A review of some species of **Berkella** and **Frustulia** occurring in freshwaters of Britain and Ireland with documentation of the types of **Berkella linearis**, **B. alpina**, **Frustulia saxonica** and **F. crassinervia**

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A review of some species of *Berkella* and *Frustulia* occurring in freshwaters of Britain and Ireland with documentation of the types of *Berkella linearis*, *B. alpina*, *Frustulia saxonica* and *F. crassinervia*

Ingrid Jüttner[1*], Bart Van de Vijver[2,3], David M. Williams[4], Eileen J. Cox[4], Carlos E. Wetzel[5]

[1*]Amgueddfa Cymru − Museum Wales, Department of Natural Sciences, Cathays Park, Cardiff, CF10 3NP, UK;

[2]Meise Botanic Garden, Research Department, Nieuwelaan 38, 1860 Meise, Belgium

[3]University of Antwerp, Department of Biology – ECOSPHERE, Universiteitsplein 1, 2610 Wilrijk, Belgium

[4]The Natural History Museum, London, SW7 5BD, UK

[5]Luxembourg Institute of Science and Technology (LIST), Environmental Research and Innovation Department (ERIN), Observatory for Climate, Environment and Biodiversity (OCEB), 41 rue du Brill, L−4422 Belvaux, Luxembourg

*Corresponding author: ingrid.juettner@museumwales.ac.uk

†In memory of our friend and colleague Luc Ector (1962–2022)

and my husband Alan Orange (1955–2023)

With 158 figures

Abstract: We investigated the type material of *Berkella linearis*, *B. alpina, Frustulia saxonica*, and *F. crassinervia*, and populations of these taxa and of *F. vulgaris*, *F. quadrisinuata*, *F. erifuga*, and *F. amphipleuroides* from Scotland and Wales with light and scanning electron microscopy. The species are distinguished from each other in light

microscopy by differences in the shape of the valves, apices and central areas, and in scanning electron microscopy by differences in the raphe endings, striation and areola occlusions. Raphe curvature and the shape of the raphe endings vary within species currently in *Frustulia* and on this basis *B. linearis* might belong to *Frustulia*. However, a recent molecular analysis showed that several *Frustulia* taxa formed a separate lineage and further analysis is required to study relationships of species currently within *Frustulia* and whether some might belong to the genus *Berkella*.

Introduction

The genus *Frustulia* Rabenh. (1853, p. 50) *nom. cons.* contains predominantly freshwater species with linear, lanceolate or rhombic valves, uniseriate striae composed of small areolae aligned in apical and transapical rows, a raphe-sternum with robust internal longitudinal ribs on either side of the raphe fissures, merging with the helictoglossae near the apices to form a so-called porte-crayon ending (Greville 1863, Round et al. 1990). Many species possess T- or Y-shaped central raphe endings and terminal raphe fissures, although occasionally in some species round, teardrop-shaped or deflected endings can be found (Siver & Baskette 2004). On AlgaeBase, there are currently more than 200 names including varieties, subspecies and forms (Guiry & Guiry 2023), and over 400 names are listed on DiatomBase (Kociolek et al. 2023).

Using both light and scanning electron microscopy, we document the morphology of six species in *Frustulia* from type material and recent collections in Scotland and Wales. These investigations include the type specimens belonging to the names of *Berkella linearis* R.Ross & P.A.Sims, *Berkella alpina* (Amossé) J.R.Carter *nom. illeg.,* and a recent *Berkella* population, all are compared to *Frustulia vulgaris* (Thwaites) De Toni, a species with a similar valve shape. The type material of *Frustulia saxonica* Rabenh. and *Frustulia crassinervia* (Bréb.) Lange-Bert. & Krammer, along with several recent *Frustulia* populations from the UK are compared to *Frustulia quadrisinuata* Lange-Bert., originally described from Julma Ölkky, Finland (Lange-Bertalot & Metzeltin 1996, p. 59, pl. 38, figs 10–12, pl. 119, figs 1–2), and known from Scandinavia, Germany and Alaska (U.S.A.). Populations of *Frustulia erifuga* Lange-Bert. & Krammer in Lange-Bertalot & Metzeltin (1996, p. 58) and *Frustulia amphipleuroides* (Grunow) A.Cleve (Cleve-Euler 1934, p. 87) from Scotland and Wales, two larger species with lanceolate valves, are also illustrated.

Taxonomic history of the species under consideration

Ross & Sims (1978) established the genus *Berkella* R.Ross & P.A.Sims with *Berkella linearis* as *typus generis*, separating it from *Frustulia* because of its curved raphe, slightly reflexed, raphe endings, and the depressions with elongated areolae on either side of the raphe. In their paper, Ross & Sims (1978) discussed features shared with *Berkeleya* Grev. and *Amphipleura* Kütz. as studied by Cox (1975a, b). The description of the new genus was based on specimens from Loch Poit na h'I, Isle of Mull (Scotland, UK) with reference to the first description of this taxon as *Frustulia spicula* var. *alpina* Amossé from the French Alps by Amossé (1972), a variety separated from the nominate form because of its linear shape and non-capitate apices. Recognising that Amossé's new variety was invalid due to the lack of a type designation, Ross & Sims (1978) proposed a new epithet '*linearis*' for the species. Contrary to the statement in Carter (1993 [that Ross & Sims regarded *B. linearis* as being identical to *Frustulia spicula* Amossé]), Ross & Sims (1978) were "reasonably certain" that *Berkella linearis* and *Frustulia spicula* var. *alpina* were conspecific, and also stated that the latter is not identical with *F. spicula*, but differed in valve outline and the arrangement of the central striae. Carter (1993, figs 1–23) illustrated capitate specimens as *B. linearis* and regarded specimens with rostrate apices ('poles non-capitate') not as a variety of the latter but transferred them to *Berkella* and elevated them to species rank, *Berkella alpina* (Amossé) J.R.Carter *nom. illeg*.

Rumrich et al. (2000) rejected the characters used to distinguish *Berkella* from *Frustulia* because they vary between species in *Frustulia*. They proposed the name *Frustulia amosseana* Lange-Bert. for '*Frustulia spicula* var. *alpina*' because of the earlier homonym *Frustulia linearis* C.Agardh. They illustrated their concept with a specimen from Chile, possessing weakly subcapitate, broadly rounded apices, and listed as synonyms *B. linearis*, *Frustulia vulgaris* var. *capitata* Krasske (holotype in Lange-Bertalot 2001, pl. 137, fig. 1), *F.*

spicula var. *alpina* and *F. spicula* var. *spicula* partim (excluding the type of *F. spicula* [with capitate valve apices] from a location near Nantes [Amossé 1932, figs 6, 7; Amossé 1972, pl. 23, figs 7–10]). Krammer & Lange-Bertalot (1986) and Rumrich et al. (2000) questioned the usefulness of the valve apex shape to distinguish between the varieties of *F. spicula*. Krammer & Lange-Bertalot (1986) could not observe populations of *F. spicula* with transitions from rostrate to capitate apices, but rejected the recognition of species or varieties based on this character because of their observations on *Frustulia vulgaris* (Krammer & Lange-Bertalot 1986, p. 261).

Rumrich et al. (2000) and Lange-Bertalot (2001) stated that there is a continuum between capitate and non-capitate forms of *F. amosseana*, i.e., the specimen illustrated as '*F. spicula* Amossé des Alpes' (Amossé 1972, pl. 23, fig. 1) and *F. spicula* var. *alpina* (Amossé 1972, pl. 23, figs 2–6), and those from different geographical locations, i.e. from Germany, Syria, Chile and Sardinia (Lange-Bertalot 2001, pl. 137, figs 1–12, pl. 139, figs 7, 8). Specimens of *F. amosseana* showing a continuum of valves with short, protracted, rostrate valve apices to valves with sub-capitate apices are illustrated from Sardinia (Lange-Bertalot et al. 2003, pl. 71, figs 4–16). Rumrich et al. (2000) separated *F. spicula* sensu stricto from *F. amosseana* based on the shape of the central nodule, small round or elliptic in the former and elongate, linear in the latter. Lange-Bertalot (2001) illustrated a population of *F. spicula* from Ecuador referring to the type (Amossé 1932, figs 6, 7) and illustrations in Carter & Bailey-Watts (1981, pl. 2, fig. 38, pl. 24, fig. 12). The morphology of *B. linearis* is here compared with *F. vulgaris*, first described as *Schizonema vulgare* Thwaites (1848, pl. 12, fig. H), a cosmopolitan species apparently found across a wide range of environmental conditions from oligotrophic to polluted waters.

Frustulia saxonica was first described from moist rocks in Saxony, Germany, the protologue stating that the valves (in valve view) have narrower, bluntly rounded apices '[...] gegen beide Enden nachenförmig, verschmälert und stumpf gerundet [...]', with drawings of one frustule from both valve and girdle view, (Rabenhorst 1851, tab. III); four valves and one frustule were illustrated in Rabenhorst (1853, p. 50, tab. VII, Frustulia fig. 1). Type material has been examined by Lange-Bertalot & Metzeltin (1996) and Lange-Bertalot & Jahn (2000). It was composed of two sets of valves that differ in size ('morphotype I': 60–105µm long, 15–19µm wide, max. width central nodule 3µm; 'morphotype II': 36–76µm long, 10.5–14µm wide, max. width central nodule 2–2.6µm), previously identified as *Frustulia rhomboides* var. *rhomboides* (Ehrenb.) De Toni and *Frustulia rhomboides* var. *saxonica* (Rabenh.) de Toni, respectively. Both were found associated with each other elsewhere and were illustrated from a peat bog in the Rhön Mountains, Germany, and from Julma Ölkky, Finland (Lange-Bertalot & Metzeltin 1996, figs 1–6, Lange-Bertalot & Jahn 2000, figs 7–11).

Frustulia crassinervia was described as *Navicula crassinervia* Bréb. in W.Smith (Smith 1853, p.47, suppl. pl. 31, fig. 271) and later transferred to *Frustulia* (Lange-Bertalot & Metzeltin 1996, p. 57). Both species have been frequently reported and studied from low pH environments in the northern hemisphere, and are abundant in habitats with high humic acid content such as peat bogs in the Holarctic (Lange-Bertalot 2001, Siver et al. 2005, Siver & Hamilton 2011).

Two other less frequently recorded species of *Frustulia* are also considered. *Frustulia erifuga*, the current name for *Frustulia rhomboides* var. *viridula* (Bréb.) Cleve and based on *Colletonema viridulum* Bréb. ex Kütz. (1849, p. 105, Lange-Bertalot & Metzeltin 1996, Cleve 1894), is found in oligotrophic waters with low electrolyte content in the Holarctic (Lange-Bertalot 2001). The name *Colletonema* needs further investigation. It is attributed to de Brébisson and its first place of publication is usually given as Kützing (1849, p. 105). In this account, Kützing included three species: *Colletonema viridulum*, *C. lacustre* (Kützing 1849, p. 105) and, in the errata, *C. eximium* (Kützing 1849, p. 891). The first appearance of *Colletonema* is actually in d'Orbigny's *Dictionnaire universel d'histoire naturelle* ([9th Sept.] 1848, pp. 418-9, nouvelle edition, v. 12, 1867, pp. 390-1), which includes a brief description of *C. viridulum* Bréb., with a somewhat different synonymy than usual. This needs further investigation. *Frustulia amphipleuroides*, a distinct species rather than a variety, replacing *Navicula rhomboides* var. *amphipleuroides* Grunow (Cleve & Grunow 1880, pl. 3, fig. 59), has been reported across a range of environmental conditions from oligotrophic to slightly polluted waters (Lange-Bertalot 2001).

Methods and materials

Type material of *Berkella alpina, B. linearis*, *Frustulia saxonica*, and *Navicula crassinervia* Bréb. ex. W.Sm., from the diatom collections at Natural History Museum, London, (BM) and Meise Botanic Garden (BR), and recently collected populations of *Berkella linearis*, *Frustulia amphipleuroides*, *F. crassinervia*, *F. erifuga*, *F. quadrisinuata*, *F. saxonica*, and *F. vulgaris*, collected from streams, a waterfall and a ditch in Scotland and Wales, were investigated. Diatom biofilms were either removed from stone surfaces with toothbrushes, or collected by cutting off small amounts of aquatic plant material or scraping off surface sediment with a spoon. All material was subsequently placed in plastic vials and preserved with 95% ethanol. Samples were heated and oxidised using H_2O_2 to remove organic material and HCl to remove calcium deposits, cleaned by rinsing with distilled water and repeated centrifugation, and mounted on glass slides using Naphrax®.

Herbarium names (sources of material) are abbreviated according to Index Herbariorum (http://sweetgum.nybg.org/science/ih/). Diatom slides and suspensions are stored in the following collections NMW (Amgueddfa Cymru – Museum Wales), BM, and BR. For light microscopy (LM), diatoms were investigated at 1000× magnification and photographed using a NIKON E600 microscope (DIC, 100× objective, N.A. 1.40) equipped with an IMAGINGSOURCE camera (DFK NME72AUC02) and using the NIS-Elements D Software (NMW). For scanning electron microscopy (SEM) a small amount of suspension was air dried onto cover glasses and mounted on stubs. They were then sputter-coated with a layer of platinum or with gold-palladium and studied with a Zeiss Gemini Ultra plus SEM microscope (working distance 3–12 mm, 3–5 kV, NHM). Photo plates were made using CorelDraw v.12 (NMW). Terminology follows Anonymous (1975), Ross et al. (1979) and Round et al. (1990).

Observations

Berkella linearis R.Ross & P.A.Sims 1978, p. 156, 157, pl. 2, figs 20–27

= *Frustulia spicula* var. *alpina* Amossé (1972, pl. 23, figs 2–6) *nom. inval.*

= *Berkella alpina* (Amossé) J.R.Carter (1993, figs 24, 25) *nom. illeg.*

TYPE *Berkella linearis*:—UNITED KINGDOM, Loch Poit na h'I, Isle of Mull, Scotland, 56.32070160˚N, -6.34455601˚W, BM 78075 https://data.nhm.ac.uk/object/ef906ed7-0da2-4edf-981f-b3dd66f72253

TYPE *Berkella alpina*:—UK, Ettrick Valley, Scottish Borders, Scotland, slide 'Tushie Law Valley, Ettrick, Gordon Arms, flush', BM 94636 https://data.nhm.ac.uk/object/408da237-47b2-4358-9e2b-f563bc566803

ADDITIONAL MATERIAL: NMW.C.2022.06.Wales.2021.3bryo, Sgwd yr Eira waterfall, River Hepste, Powys, Wales, 51.778265˚N, -3.553872˚W, on moist, subaerial bryophytes behind waterfall Sgwd yr Eira.

OBSERVATIONS: Valves linear with short protracted, subrostrate apices (Figs 1–35). Valve dimensions: type *B. linearis* (n=15): length 26.5–48.5 µm, width 5.5–7.0 µm, type *B. alpina* (n=7): length 32.0–47.5 µm, width 6.0–7.0 µm, population from waterfall Sgwd yr Eira waterfall, River Hepste (n=19): length 24.5–51.0 µm, width 5.5–7.0 µm. Striae fine, discernible in LM, punctate, parallel, becoming convergent towards valve ends, type *B. linearis* and type *B. alpina*: 30–31 in 10 µm, population from waterfall Sgwd yr Eira: 29–31 in 10 µm. Striae encircling apices consist of 2–6 areolae. External areola openings round to oval, transapically elongated (Figs 36–39). External valve surface sometimes covered by a silica layer (Figs 40–43). Internally areola openings transapically elongated, occluded by individual hymenes (Figs 44–47). Axial area narrow, lanceolate, not continuing to apex, terminating at short distance from raphe endings, separated from apex by encircling striae. Central area narrow, linear, sometimes indistinct. Raphe slightly curved, terminating in hardly widened, straight central and terminal endings, terminal raphe fissures absent (Figs 36–38). Shallow grooves present adjacent to central raphe endings (Figs 37, 38). Internally, longitudinal ribs on both sides of raphe interrupted at valve centre, terminating beside ends of elongated central nodule. Near valve apices ribs terminating beside or fusing with elongated helictoglossae to form porte-crayon endings (Figs 44–46). Internal areola openings oval, transapically elongated, occluded by individual hymenes (Fig. 47).

Frustulia vulgaris (Thwaites) De Toni 1891, p. 280

BASIONYM: *Schizonema vulgare* Thwaites 1848, p. 170, pl. XII, fig. H 1–5

ANALYSED MATERIAL: NMW.C.2011.025.2011.Wales.3, ditch at RSPB Newport Wetlands, Newport, Wales, 51.543291˚N, -2.961348˚W.

OBSERVATIONS: Valves linear to linear-elliptic with short protracted, subrostrate, rounded apices (Figs 48–57). Valve dimensions: population from ditch at RSPB Newport Wetlands, Newport, Wales (n=10): length 45.0–50.0 µm, width 9.0–10.5 µm. Striae fine, discernible in LM, punctate, radiate in valve centre, becoming parallel and slightly convergent near valve ends, 29–30 in 10 µm. Striae encircling apices consisting of 2–4 areolae. External areola openings small, mostly round, sometimes oval, transapically elongated. One row of areolae beside axial and central areas slightly at a distance from other stria areolae (Figs 58, 60, 62). Axial area narrow, lanceolate, not continuing to valve apices, terminating some distance from raphe endings, separated from apices by encircling striae (Fig. 62). Central area small oval. Raphe slightly curved, terminating in small, Y-shaped raphe endings (Figs 58, 60, 62). Internally, longitudinal ribs on both sides of raphe interrupted at valve centre, terminating beside ends of central nodule (Figs 59, 61). At valve apices, ribs fusing with elongated helictoglossae to form porte-crayon endings (Fig. 63). Virgae slightly thickened, particularly at valve centre. Internal areola openings larger, transapically elongated, occluded by individual hymenes (Fig. 61, 63).

Frustulia saxonica Rabenh. ([Jul] 1851), no. 42, Tab. III [‘*Frustulia saxonica* 42’]

≡ *Frustulia rhomboides* var. *saxonica* (Rabenh.) Pfitzer (1872, p. 164)

≡ *Frustulia rhomboides* var. *saxonica* (Rabenh.) De Toni (1891, p. 277)

≡ *Navicula saxonica* (Rabenh.) Lagerst. (1873, p. 32)

≡ *Vanheurckia rhomboides* var. *saxonica* (Rabenh.) Perag. (1897, p. 382)

≡ *Vanheurckia rhomboides* var. *saxonica* (Rabenh.) Holmboe (1899, p. 44)

≡ *Navicula rhomboides* var. *saxonica* (Rabenh.) Budde (1928, p. 510)

≡ *Navicula rhomboides* var. *saxonica* (Rabenh.) Mills (1934, p. 1137)

TYPE:—GERMANY, Saxony, '[…] (Rabenhorst 1851, no., 42) […]', Naturmuseum Senckenberg, Frankfurt am Main, Germany, lectotype (see Lange-Bertalot & Jahn 2000, figs 2, 3, 'lectotype from Exsicc. Algen Sachsens [sic, see below]'); BM 55338, 'Rabenhorst […] no. 42' in PC TA 56710, L4020483, and RO s.n., isolectotypes

ADDITIONAL MATERIAL: NMW.C.2022.02.Esgair.Forest.Lliwdy.1.7/2016, Nant Lliwdy, Esgair Forest, Pantperthog, Machynlleth, Gwynedd, Wales, 52.63113°N, -3.89190°W.

OBSERVATIONS: Valves rhombic, lanceolate to elliptic-lanceolate with cuneate or slightly protracted, subrostrate to rostrate apices (Figs 64–89). Valve dimensions: type population Rabenhorst 41: (n = 15): length 47.0–78.5 µm, width 12.0–16.0 µm; population from Nant Lliwdy, Gwynedd, Wales: (n = 18): length 45.5–87.5 µm, width 12.5–18.0 µm. Striae fine, discernible in LM, parallel in central part of valve, becoming slightly convergent towards apices, type population: 32–38 in 10 µm, Nant Lliwdy: 30–33 in 10 µm. Striae encircling apices reduced to one or two areolae. External areola openings small rounded to oval, apically elongated. Areola openings beside central area small rounded to oval, transapically elongated (Figs 92, 94). Internal areola openings larger, circular, elongated near apices, occluded by raised hymenes (Figs 93, 95). Axial area narrow, linear, not continuing to valve apices, terminating some distance from raphe endings, separated from apex by one or two rows of areolae. Central area short, elongate, either lacking constriction or with small constriction on one or both sides. Raphe straight, terminating in T-shaped, slightly recurved, raphe endings (Figs 90, 92, 94). Internally, longitudinal ribs on both sides of raphe widening slightly towards valve centre, then narrowing slightly on one or both sides beside central nodule (Figs 91, 93). Ribs fusing near valve apices with elongate, linear helictoglossae to form short porte-crayon endings (Fig. 95).

Frustulia crassinervia (Bréb. ex. W.Sm.) Lange-Bert. & Krammer 1996, p. 57, pl. 38, figs 7–9

Basionym: *Navicula crassinervia* Bréb. ex W.Sm. 1853, p. 47, pl. 31, fig. 271

≡ *Navicula crassinervia* Bréb. ex W.Sm. (1853, p. 47)

≡ *Navicula rhomboides* var. *crassinervia* (Bréb. ex W.Sm.) Grunow (1880)

≡ *Frustulia rhomboides* var. *crassinervia* (Bréb. ex W.Sm.) R.Ross (1947, p. 212)

= *Frustulia rhomboides* f. *undulata* Hust. (1930, p. 221)

= *Vanheurckia rhomboides* f. *undulata* (Hust.) Freng. (1942, p. 104)

TYPE:—FRANCE, Falaise, sample *Navicula crassinervia*, July 23, 1852, leg. A. de Brébisson (Smith 1853, p. 47), BR-4805, **lectotype here designated**; Falaise, BM 18883 (Kützing 1674), isolectotype.

REGISTRATION: —http://phycobank.org/XXXX

Casa et al. (2018, p. 57) discussed the origin of the type material of *N. crassinervia*. The protologue for *N. crassinervia* in Smith (1853) lists syntype material from Wareham ('September 1849, *W.Sm.*') 'Snow Mud, Grampians' (collected by *'Dr. Dickie'*) and Dolgelly (collected by '*Mr. Ralfs*') as well as 'ad specimina sub hoc nomine quae misit cl. De Brebisson, Sept. 1852' (Smith 1853, p. 47). A search in the Van Heurck diatom collection at BR yielded the original Brébisson material from Falaise, France, which should correspond to the 'Sept. 1852'material noted. It contains a fairly large population of *Navicula crassinervia*. This material should be considered as the lectotype material for the species. As Casa et al. (2018) did not lectotypify the material we designate BR-4805 as lectotype for *N. crassinervia*.

ADDITIONAL MATERIAL: NMW.C.2021.02.Scotland.11/21.24aeropeat.filalg, stream at Ryvoan, Aberneth National Nature Reserve, Highland, Scotland, 57.181439˚N, -3.6472372˚W.

OBSERVATIONS: Valves lanceolate to elliptic-lanceolate with protracted, rostrate apices (Figs 96–112). Valve dimensions: type population Brébisson: (n = 15): length 46.5–51.0 µm, width 12.0–13.5 µm; population from a stream at Ryvoan, Aberneth National Nature Reserve, Highland, Scotland (n = 12): length 44.0–54.5 µm, width 10.5–13.0 µm. Striae fine, discernible in LM, parallel, near apices parallel or slightly convergent, type population Brébisson: 35–40 in 10 µm, stream at Ryvoan: 33 in 10 µm; longitudinal striae slightly wavy. Striae encircling valve apices reduced to 2–3 areolae, one at centre of apex (Figs 114, 116). External areola openings small, slit-like, apically elongated. Areola openings beside central area small, rounded to oval, transapically elongated (Figs 115, 116). Internal areola openings larger, circular, elongated near apices, occluded by raised individual hymenes (Fig. 118). Axial area narrow, linear, not continuing to valve apices, terminating some distance from raphe endings, separated from apex by one row of areolae. Central area short, elongate, either lacking or with small constriction on one or both sides. Raphe straight, terminating in T-shaped, slightly recurved, raphe endings (Figs 113–116). Internally, longitudinal ribs on both sides of raphe widening slightly towards valve centre, then narrowing slightly on one or both sides beside central nodule. Ribs fusing at valve apices with elongate, linear helictoglossae to form short porte-crayon endings (Figs 117–118).

Frustulia quadrisinuata Lange-Bert.in Lange-Bertalot & Metzeltin 1996, p. 59, pl. 38, figs 10–12, pl. 119, figs 1–2

ANALYSED MATERIAL: NMW.C.2021.02.Scot.11/21.15sed, Loch Mallachie, Highland, Scotland, 57.236065˚N, -3.7149879˚W.

OBSERVATIONS: Valves rhombic to rhombic-lanceolate with short protracted, rostrate, broadly rounded apices (Figs 119–125). Valve dimensions: population from Loch Mallachie, Highland, Scotland (n=10): length 56.0–61.0 µm, width 13.5–14.0 µm. Striae fine, discernible in LM, striae parallel in valve centre, convergent towards apices, 30–31 in 10 µm. External areola openings small, round or oval, apically elongated. Areolae beside central area and central raphe branches round, slightly larger than other areolae, forming distinct line. Areola adjacent to this line at centre of valve smaller than other areolae. Areolae beside axial area may be fused forming longitudinal lines (Figs 126–129). Internal areola openings larger, circular or oval, occluded by raised individual hymenes (Figs 131–133). Axial area narrow, linear, extending to valve margin at valve ends (Fig. 129). Central area short, elongate. Raphe straight, terminating in T-shaped, slightly recurved, raphe endings (Figs 126–129). Internally, longitudinal ribs on both sides of raphe widening slightly near valve centre, then narrowing slightly on both sides beside central nodule. Ribs fusing with elongated, linear helictoglossae to form porte-crayon endings at valve apices (Figs 130, 133).

Frustulia erifuga Lange-Bert. & Krammer in Lange-Bertalot & Metzeltin1996, p. 58, pl. 39, figs 1–4, pl. 120, figs 1–3

Replaced synonym: *Frustulia rhomboides* var. *viridula* (Bréb. ex Kütz.) Cleve 1894, p. 123, non = *Frustulia viridula* Kütz.

Basionym: *Colletonema viridulum* Bréb. ex Kütz. (1849, p. 105)

= *Schizonema viridulum* (Bréb.) Rabenh. (1864, p. 266)

= *Vanheurckia viridula* (Bréb. ex Kütz.) Bréb. (1869, p. 203, figs 1-4)

= *Frustulia viridula* (Bréb.) F.Schaarschm. (1881, p. 158), non = *Frustulia viridula* Kütz.

= *Frustulia viridula* (Bréb.) De Toni (1891, p. 278)

= *Frustulia rhomboides* var. *viridula* (Bréb. ex Kütz.) Cleve (1894, p. 123)

= *Navicula rhomboides* var. *viridula* (Bréb. ex Kutz**.**) Mills (1934, p. 1137)

= *Vanheurckia rhomboides* var. *viridula* (Bréb.) Mills (1935, p. 1680)

TYPE:—FRANCE, Falaise, BM 19417 (‘Circa Falaise in aqua dulci legit clar. De Brebisson!’, Kützing 1508, de Brébisson); ?Calvados, La Tour, H.L. Smith 88; L 4020493, 5 https://data.biodiversitydata.nl/naturalis/specimen/L.4020495 https://data.biodiversitydata.nl/naturalis/specimen/L.4020493

ANALYSED MATERIAL: NMW.C.2021.02.Scot.11/21.24aeropeat.filalg, stream at Ryvoan, Aberneth National Nature Reserve, Highland, Scotland, 57.181439˚N, -3.6472372˚W; NMW.C.2011.019.06/11.IF34, Nant Hir, tributary to River Irfon, Powys, Wales, 52.174333˚N, -3.700467˚W.

OBSERVATIONS: Valves lanceolate with rounded or cuneate apices, not or hardly protracted (Figs 134–139). Valve dimensions: population from stream at Ryvoan, Aberneth National Nature Reserve, Highland, Scotland (n = 5): length 94.0–130.0 µm, width 17.0–19.5 µm; population from the stream Nant Hir (n = 11): length 63.0–95 µm, width 14.5–17.5 µm. Striae fine, discernible in LM, punctate, 26–27 in 10 µm in both populations, parallel in central part of valve, becoming slightly convergent towards apices. External areola openings small, oval, apically elongated. Areola openings beside central area round (Figs 142, 144). Internal areola openings larger, occluded by raised, quadrangular individual hymenes (Figs 143, 145–147). Axial area narrow, linear, terminating some distance from raphe endings, continuing to valve apices or separated from apices by one or two rows of areolae (Figs 144, 145). Central area narrow, oval. Raphe straight, terminating in T-shaped, slightly recurved, raphe endings (Figs 140, 142, 144). Internally, longitudinal ribs on sides of raphe widening slightly on one or both sides at valve centre adjacent to central nodule (Fig. 143). Ribs fusing with elongate, linear helictoglossae to form long porte-crayon endings at valve apices (Fig. 145).

See introduction for some comments on the nomenclature of *Colletonema*.

Frustulia amphipleuroides (Grunow) A.Cleve 1934, p. 87

Basionym: *Navicula rhomboides* var. *amphipleuroides* Grunow in Cleve & Grunow (1880: 47)

≡ *Frustulia rhomboides* var. *amphipleuroides* (Grunow) De Toni (1891, p. 277)

≡ *Vanheurckia rhomboides* var. *amphipleuroides* (Grunow) Freng. (1942, p. 102)

≡ *Vanheurckia rhomboides* var. *amphipleuroides* (Grunow) R.M.Patrick (1945, p. 170)

= *Vanheurckia rhomboides* var. *amphipleuroides* Grunow (1880, p. 47)

= *Frustulia amphipleuroides* var. *typica* A.Cleve (1952, p. 7)

ANALYSED MATERIAL: NMW.C.2012.018.SEPA.2048545, Coy Burn at Damhead, Aberdeenshire, Scotland 57.072939°N, -2.400922°W.

OBSERVATIONS: Valves lanceolate with rounded apices, not or hardly protracted (Figs 148–152). Valve dimensions: population from Coy Burn at Damhead, Aberdeenshire, Scotland (n=7) length 109.0–116.0 µm, width 18.5–20.5 µm. Striae fine, discernible in LM, punctate, 23–24 in 10 µm, parallel in central part of valve, becoming slightly convergent towards apices. Striae around valve apices comprising 3–7 areolae (Fig. 157). External areola openings small, oval, apically elongated. Areola openings of row beside central area round (Fig. 155). Internal areola openings larger, occluded by raised, oval, transapically elongated individual hymenes (Figs 156, 158). Axial area narrow, linear, terminating some distance from raphe endings, narrowing towards valve apices, separated from apices by peripheral striae (Fig. 157). Central area long, narrow, linear. Raphe slightly curved with slightly deflected central raphe endings, terminating in small, Y-shaped raphe endings (Figs 155, 157). Internally, longitudinal ribs on sides of the raphe widening slightly and merging with central nodule (Figs 154, 156). Ribs fusing with elongate, linear helictoglossae to form long porte-crayon endings at valve apices (Fig. 158).

Discussion

Berkella linearis, Frustulia amphipleuroides, *F. crassinervia*, *F. erifuga*, *F. quadrisinuata*, *F. saxonica* and *F. vulgaris*, can be distinguished from each other in LM by differences in the shape of the valves, apices and central area, and in SEM by differences in the external raphe endings, striation and areola occlusions (Table 1).

***Frustulia vulgaris*, *Berkella linearis* and other *Frustulia* spp. with linear valves**

Frustulia vulgaris and *B. linearis* are smaller species, differing from each other in valve shape, striation and the shape of the central area. Valves of *F. vulgaris* are linear to linear-elliptic, with valve margins forming a small shoulder when tapering towards the valve apices. Valves of *B. linearis* are linear, sometimes slightly constricted in the central part of the valve and margins taper gradually towards the apices. Striae at the valve centre are parallel in *B. linearis* but radiate with internally slightly thickened virgae in *F. vulgaris*. The central area of *F. vulgaris* is small and oval. Most valves of *B. linearis* examined in this study have a narrow, linear elongate central area; in one valve the central area was indistinct (Fig. 36). The raphe branches of *B. linearis* and *F. vulgaris* are slightly curved, terminating in small round or Y-shaped external raphe endings. The curvature of the raphe and the shape of the raphe endings were discussed by Ross & Sims (1978) as characters distinguishing *Berkella* from *Frustulia*. However, raphe structure varies between species currently assigned to *Frustulia*. Many species have a straight raphe with T-shaped external raphe endings, but others have a raphe similar to that in *B. linearis* and *F. vulgaris*.

Frustulia pumilio Lange-Bert. & Rumrich in Rumrich et al. (2000), a species described from wet rocks in Ecuador and similar in shape to *B. linearis,* has small, round proximal and distal raphe endings and adjacent shallow grooves. It differs from *B. linearis* by two oval, hyaline areas in the central part of the valve. *Frustulia kosmolliana* Lange-Bert. & Rumrich in Rumrich et al. (2000), described from Chile, is similar to *F. vulgaris* with respect to the curved raphe with small Y-shaped proximal and distal raphe ends, and the oval central area, but differs in width and in the arrangement of the marginal areolae. *Frustulia amphipleuroides* has the same raphe structure as *F. vulgaris* and *F. kosmolliana*.

Frustulia lange-bertalotii Metzeltin in Lange-Bertalot & Genkal (1999), described from Greenland, is similar to *F. vulgaris* when considering the overall valve shape and striation but the raphe is more or less straight with T-shaped raphe endings and the central area is elongate oval to linear (Lange-Bertalot & Genkal 1999). Another feature mentioned by Ross & Sims (1978), the depressions on either side of the raphe in *B. linearis*, is not a character that distinguishes *Berkella* from *Frustulia* but an erosion of the external valve surface, which we observed in some valves (Figs 37, 39) but not in others (Figs 36, 38). The separation of *Berkella* from *Frustulia* based on these morphological features is thus unsatisfactory (cf. Rumrich et al. 2000) while their new name, *F. amosseana* avoided the creation of a homonym.

It is questionable whether all specimens illustrated as *F. amosseana* by Lange-Bertalot (2001, figs 1–8) belong to the same taxon. The specimen from the Río Loa in Chile illustrated when

F. amosseana was first established (Rumrich et al. 2000, pl. 92, fig. 9 = Lange-Bertalot 2001, pl. 137, fig. 7) has broadly rounded, rostrate valve ends. This and other specimens including those with subcapitate ends (Lange-Bertalot 2001, figs 1–4, 7, 8 [including the holotype of *Frustulia vulgaris* var. *capitata* Krasske = fig. 1]; Lange-Bertalot et al. 2003, figs 4–16 [except fig. 9]) do not resemble the specimens with rostrate, narrowly rounded or cuneate valve ends from a variety of locations, which include Scotland and the type of *B. linearis* (Figs 1–14; Ross & Sims 1978, pl. 3, figs 22, 23), populations from the Shetland Islands (Carter & Bailey-Watts 1981, pl. 2, fig. 39, pl. 24, fig. 7, Carter 1993, figs 24, [25 is broadly rostrate] as *Berkella alpina*), from the Rhône-Alpes region in France (Bey & Ector 2013, p. 441, figs 1–28 as *B. amosseana*), from the Buenos Aires region, Argentina (Egüés-Weber & Maidana 1994, figs 2a–d), from Wales (Figs 22–35), and the type of *F. spicula* var. *alpina* from the French Alps (Figs 15–21; Amossé 1972, pl. 23, figs 2–6). A study of the type material of *Frustulia spicula* Amossé is needed to determine whether there is variability in the shape of the raphe endings and the central area, and whether specimens illustrated as *F. amosseana* in fact belong to *F. spicula*. The specimens of *B. linearis*, as illustrated here, are likely to be different to most of the specimens shown as *F. amosseana* by Rumrich et al. (2000), Lange-Bertalot (2001) and Lange-Bertalot et al. (2003), and the specimens from South America may well belong to a different species. We suggest that the name *B. linearis* should be retained for specimens resembling the type until further evidence can determine whether they belong to *Frustulia* or to the separate genus *Berkella*.

Peculiarities in valve structure in *Berkella*

The specimens of *B. linearis* found in Wales on subaerial bryophytes have two types of valves, those with structures typical for *Frustulia*, and those with a silica surface apparently lacking perforations, with barely discernible striae or raphe, and with a faint row of areolae beside the axial area. In his description of the *F. spicula* specimens found on wet rocks, Amossé (1932) referred to these two types of valves, the one with few structures (fig. 7) being an external valve. When establishing *F. spicula* var. *alpina*, Amossé (1972) described the abnormal valves as internal valves and because they were found in a ditch with permanently flowing water, dismissed desiccation as factor in their formation. According to Carter (1993), no internal plates were observed in specimens found at ten sites on the Isle of Mull (Ross & Sims 1978) or at five sites in southern Scotland and in the Shetland Islands. However, Carter (1993) found frequent 'internal plates' in capitate specimens (illustrated as *B. linearis*) collected from the surface of wet earth near Inverkirkraig, Sutherland, Scotland. The occurrence of these valves on wet earth and subaerial bryophytes suggests that the silica layer without perforations might be formed as an adaptation to protect the cells from desiccation in temporarily dry habitats.

Berkella linearis was found in a variety of habitats: in South Wales on bryophytes on a rock wall on a shaded vertical wall behind the Sgwd yr Eira waterfall of the River Hepste; in several Scottish locations including lochs, streams and a wet rock face on the island of Mull; Loch Grigadale on the west coast of Scotland north of Mull; in a bog and a flush in the Selkirk area; on Mainland, Shetland Islands; and in northern England in Slapestone Sike, a stream in the North Pennines, Upper Teesdale (Ross and Sims 1978; Carter & Bailey-Watts 1981). Amossé (1972) found *F. spicula* var. *alpina* in a calcareous stream near Pont de Brion, south of Monestier-de-Clermont in the French Alps, and Bey & Ector (2013) found it in an outlet of the Bouligons marsh at Charens, France. In the southern hemisphere, Egüés-Weber & Maidana (1994) reported it from three polluted, circumneutral to alkaline, nutrient-rich streams with high conductivity in the Buenos Aires region, Argentina.

Frustulia species with more lanceolate valves

Frustulia crassinervia, *F. quadrisinuata*, and *F. saxonica*, can be distinguished by their valve shape, and the shape and width of their valve apices. Valves of *F. saxonica* are rhombic in large and medium-sized valves, lanceolate to elliptic-lanceolate in smaller valves, with the valve margin tapering gradually to slightly protracted apices, in contrast to the clearly protracted and rostrate valve apices in *F. crassinervia* and *F. quadrisinuata*. In *F. crassinervia*, the valve margin can be slightly undulate and forms a small shoulder at the transition to the apices. *Frustulia quadrisinuata* has rhombic to rhombic-lanceolate valves and wider apices than both *F. saxonica* and *F. crassinervia*. The ultrastructure of these species is similar with respect to the T-shaped, slightly recurved, external raphe endings, continuous longitudinal ribs adjacent to the raphe internally, which can be slightly constricted at the valve centre, internally raised, rounded hymenate occlusions, and relatively short porte-crayon endings. In *F. quadrisinuata* areolae merge to form longitudinal lines on the valve surface adjacent to the raphe.

Frustulia erifuga and *F. amphipleuroides* are larger species with lanceolate valves with long porte-crayon endings. They differ in the shape of their central area, which is longer, narrow linear in the latter, and their raphe endings, which are small, v-shaped in *F. amphipleuroides* and T-shaped and slightly recurved in *F. erifuga*. Internally, areolae are occluded by large raised hymenes, quadrangular in shape in *F. erifuga* and oval, transapically elongated in *F. amphipleuroides*. Two morphotypes of *F. erifuga* were illustrated in Lange-Bertalot & Metzeltin (1996), with the specimens illustrated here conforming to 'morphotype I'. 'Morphotype II', with narrower valves and slightly protracted apices, was also found in Scotland. Material from Julma Ölkky, Kuursamo, Finland, and Scotland has recently been studied and will be described as a new species (Van de Vijver et al. unpub. res.). The presence or absence of areolae at the apices is not a character that separates these morphotypes because it is variable in both. Populations of *F. erifuga* which conform to ‘morphotype I’ contain specimens with and without a gap in the areolae at the apices.

Morphometric and molecular studies on *Frustulia*

Lange-Bertalot & Jahn (2000) distinguished between *F. saxonica* ‘morphotype I’ and ‘morphotype II’. The populations studied by the authors (unpubl. data) showed a variability in valve length and width that covers the range for both morphotypes reported by Lange-Bertalot & Jahn (2000). None of the larger cells in these populations had wider apices as shown in Lange-Bertalot & Metzeltin (1996). If populations with wider apices are found in ecological studies it might be prudent to distinguish them as ‘morphotype I’ so that data are available which allow us to investigate whether this morphotype is indicative of particular environmental conditions. Furthermore, we require better knowledge on the within species variability of the valve apices in relation to growth conditions. This can only be established by growth experiments (Rose & Cox 2014) or, perhaps, by continuous sampling in naturally changing environments, and would be helpful to determine whether environmental conditions cause the shape differences of *F. saxonica* and *F. crassinervia* given that a clear separation in molecular analysis was not possible in populations from North America (Bouchard et al. 2019). In a study of *Frustulia* from Florida, principal component analysis (PCA) based on morphology (length, width, valve shape, stria and areola density) resulted in two distinct groups, representing *F. saxonica* and *F. crassinervia*, although with some overlap (Siver & Baskette 2004). But similar to the study on North American species, molecular markers (rbcL-3P, D1-D2 region of LSU) were unable to delineate the species in the *F. saxonica - crassinervia* complex using collections from Scandinavia and Estonia. High morphological variability was matched by a wide ecological range within this complex and the inability to recognise distinct species (Urbánková et al. 2016.). Similarly, a phylogenetic analysis of *Frustulia rhomboides* sensu lato strains from across Europe using the D1-D2 region of LSU failed to separate lineages corresponding to the identified morphological taxa, perhaps due intraclonal polymorphism obscuring species boundaries of closely related species. A PCA analysis showed substantial overlap between the shapes of different lineages, while individual strains were separated. Strains of some lineages had restricted and others a wider geographical distribution. Molecular lineages and environmental factors such as hydrological conditions, pH and conductivity in different habitat types were linked (Veselá et al. 2012, Kulichová & Fialová 2016). Similar valve shape can evolve multiple times with lineages phylogenetically not always closely related resembling the same morphospecies (Bourchard et al. 2019, Mann et al. 2021). Names might also be applied inconsistently in both morphological and molecular studies, or cryptic species not recognised in morphological studies, leading to a mismatch in morphological and molecular analysis.

Conclusions

The species studied here can be distinguished using a range of morphological characters. The smallest species with linear to linear-elliptic valves, *B. linearis* and *F. vulgaris*, and the large species with lanceolate valves, *F. erifuga* and *F. amphipleuroides*, differed from each other in the shape of the central area, a character that varied little within species. *Frustulia saxonica*, *F. crassinervia* and *F. quadrisinuata* differed in valve shape, and in the shape and width of their apices. In our observations apices varied little in *F. quadrisinuata*. However, phenotypic plasticity, such as valve shape in *F. saxonica* and *F. crassinervia*, can be significant and might be linked to environmental conditions (Mann 1999, Kociolek & Stoermer 2010, Veselá et al. 2012). Both, *F. saxonica* and *F. crassinervia*, are frequently found in acid, dystrophic waters in the UK and elsewhere and further morphometric studies using shape analysis combined with an ecological analysis of their habitats would be helpful in understanding morphological variability within and between population across a range of habitat types (Kulichová & Fialová 2016, Urbánková et al. 2016, Bouchard et al. 2019, Jüttner et al. 2022). Raphe curvature and the shape of the raphe endings vary within species currently in *Frustulia*, and on this basis *B. linearis* might belong to *Frustulia*. However, a recent molecular analysis of several *Frustulia* taxa, including *F. vulgaris,* showed that the latter formed a lineage separated from others including the *F. saxonica/crassinervia* complex and *F. erifuga*. *Frustulia vulgaris* and *Frustulia cassieae* Lange-Bert. & T.Beier, a species described from New Zealand (Beier & Lange-Bertalot 2007) with small, Y-shaped raphe endings as in *F. amphipleuroides*, were separated from other *Frustulia* species and positioned close to the genera *Amphipleura*, *Berkeleya* and *Climaconeis* (Kulichová et al. 2020 suppl.). Taxa with this raphe structure might represent the genus *Berkella*, but this requires support from additional morphological and phylogenetic analysis that includes species such as *B. linearis* and *F. amphipleuroides*.

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Figure legends

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