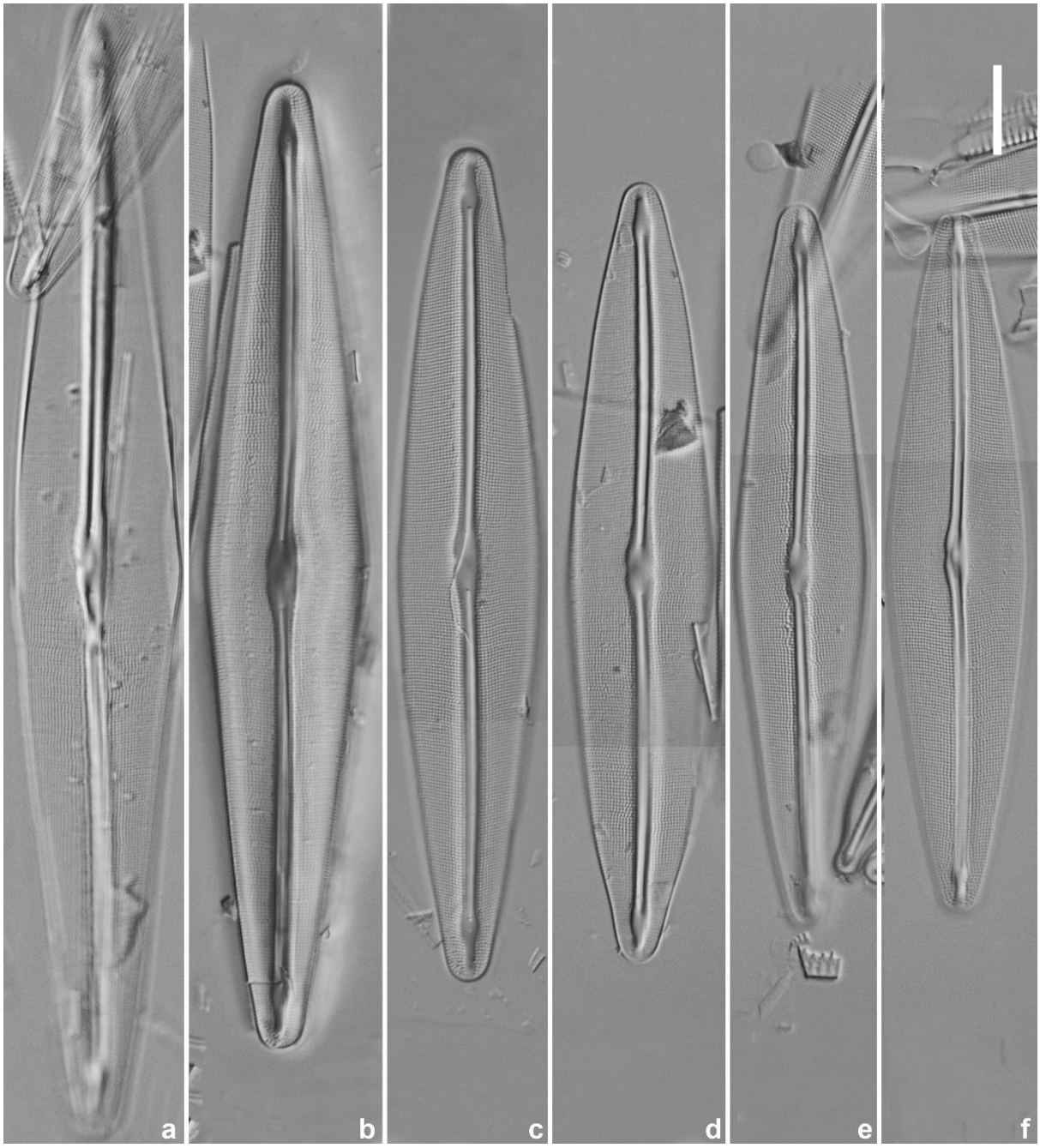

a
b
c
d
e
f

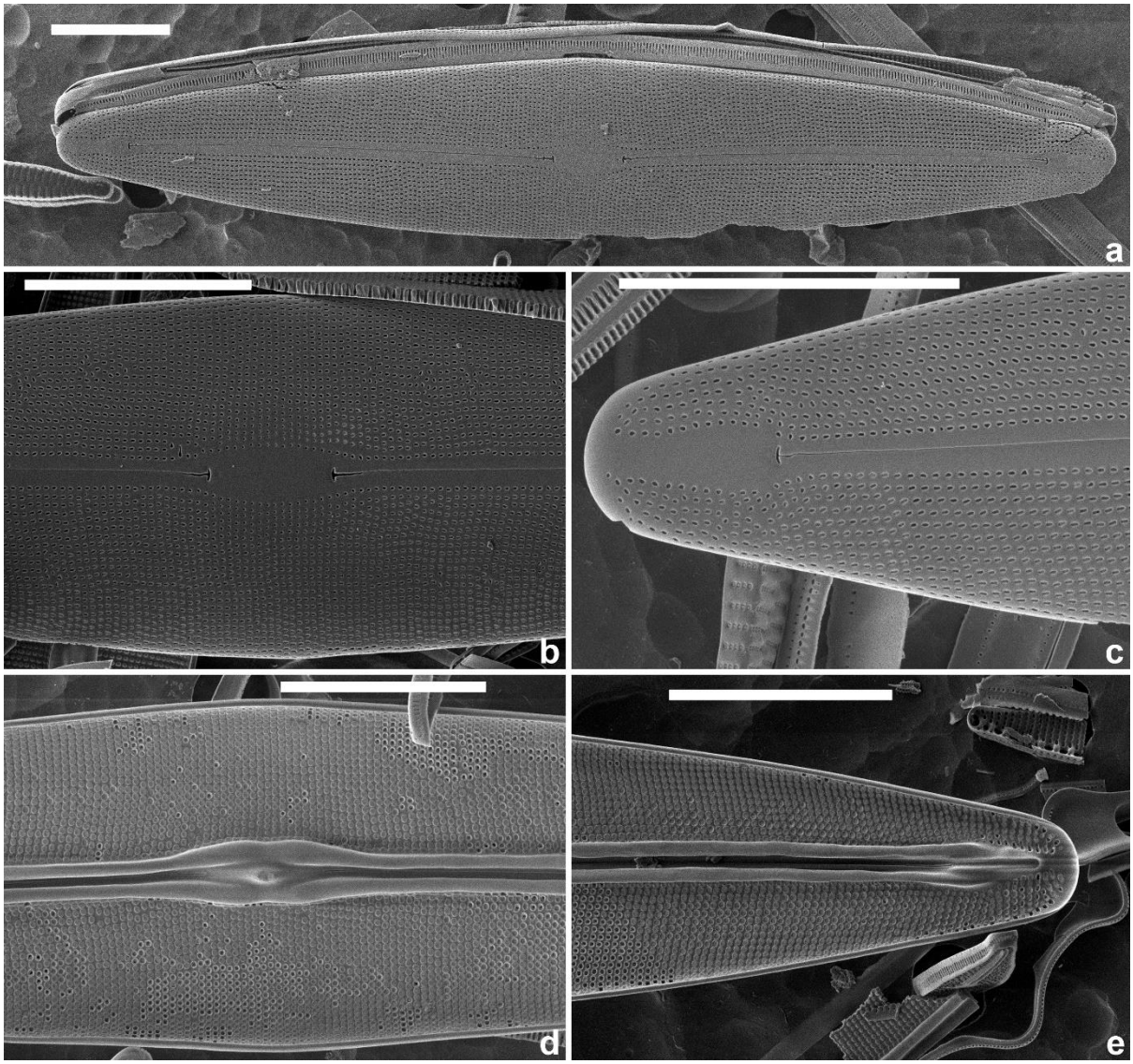

a
b
c
d
e
f

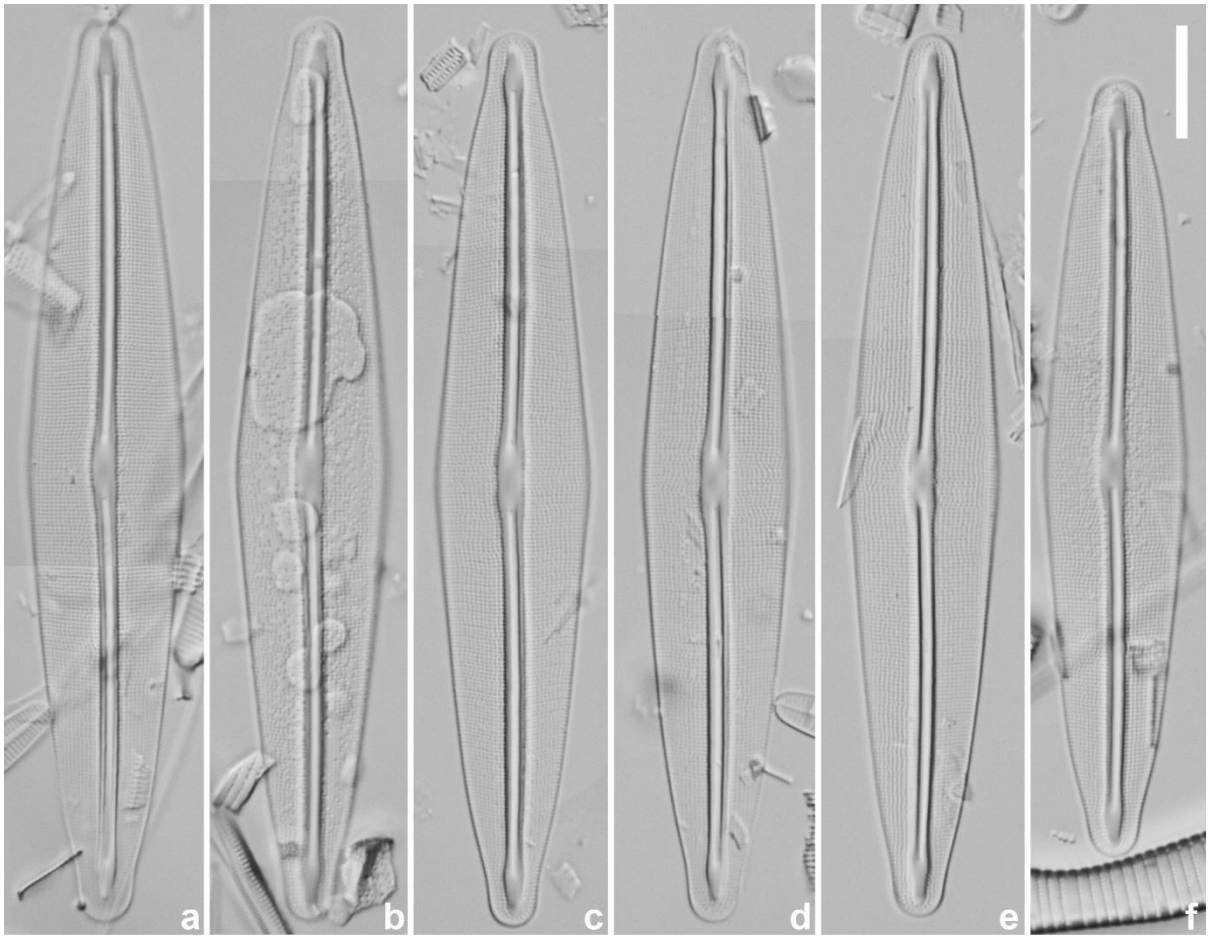

a
b
c
d
e

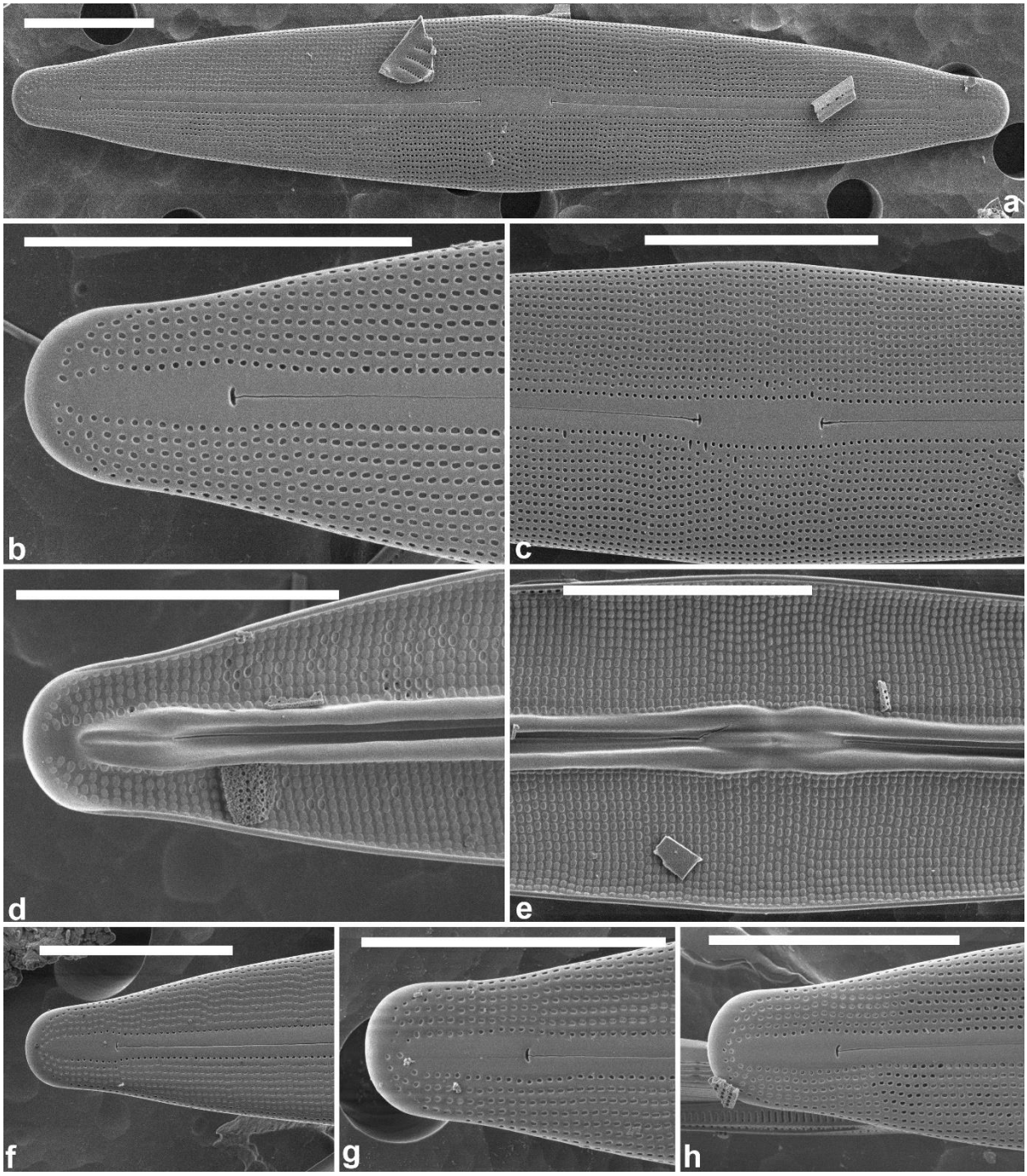

a
b
c
d
e


a
b
c
d
e


a
b
c
d
e
f


a
b
c
d
e


a
b
c
d
e
f


a
b
c
d
e
f
g
h