

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

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15

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

17 **and my husband Alan Orange (1955–2023)**

18

19 With 158 figures

20 **Abstract:** We investigated the type material of *Berkella linearis*, *B. alpina*, *Frustulia*

21 *saxonica*, and *F. crassinervia*, and populations of these taxa and of *F. vulgaris*, *F.*

22 *quadrisinuata*, *F. erifuga*, and *F. amphipleuroides* from Scotland and Wales with light and

23 scanning electron microscopy. The species are distinguished from each other in light

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

31

## 32 **Introduction**

33 The genus *Frustulia* Rabenh. (1853, p. 50) *nom. cons.* contains predominantly freshwater  
34 species with linear, lanceolate or rhombic valves, uniseriate striae composed of small areolae  
35 aligned in apical and transapical rows, a raphe-sternum with robust internal longitudinal ribs  
36 on either side of the raphe fissures, merging with the helictoglossae near the apices to form a  
37 so-called porte-crayon ending (Greville 1863, Round et al. 1990). Many species possess T- or  
38 Y-shaped central raphe endings and terminal raphe fissures, although occasionally in some  
39 species round, teardrop-shaped or deflected endings can be found (Siver & Baskette 2004).  
40 On AlgaeBase, there are currently more than 200 names including varieties, subspecies and  
41 forms (Guiry & Guiry 2023), and over 400 names are listed on DiatomBase (Kociolek et al.  
42 2023).

43 Using both light and scanning electron microscopy, we document the morphology of six  
44 species in *Frustulia* from type material and recent collections in Scotland and Wales. These  
45 investigations include the type specimens belonging to the names of *Berkella linearis* R.Ross  
46 & P.A.Sims, *Berkella alpina* (Amossé) J.R.Carter *nom. illeg.*, and a recent *Berkella*  
47 population, all are compared to *Frustulia vulgaris* (Thwaites) De Toni, a species with a  
48 similar valve shape. The type material of *Frustulia saxonica* Rabenh. and *Frustulia*  
49 *crassinervia* (Bréb.) Lange-Bert. & Krammer, along with several recent *Frustulia*  
50 populations from the UK are compared to *Frustulia quadrisinuata* Lange-Bert., originally  
51 described from Julma Ölkky, Finland (Lange-Bertalot & Metzeltin 1996, p. 59, pl. 38, figs  
52 10–12, pl. 119, figs 1–2), and known from Scandinavia, Germany and Alaska (U.S.A.).  
53 Populations of *Frustulia erifuga* Lange-Bert. & Krammer in Lange-Bertalot & Metzeltin  
54 (1996, p. 58) and *Frustulia amphipleuroides* (Grunow) A.Cleve (Cleve-Euler 1934, p. 87)  
55 from Scotland and Wales, two larger species with lanceolate valves, are also illustrated.

56 **Taxonomic history of the species under consideration**

57 Ross & Sims (1978) established the genus *Berkella* R.Ross & P.A.Sims with *Berkella*  
58 *linearis* as *typus generis*, separating it from *Frustulia* because of its curved raphe, slightly  
59 reflexed, raphe endings, and the depressions with elongated areolae on either side of the  
60 raphe. In their paper, Ross & Sims (1978) discussed features shared with *Berkeleya* Grev. and  
61 *Amphipleura* Kütz. as studied by Cox (1975a, b). The description of the new genus was based  
62 on specimens from Loch Poit na h'I, Isle of Mull (Scotland, UK) with reference to the first  
63 description of this taxon as *Frustulia spicula* var. *alpina* Amossé from the French Alps by  
64 Amossé (1972), a variety separated from the nominate form because of its linear shape and  
65 non-capitate apices. Recognising that Amossé's new variety was invalid due to the lack of a  
66 type designation, Ross & Sims (1978) proposed a new epithet '*linearis*' for the species.

67 Contrary to the statement in Carter (1993 [that Ross & Sims regarded *B. linearis* as being  
68 identical to *Frustulia spicula* Amossé]), Ross & Sims (1978) were "reasonably certain" that  
69 *Berkella linearis* and *Frustulia spicula* var. *alpina* were conspecific, and also stated that the  
70 latter is not identical with *F. spicula*, but differed in valve outline and the arrangement of the  
71 central striae. Carter (1993, figs 1–23) illustrated capitate specimens as *B. linearis* and  
72 regarded specimens with rostrate apices ('poles non-capitate') not as a variety of the latter but  
73 transferred them to *Berkella* and elevated them to species rank, *Berkella alpina* (Amossé)  
74 J.R.Carter *nom. illeg.*

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

81 *spicula* var. *alpina* and *F. spicula* var. *spicula* partim (excluding the type of *F. spicula* [with  
82 capitate valve apices] from a location near Nantes [Amossé 1932, figs 6, 7; Amossé 1972, pl.  
83 23, figs 7–10]). Krammer & Lange-Bertalot (1986) and Rumrich et al. (2000) questioned the  
84 usefulness of the valve apex shape to distinguish between the varieties of *F. spicula*.  
85 Krammer & Lange-Bertalot (1986) could not observe populations of *F. spicula* with  
86 transitions from rostrate to capitate apices, but rejected the recognition of species or varieties  
87 based on this character because of their observations on *Frustulia vulgaris* (Krammer &  
88 Lange-Bertalot 1986, p. 261).

89 Rumrich et al. (2000) and Lange-Bertalot (2001) stated that there is a continuum between  
90 capitate and non-capitate forms of *F. amosseana*, i.e., the specimen illustrated as '*F. spicula*  
91 Amossé des Alpes' (Amossé 1972, pl. 23, fig. 1) and *F. spicula* var. *alpina* (Amossé 1972, pl.  
92 23, figs 2–6), and those from different geographical locations, i.e. from Germany, Syria,  
93 Chile and Sardinia (Lange-Bertalot 2001, pl. 137, figs 1–12, pl. 139, figs 7, 8). Specimens of  
94 *F. amosseana* showing a continuum of valves with short, protracted, rostrate valve apices to  
95 valves with sub-capitate apices are illustrated from Sardinia (Lange-Bertalot et al. 2003, pl.  
96 71, figs 4–16). Rumrich et al. (2000) separated *F. spicula* sensu stricto from *F. amosseana*  
97 based on the shape of the central nodule, small round or elliptic in the former and elongate,  
98 linear in the latter. Lange-Bertalot (2001) illustrated a population of *F. spicula* from Ecuador  
99 referring to the type (Amossé 1932, figs 6, 7) and illustrations in Carter & Bailey-Watts  
100 (1981, pl. 2, fig. 38, pl. 24, fig. 12). The morphology of *B. linearis* is here compared with *F.*  
101 *vulgaris*, first described as *Schizonema vulgare* Thwaites (1848, pl. 12, fig. H), a  
102 cosmopolitan species apparently found across a wide range of environmental conditions from  
103 oligotrophic to polluted waters.

104 *Frustulia saxonica* was first described from moist rocks in Saxony, Germany, the protologue  
105 stating that the valves (in valve view) have narrower, bluntly rounded apices '[...] gegen

106 beide Enden nachenförmig, verschmälert und stumpf gerundet [...]', with drawings of one  
107 frustule from both valve and girdle view, (Rabenhorst 1851, tab. III); four valves and one  
108 frustule were illustrated in Rabenhorst (1853, p. 50, tab. VII, *Frustulia* fig. 1). Type material  
109 has been examined by Lange-Bertalot & Metzeltin (1996) and Lange-Bertalot & Jahn (2000).  
110 It was composed of two sets of valves that differ in size ('morphotype I': 60–105µm long,  
111 15–19µm wide, max. width central nodule 3µm; 'morphotype II': 36–76µm long, 10.5–14µm  
112 wide, max. width central nodule 2–2.6µm), previously identified as *Frustulia rhomboides*  
113 var. *rhomboides* (Ehrenb.) De Toni and *Frustulia rhomboides* var. *saxonica* (Rabenh.) de  
114 Toni, respectively. Both were found associated with each other elsewhere and were illustrated  
115 from a peat bog in the Rhön Mountains, Germany, and from Julma Ölkky, Finland (Lange-  
116 Bertalot & Metzeltin 1996, figs 1–6, Lange-Bertalot & Jahn 2000, figs 7–11).

117 *Frustulia crassinervia* was described as *Navicula crassinervia* Bréb. in W. Smith (Smith  
118 1853, p.47, suppl. pl. 31, fig. 271) and later transferred to *Frustulia* (Lange-Bertalot &  
119 Metzeltin 1996, p. 57). Both species have been frequently reported and studied from low pH  
120 environments in the northern hemisphere, and are abundant in habitats with high humic acid  
121 content such as peat bogs in the Holarctic (Lange-Bertalot 2001, Siver et al. 2005, Siver &  
122 Hamilton 2011).

123 Two other less frequently recorded species of *Frustulia* are also considered. *Frustulia*  
124 *erifuga*, the current name for *Frustulia rhomboides* var. *viridula* (Bréb.) Cleve and based on  
125 *Colletonema viridulum* Bréb. ex Kütz. (1849, p. 105, Lange-Bertalot & Metzeltin 1996,  
126 Cleve 1894), is found in oligotrophic waters with low electrolyte content in the Holarctic  
127 (Lange-Bertalot 2001). The name *Colletonema* needs further investigation. It is attributed to  
128 de Brébisson and its first place of publication is usually given as Kützing (1849, p. 105). In  
129 this account, Kützing included three species: *Colletonema viridulum*, *C. lacustre*  
130 (Kützing 1849, p. 105) and, in the errata, *C. eximium* (Kützing 1849, p. 891). The first

131 appearance of *Colletonema* is actually in d'Orbigny's *Dictionnaire universel d'histoire*  
132 *naturelle* ([9<sup>th</sup> Sept.] 1848, pp. 418-9, nouvelle edition, v. 12, 1867, pp. 390-1), which  
133 includes a brief description of *C. viridulum* Bréb., with a somewhat different synonymy than  
134 usual. This needs further investigation. *Frustulia amphipleuroides*, a distinct species rather  
135 than a variety, replacing *Navicula rhomboides* var. *amphipleuroides* Grunow (Cleve &  
136 Grunow 1880, pl. 3, fig. 59), has been reported across a range of environmental conditions  
137 from oligotrophic to slightly polluted waters (Lange-Bertalot 2001).

138

### 139 **Methods and materials**

140 Type material of *Berkella alpina*, *B. linearis*, *Frustulia saxonica*, and *Navicula crassinervia*  
141 Bréb. ex. W.Sm., from the diatom collections at Natural History Museum, London, (BM) and  
142 Meise Botanic Garden (BR), and recently collected populations of *Berkella linearis*,  
143 *Frustulia amphipleuroides*, *F. crassinervia*, *F. erifuga*, *F. quadrisinuata*, *F. saxonica*, and *F.*  
144 *vulgaris*, collected from streams, a waterfall and a ditch in Scotland and Wales, were  
145 investigated. Diatom biofilms were either removed from stone surfaces with toothbrushes, or  
146 collected by cutting off small amounts of aquatic plant material or scraping off surface  
147 sediment with a spoon. All material was subsequently placed in plastic vials and preserved  
148 with 95% ethanol. Samples were heated and oxidised using H<sub>2</sub>O<sub>2</sub> to remove organic material  
149 and HCl to remove calcium deposits, cleaned by rinsing with distilled water and repeated  
150 centrifugation, and mounted on glass slides using Naphrax®.

151 Herbarium names (sources of material) are abbreviated according to Index Herbariorum  
152 (<http://sweetgum.nybg.org/science/ih/>). Diatom slides and suspensions are stored in the  
153 following collections NMW (Amgueddfa Cymru – Museum Wales), BM, and BR. For light  
154 microscopy (LM), diatoms were investigated at 1000× magnification and photographed using

155 a NIKON E600 microscope (DIC, 100× objective, N.A. 1.40) equipped with an  
156 IMAGINGSOURCE camera (DFK NME72AUC02) and using the NIS-Elements D Software  
157 (NMW). For scanning electron microscopy (SEM) a small amount of suspension was air  
158 dried onto cover glasses and mounted on stubs. They were then sputter-coated with a layer of  
159 platinum or with gold-palladium and studied with a Zeiss Gemini Ultra plus SEM microscope  
160 (working distance 3–12 mm, 3–5 kV, NHM). Photo plates were made using CorelDraw v.12  
161 (NMW). Terminology follows Anonymous (1975), Ross et al. (1979) and Round et al.  
162 (1990).

163

#### 164 **Observations**

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

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

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

168 TYPE *Berkella linearis*:—UNITED KINGDOM, Loch Poit na h'I, Isle of Mull, Scotland,  
169 56.32070160°N, -6.34455601°W, BM 78075 [https://data.nhm.ac.uk/object/ef906ed7-0da2-](https://data.nhm.ac.uk/object/ef906ed7-0da2-4edf-981f-b3dd66f72253)  
170 [4edf-981f-b3dd66f72253](https://data.nhm.ac.uk/object/ef906ed7-0da2-4edf-981f-b3dd66f72253)

171 TYPE *Berkella alpina*:—UK, Ettrick Valley, Scottish Borders, Scotland, slide 'Tushie Law  
172 Valley, Ettrick, Gordon Arms, flush', BM 94636 [https://data.nhm.ac.uk/object/408da237-](https://data.nhm.ac.uk/object/408da237-47b2-4358-9e2b-f563bc566803)  
173 [47b2-4358-9e2b-f563bc566803](https://data.nhm.ac.uk/object/408da237-47b2-4358-9e2b-f563bc566803)

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



177 OBSERVATIONS: Valves linear with short protracted, subrostrate apices (Figs 1–35). Valve  
178 dimensions: type *B. linearis* (n=15): length 26.5–48.5 µm, width 5.5–7.0 µm, type *B. alpina*  
179 (n=7): length 32.0–47.5 µm, width 6.0–7.0 µm, population from waterfall Sgwd yr Eira  
180 waterfall, River Hepste (n=19): length 24.5–51.0 µm, width 5.5–7.0 µm. Striae fine,  
181 discernible in LM, punctate, parallel, becoming convergent towards valve ends, type *B.*  
182 *linearis* and type *B. alpina*: 30–31 in 10 µm, population from waterfall Sgwd yr Eira: 29–31  
183 in 10 µm. Striae encircling apices consist of 2–6 areolae. External areola openings round to  
184 oval, transapically elongated (Figs 36–39). External valve surface sometimes covered by a  
185 silica layer (Figs 40–43). Internally areola openings transapically elongated, occluded by  
186 individual hymenes (Figs 44–47). Axial area narrow, lanceolate, not continuing to apex,  
187 terminating at short distance from raphe endings, separated from apex by encircling striae.  
188 Central area narrow, linear, sometimes indistinct. Raphe slightly curved, terminating in  
189 hardly widened, straight central and terminal endings, terminal raphe fissures absent (Figs  
190 36–38). Shallow grooves present adjacent to central raphe endings (Figs 37, 38). Internally,  
191 longitudinal ribs on both sides of raphe interrupted at valve centre, terminating beside ends of  
192 elongated central nodule. Near valve apices ribs terminating beside or fusing with elongated  
193 helictoglossae to form porte-crayon endings (Figs 44–46). Internal areola openings oval,  
194 transapically elongated, occluded by individual hymenes (Fig. 47).

195

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

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

198 ANALYSED MATERIAL: NMW.C.2011.025.2011.Wales.3, ditch at RSPB Newport Wetlands,

199 Newport, Wales, 51.543291°N, -2.961348°W.

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

215

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

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

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

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

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

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

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

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

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

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

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

247

248 *Frustulia crassinervia* (Bréb. ex. W.Sm.) Lange-Bert. & Krammer 1996, p. 57, pl. 38, figs  
249 7–9

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

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

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

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

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

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

256 TYPE:—FRANCE, Falaise, sample *Navicula crassinervia*, July 23, 1852, leg. A. de Brébisson  
257 (Smith 1853, p. 47), BR-4805, **lectotype here designated**; Falaise, BM 18883 (Kützing  
258 1674), isolectotype.

259 REGISTRATION: —<http://phycobank.org/XXXX>

260 Casa et al. (2018, p. 57) discussed the origin of the type material of *N. crassinervia*. The  
261 protologue for *N. crassinervia* in Smith (1853) lists syntype material from Wareham  
262 (‘September 1849, W.Sm.’) ‘Snow Mud, Grampians’ (collected by ‘Dr. Dickie’) and Dolgelly  
263 (collected by ‘Mr. Ralfs’) as well as ‘ad specimina sub hoc nomine quae misit cl. De  
264 Brebisson, Sept. 1852’ (Smith 1853, p. 47). A search in the Van Heurck diatom collection at  
265 BR yielded the original Brébisson material from Falaise, France, which should correspond to  
266 the ‘Sept. 1852’ material noted. It contains a fairly large population of *Navicula crassinervia*.  
267 This material should be considered as the lectotype material for the species. As Casa et al.  
268 (2018) did not lectotypify the material we designate BR-4805 as lectotype for *N.*  
269 *crassinervia*.

270 ADDITIONAL MATERIAL: NMW.C.2021.02.Scotland.11/21.24aeropeat.filalg, stream at  
271 Ryvoan, Aberneth National Nature Reserve, Highland, Scotland, 57.181439°N, -  
272 3.6472372°W.

273 OBSERVATIONS: Valves lanceolate to elliptic-lanceolate with protracted, rostrate apices (Figs  
274 96–112). Valve dimensions: type population Brébisson: (n = 15): length 46.5–51.0 µm, width  
275 12.0–13.5 µm; population from a stream at Ryvoan, Aberneth National Nature Reserve,  
276 Highland, Scotland (n = 12): length 44.0–54.5 µm, width 10.5–13.0 µm. Striae fine,  
277 discernible in LM, parallel, near apices parallel or slightly convergent, type population  
278 Brébisson: 35–40 in 10 µm, stream at Ryvoan: 33 in 10 µm; longitudinal striae slightly wavy.  
279 Striae encircling valve apices reduced to 2–3 areolae, one at centre of apex (Figs 114, 116).  
280 External areola openings small, slit-like, apically elongated. Areola openings beside central  
281 area small, rounded to oval, transapically elongated (Figs 115, 116). Internal areola openings  
282 larger, circular, elongated near apices, occluded by raised individual hymenes (Fig. 118).  
283 Axial area narrow, linear, not continuing to valve apices, terminating some distance from  
284 raphe endings, separated from apex by one row of areolae. Central area short, elongate, either  
285 lacking or with small constriction on one or both sides. Raphe straight, terminating in T-  
286 shaped, slightly recurved, raphe endings (Figs 113–116). Internally, longitudinal ribs on both  
287 sides of raphe widening slightly towards valve centre, then narrowing slightly on one or both  
288 sides beside central nodule. Ribs fusing at valve apices with elongate, linear helictoglossae to  
289 form short porte-crayon endings (Figs 117–118).

290

291 *Frustulia quadrisinuata* Lange-Bert.in Lange-Bertalot & Metzeltin 1996, p. 59, pl. 38, figs  
292 10–12, pl. 119, figs 1–2

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

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

309

310 *Frustulia erifuga* Lange-Bert. & Krammer in Lange-Bertalot & Metzeltin 1996, p. 58, pl. 39,  
311 figs 1–4, pl. 120, figs 1–3

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

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

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

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

317 = *Frustulia viridula* (Bréb.) F.Schaarschm. (1881, p. 158), non = *Frustulia viridula* Kütz.  
318 = *Frustulia viridula* (Bréb.) De Toni (1891, p. 278)  
319 = *Frustulia rhomboides* var. *viridula* (Bréb. ex Kütz.) Cleve (1894, p. 123)  
320 = *Navicula rhomboides* var. *viridula* (Bréb. ex Kütz.) Mills (1934, p. 1137)  
321 = *Vanheurckia rhomboides* var. *viridula* (Bréb.) Mills (1935, p. 1680)

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

326 ANALYSED MATERIAL: NMW.C.2021.02.Scot.11/21.24aeropeat.filalg, stream at Ryvoan,  
327 Aberneth National Nature Reserve, Highland, Scotland, 57.181439°N, -3.6472372°W;  
328 NMW.C.2011.019.06/11.IF34, Nant Hir, tributary to River Irfon, Powys, Wales,  
329 52.174333°N, -3.700467°W.

330 OBSERVATIONS: Valves lanceolate with rounded or cuneate apices, not or hardly protracted  
331 (Figs 134–139). Valve dimensions: population from stream at Ryvoan, Aberneth National  
332 Nature Reserve, Highland, Scotland (n = 5): length 94.0–130.0 µm, width 17.0–19.5 µm;  
333 population from the stream Nant Hir (n = 11): length 63.0–95 µm, width 14.5–17.5 µm.  
334 Striae fine, discernible in LM, punctate, 26–27 in 10 µm in both populations, parallel in  
335 central part of valve, becoming slightly convergent towards apices. External areola openings  
336 small, oval, apically elongated. Areola openings beside central area round (Figs 142, 144).  
337 Internal areola openings larger, occluded by raised, quadrangular individual hymenes (Figs  
338 143, 145–147). Axial area narrow, linear, terminating some distance from raphe endings,  
339 continuing to valve apices or separated from apices by one or two rows of areolae (Figs 144,  
340 145). Central area narrow, oval. Raphe straight, terminating in T-shaped, slightly recurved,

341 raphe endings (Figs 140, 142, 144). Internally, longitudinal ribs on sides of raphe widening  
342 slightly on one or both sides at valve centre adjacent to central nodule (Fig. 143). Ribs fusing  
343 with elongate, linear helictoglossae to form long porte-crayon endings at valve apices (Fig.  
344 145).

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

346

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

348 Basionym: *Navicula rhomboides* var. *amphipleuroides* Grunow in Cleve & Grunow (1880:  
349 47)

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

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

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

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

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

355 ANALYSED MATERIAL: NMW.C.2012.018.SEPA.2048545, Coy Burn at Damhead,

356 Aberdeenshire, Scotland 57.072939°N, -2.400922°W.

357 OBSERVATIONS: Valves lanceolate with rounded apices, not or hardly protracted (Figs 148–  
358 152). Valve dimensions: population from Coy Burn at Damhead, Aberdeenshire, Scotland  
359 (n=7) length 109.0–116.0 µm, width 18.5–20.5 µm. Striae fine, discernible in LM, punctate,  
360 23–24 in 10 µm, parallel in central part of valve, becoming slightly convergent towards  
361 apices. Striae around valve apices comprising 3–7 areolae (Fig. 157). External areola  
362 openings small, oval, apically elongated. Areola openings of row beside central area round  
363 (Fig. 155). Internal areola openings larger, occluded by raised, oval, transapically elongated  
364 individual hymenes (Figs 156, 158). Axial area narrow, linear, terminating some distance



365 from raphe endings, narrowing towards valve apices, separated from apices by peripheral  
366 striae (Fig. 157). Central area long, narrow, linear. Raphe slightly curved with slightly  
367 deflected central raphe endings, terminating in small, Y-shaped raphe endings (Figs 155,  
368 157). Internally, longitudinal ribs on sides of the raphe widening slightly and merging with  
369 central nodule (Figs 154, 156). Ribs fusing with elongate, linear helictoglossae to form long  
370 porte-crayon endings at valve apices (Fig. 158).

371

## 372 **Discussion**

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

377

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

379 *Frustulia vulgaris* and *B. linearis* are smaller species, differing from each other in valve  
380 shape, striation and the shape of the central area. Valves of *F. vulgaris* are linear to linear-  
381 elliptic, with valve margins forming a small shoulder when tapering towards the valve apices.  
382 Valves of *B. linearis* are linear, sometimes slightly constricted in the central part of the valve  
383 and margins taper gradually towards the apices. Striae at the valve centre are parallel in *B.*  
384 *linearis* but radiate with internally slightly thickened virgae in *F. vulgaris*. The central area of  
385 *F. vulgaris* is small and oval. Most valves of *B. linearis* examined in this study have a  
386 narrow, linear elongate central area; in one valve the central area was indistinct (Fig. 36). The  
387 raphe branches of *B. linearis* and *F. vulgaris* are slightly curved, terminating in small round  
388 or Y-shaped external raphe endings. The curvature of the raphe and the shape of the raphe

389 endings were discussed by Ross & Sims (1978) as characters distinguishing *Berkella* from  
390 *Frustulia*. However, raphe structure varies between species currently assigned to *Frustulia*.  
391 Many species have a straight raphe with T-shaped external raphe endings, but others have a  
392 raphe similar to that in *B. linearis* and *F. vulgaris*.

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

401 *Frustulia lange-bertalotii* Metzeltin in Lange-Bertalot & Genkal (1999), described from  
402 Greenland, is similar to *F. vulgaris* when considering the overall valve shape and striation but  
403 the raphe is more or less straight with T-shaped raphe endings and the central area is elongate  
404 oval to linear (Lange-Bertalot & Genkal 1999). Another feature mentioned by Ross & Sims  
405 (1978), the depressions on either side of the raphe in *B. linearis*, is not a character that  
406 distinguishes *Berkella* from *Frustulia* but an erosion of the external valve surface, which we  
407 observed in some valves (Figs 37, 39) but not in others (Figs 36, 38). The separation of  
408 *Berkella* from *Frustulia* based on these morphological features is thus unsatisfactory (cf.  
409 Rumrich et al. 2000) while their new name, *F. amosseana* avoided the creation of a  
410 homonym.

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

413 *F. amosseana* was first established (Rumrich et al. 2000, pl. 92, fig. 9 = Lange-Bertalot 2001,  
414 pl. 137, fig. 7) has broadly rounded, rostrate valve ends. This and other specimens including  
415 those with subcapitate ends (Lange-Bertalot 2001, figs 1–4, 7, 8 [including the holotype of  
416 *Frustulia vulgaris* var. *capitata* Krasske = fig. 1]; Lange-Bertalot et al. 2003, figs 4–16  
417 [except fig. 9]) do not resemble the specimens with rostrate, narrowly rounded or cuneate  
418 valve ends from a variety of locations, which include Scotland and the type of *B. linearis*  
419 (Figs 1–14; Ross & Sims 1978, pl. 3, figs 22, 23), populations from the Shetland Islands  
420 (Carter & Bailey-Watts 1981, pl. 2, fig. 39, pl. 24, fig. 7, Carter 1993, figs 24, [25 is broadly  
421 rostrate] as *Berkella alpina*), from the Rhône-Alpes region in France (Bey & Ector 2013, p.  
422 441, figs 1–28 as *B. amosseana*), from the Buenos Aires region, Argentina (Egüés-Weber &  
423 Maidana 1994, figs 2a–d), from Wales (Figs 22–35), and the type of *F. spicula* var. *alpina*  
424 from the French Alps (Figs 15–21; Amossé 1972, pl. 23, figs 2–6). A study of the type  
425 material of *Frustulia spicula* Amossé is needed to determine whether there is variability in  
426 the shape of the raphe endings and the central area, and whether specimens illustrated as *F.*  
427 *amosseana* in fact belong to *F. spicula*. The specimens of *B. linearis*, as illustrated here, are  
428 likely to be different to most of the specimens shown as *F. amosseana* by Rumrich et al.  
429 (2000), Lange-Bertalot (2001) and Lange-Bertalot et al. (2003), and the specimens from  
430 South America may well belong to a different species. We suggest that the name *B. linearis*  
431 should be retained for specimens resembling the type until further evidence can determine  
432 whether they belong to *Frustulia* or to the separate genus *Berkella*.

433

#### 434 **Peculiarities in valve structure in *Berkella***

435 The specimens of *B. linearis* found in Wales on subaerial bryophytes have two types of  
436 valves, those with structures typical for *Frustulia*, and those with a silica surface apparently

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

450 *Berkella linearis* was found in a variety of habitats: in South Wales on bryophytes on a rock  
451 wall on a shaded vertical wall behind the Sgwd yr Eira waterfall of the River Hepste; in  
452 several Scottish locations including lochs, streams and a wet rock face on the island of Mull;  
453 Loch Grigadale on the west coast of Scotland north of Mull; in a bog and a flush in the  
454 Selkirk area; on Mainland, Shetland Islands; and in northern England in Slapestone Sike, a  
455 stream in the North Pennines, Upper Teesdale (Ross and Sims 1978; Carter & Bailey-Watts  
456 1981). Amossé (1972) found *F. spicula* var. *alpina* in a calcareous stream near Pont de Brion,  
457 south of Monestier-de-Clermont in the French Alps, and Bey & Ector (2013) found it in an  
458 outlet of the Bouligons marsh at Charens, France. In the southern hemisphere, Egiús-Weber  
459 & Maidana (1994) reported it from three polluted, circumneutral to alkaline, nutrient-rich  
460 streams with high conductivity in the Buenos Aires region, Argentina.

461

462 ***Frustulia* species with more lanceolate valves**

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

476 *Frustulia erifuga* and *F. amphipleuroides* are larger species with lanceolate valves with long  
477 porte-crayon endings. They differ in the shape of their central area, which is longer, narrow  
478 linear in the latter, and their raphe endings, which are small, v-shaped in *F. amphipleuroides*  
479 and T-shaped and slightly recurved in *F. erifuga*. Internally, areolae are occluded by large  
480 raised hymenes, quadrangular in shape in *F. erifuga* and oval, transapically elongated in *F.*  
481 *amphipleuroides*. Two morphotypes of *F. erifuga* were illustrated in Lange-Bertalot &  
482 Metzeltin (1996), with the specimens illustrated here conforming to ‘morphotype I’.  
483 ‘Morphotype II’, with narrower valves and slightly protracted apices, was also found in  
484 Scotland. Material from Julma Ölkky, Kuorsamo, Finland, and Scotland has recently been  
485 studied and will be described as a new species (Van de Vijver et al. unpub. res.). The  
486 presence or absence of areolae at the apices is not a character that separates these

487 morphotypes because it is variable in both. Populations of *F. erifuga* which conform to  
488 ‘morphotype I’ contain specimens with and without a gap in the areolae at the apices.

489

#### 490 **Morphometric and molecular studies on *Frustulia***

491 Lange-Bertalot & Jahn (2000) distinguished between *F. saxonica* ‘morphotype I’ and  
492 ‘morphotype II’. The populations studied by the authors (unpubl. data) showed a variability  
493 in valve length and width that covers the range for both morphotypes reported by Lange-  
494 Bertalot & Jahn (2000). None of the larger cells in these populations had wider apices as  
495 shown in Lange-Bertalot & Metzeltin (1996). If populations with wider apices are found in  
496 ecological studies it might be prudent to distinguish them as ‘morphotype I’ so that data are  
497 available which allow us to investigate whether this morphotype is indicative of particular  
498 environmental conditions. Furthermore, we require better knowledge on the within species  
499 variability of the valve apices in relation to growth conditions. This can only be established  
500 by growth experiments (Rose & Cox 2014) or, perhaps, by continuous sampling in naturally  
501 changing environments, and would be helpful to determine whether environmental conditions  
502 cause the shape differences of *F. saxonica* and *F. crassinervia* given that a clear separation in  
503 molecular analysis was not possible in populations from North America (Bouchard et al.  
504 2019). In a study of *Frustulia* from Florida, principal component analysis (PCA) based on  
505 morphology (length, width, valve shape, stria and areola density) resulted in two distinct  
506 groups, representing *F. saxonica* and *F. crassinervia*, although with some overlap (Siver &  
507 Baskette 2004). But similar to the study on North American species, molecular markers  
508 (rbcL-3P, D1-D2 region of LSU) were unable to delineate the species in the *F. saxonica* -  
509 *crassinervia* complex using collections from Scandinavia and Estonia. High morphological  
510 variability was matched by a wide ecological range within this complex and the inability to

511 recognise distinct species (Urbánková et al. 2016.). Similarly, a phylogenetic analysis of  
512 *Frustulia rhomboides* sensu lato strains from across Europe using the D1-D2 region of LSU  
513 failed to separate lineages corresponding to the identified morphological taxa, perhaps due  
514 intraclonal polymorphism obscuring species boundaries of closely related species. A PCA  
515 analysis showed substantial overlap between the shapes of different lineages, while individual  
516 strains were separated. Strains of some lineages had restricted and others a wider  
517 geographical distribution. Molecular lineages and environmental factors such as hydrological  
518 conditions, pH and conductivity in different habitat types were linked (Veselá et al. 2012,  
519 Kulichová & Fialová 2016). Similar valve shape can evolve multiple times with lineages  
520 phylogenetically not always closely related resembling the same morphospecies (Bourchard  
521 et al. 2019, Mann et al. 2021). Names might also be applied inconsistently in both  
522 morphological and molecular studies, or cryptic species not recognised in morphological  
523 studies, leading to a mismatch in morphological and molecular analysis.

524

## 525 **Conclusions**

526 The species studied here can be distinguished using a range of morphological characters. The  
527 smallest species with linear to linear-elliptic valves, *B. linearis* and *F. vulgaris*, and the large  
528 species with lanceolate valves, *F. erifuga* and *F. amphipleuroides*, differed from each other in  
529 the shape of the central area, a character that varied little within species. *Frustulia saxonica*,  
530 *F. crassinervia* and *F. quadrisinuata* differed in valve shape, and in the shape and width of  
531 their apices. In our observations apices varied little in *F. quadrisinuata*. However, phenotypic  
532 plasticity, such as valve shape in *F. saxonica* and *F. crassinervia*, can be significant and  
533 might be linked to environmental conditions (Mann 1999, Kociolek & Stoermer 2010, Veselá  
534 et al. 2012). Both, *F. saxonica* and *F. crassinervia*, are frequently found in acid, dystrophic

535 waters in the UK and elsewhere and further morphometric studies using shape analysis  
536 combined with an ecological analysis of their habitats would be helpful in understanding  
537 morphological variability within and between population across a range of habitat types  
538 (Kulichová & Fialová 2016, Urbánková et al. 2016, Bouchard et al. 2019, Jüttner et al. 2022).  
539 Raphe curvature and the shape of the raphe endings vary within species currently in  
540 *Frustulia*, and on this basis *B. linearis* might belong to *Frustulia*. However, a recent  
541 molecular analysis of several *Frustulia* taxa, including *F. vulgaris*, showed that the latter  
542 formed a lineage separated from others including the *F. saxonica/crassinervia* complex and  
543 *F. erifuga*. *Frustulia vulgaris* and *Frustulia cassieae* Lange-Bert. & T.Beier, a species  
544 described from New Zealand (Beier & Lange-Bertalot 2007) with small, Y-shaped raphe  
545 endings as in *F. amphipleuroides*, were separated from other *Frustulia* species and positioned  
546 close to the genera *Amphipleura*, *Berkeleya* and *Climaconeis* (Kulichová et al. 2020 suppl.).  
547 Taxa with this raphe structure might represent the genus *Berkella*, but this requires support  
548 from additional morphological and phylogenetic analysis that includes species such as *B.*  
549 *linearis* and *F. amphipleuroides*.

550

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557

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596 phénomènes de la nature l’étymologie et la définition des noms scientifiques, les  
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686 **Figure legends**

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689 Valley, Scottish Borders, Scotland; Figs 22–35. NMW.C.2022.06.Wales.2021.3bryo,  
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702 Scale bar = 10  $\mu\text{m}$ . Figs 58–63. SEM. Fig. 58. External view of whole valve. Fig. 59. Internal  
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704 centre. Fig. 62. External view of valve end. Fig. 63. Internal view of valve end. Scale bars:  
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709 NMW.C.2022.02.Esgair.Forest.Lliwdy.1.7/2016, stream Nant Lliwdy, Gwynedd, Wales.  
710 Scale bar = 10  $\mu$ m.

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712 stream Nant Lliwdy, Gwynedd, Wales. Fig. 90. External view of whole valve. 91. Internal  
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717 *Navicula crassinervia*, BR-4805, lectotype; Figs 104–112.  
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719 Nature Reserve, Highland, Scotland. Scale bar = 10  $\mu$ m.

720 Figs 113–118. *Frustulia crassinervia*. SEM.  
721 NMW.C.2021.02.Scotland.11/21.24aeropeat.filalg, stream at Ryvoan, Aberneth National  
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727 NMW.C.2021.02.Scot.11/21.15sed, Loch Mallachie, Highland, Scotland. Scale bar = 10  $\mu$ m.

728 Figs 126–133. *Frustulia quadrisinuata* SEM. NMW.C.2021.02.Scot.11/21.15sed, Loch  
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734 Fig. 131 = 400 nm.

735 Figs 134–139. *Frustulia erifuga*. LM, valve views. Figs 134, 135.  
736 NMW.C.2021.02.Scotland.11/21.24aeropeat.filalg, stream at Ryvoan, Aberneth National  
737 Nature Reserve, Highland, Scotland; Figs 136–139. NMW.C.2011.019.06/11.IF34, stream  
738 Nant Hir, tributary to River Irfon, Powys, Wales. Scale bar = 10  $\mu\text{m}$ .

739 Figs 140–147. *Frustulia erifuga*. SEM. NMW.C.2021.02.Scotland.11/21.24aeropeat.filalg,  
740 stream at Ryvoan, Aberneth National Nature Reserve, Highland, Scotland. Fig. 140. External  
741 view of whole valve. Fig. 141. Internal view of whole valve. Fig. 142. External view of valve  
742 centre. Fig. 143. Internal view of valve centre. Fig. 144. External view of valve end. Fig. 145.  
743 Internal view of valve end. Fig. 146, 147. View of internal areola occlusions. Scale bars: Figs  
744 140, 141 = 10  $\mu\text{m}$ , Figs 142, 144 = 2  $\mu\text{m}$ , Figs 143, 145 = 1  $\mu\text{m}$ , Fig. 146 = 400 nm, Fig. 147  
745 = 100 nm.

746 Figs 148–152. *Frustulia amphipleuroides* LM, valve views.  
747 NMW.C.2012.018.SEPA.2048545, Coy Burn at Damhead, Aberdeenshire, Scotland. Scale  
748 bar = 10  $\mu\text{m}$ .

749 Figs 153–158. *Frustulia amphipleuroides* SEM. NMW.C.2012.018.SEPA.2048545, Coy  
750 Burn at Damhead, Aberdeenshire, Scotland. Fig. 153. External view of whole valve. Fig. 154.  
751 Internal view of whole valve. Fig. 155. External view of valve centre. Fig. 156. Internal view  
752 of valve centre. Fig. 157. External view of valve end. Fig. 158. Internal view of valve end.  
753 Scale bars: Figs 153, 154 = 10  $\mu\text{m}$ , Figs 155–157 = 2  $\mu\text{m}$ , Fig. 158 = 1  $\mu\text{m}$ .

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