Lectotypification of *Fragilariforma undata* (W.Smith) Heudre & al. (*Fragilariaceae, Bacillariophyceae*)

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In 1855, the Reverend William Smith (1808–1857) reported on a collection trip he made in May and June 1854 to southern France and the Auvergne (Smith 1855), during which he collected almost 50 samples from both marine and freshwater habitats. In his report, he described several new species such as Orthoseira spinosa W.Smith (Kochman-Kędziora & al. 2023) and Fragilaria undata W.Smith. The latter species, illustrated by a few line drawings (Fig. 1) was observed in a sample collected on 24.vi.1854 from Lake Guéry, at an elevation of 4066 ft, not far from the city of Clermont-Ferrand in the Massif Central, France (Fig. 2). Smith (1855: 7) provided a short description: "Filaments imperfectly tenacious; frustules frequently cohering by their angles; valve oval or linear, acuminate. Striae 42 in .001". Length of frustule .0006" to .0008". Smith (1856: 24) repeated this description in his Synopsis of the British Diatomaceae and illustrated it a second time (Fig. 2) but omitted the word 'linear' from the original description. He separated two varieties, with the un-named "var. β " characterised as "Valve linear, acuminate. Length of frustule $\cdot 0008$ " to \cdot 0012". v.v.*" and the un-named "var. γ " as "Valve constricted in the centre. Length of frustule $\cdot 0008$ " to $\cdot 0021$ ". v.v.". Smith (1856: 24) attributed the "var. γ " to a sporangial form of *Odontidium* tabellariae referring to "Greg. M.J. vol. ii, pl. iv 22", a paper published in 1854 by William Gregory (1803–1858) on the Mull deposit where the latter illustrated two valves as "*Remarkable* sporangial frustules of Odontidium tabellariae β " (Gregory 1854: legend to pl. IV, incorrectly indicating 'pustules' in lieu of 'frustules').

Apart from the Mull deposit sample, Smith (1855,1856) indicated two other localities, although the third locality, Christiana (Norway) attributed to "Dr. Arnott" [George Arnott Walker Arnott (1799–1868)], was only added in Smith (1856). Analysis of Walker Arnott sample S171 from Christiana (Norway), a sample collected by Norman according to the hand-written catalogue that accompanied the Walker Arnott collection in **BR** (Meise Botanic Garden), showed that only a handful of valves identified as *F. undata* could be observed, together with hundreds of valves of *F. virescens* Ralfs (Van de Vijver, pers. obs.). The main source material for the description, therefore, seems to be the *River Mortes, Mont Dore, elev. 4066 ft., June 1854, leg. W. Sm.* for 'all three forms' of *F. undata*. This River Mortes is most likely known nowadays as the Ruisseau des Mortes de Guéry, a small brook starting on the slopes of the Puy Gros and flowing into the Lac du Guéry (Guéry Lake). In the Van Heurck collection, part of **BR**, a major part of the samples collected by W. Smith for his *Synopsis of the British Diatomaceae*, is conserved (Hoover 1976). Among the hundreds of samples from Britain and Ireland, there are ca. 20 samples that were collected in 1854 during the trip William Smith made in the Auvergne. One of these samples was collected from the River Mortes (Fig. 8). The sample label contains all the necessary information to justify the choice of the latter as

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^{*}vidi vivam: seen in the living state.

type material for the species, including a small line drawing showing the typical valve outline of F. *undata*.

Grunow (1862: 374) discussed the taxonomic identity of *F. undata* and concluded that "*Ich weiss nicht aus welchem Grunde Smith* Fragilaria undata *als Art abgeschieden hat, da er selbst* Fragilaria virescens *als in Zickzackketten vorkommend abbildet. Die eine Schalenansicht der* Fragilaria undata *ohne mittlere Einschnürung unterscheidet sich durchaus nicht von kurzen breiten Formen der* Fragilaria virescens" [I know not why Smith separated *Fragilaria undata* as a species, he himself illustrated *Fragilaria virescens* as living in zigzag chains. The single valve face view of *Fragilaria undata undata* without the central constriction can usually not be separated from the shorter, broader forms of *Fragilaria virescens*]. Grunow (1862: 373) described *F. virescens* var. β *diatomacea* Grunow with *F. undata* W.Smith as a synonym, that formed zigzag-chains. Additionally, he included the varieties β and γ of *F. undata*, in his new variety *F. virescens* var. γ *undata* Grunow together with *F. constricta sensu* Ehrenberg (1854: pl. XVI [16]. II. 34, 35) and *F. binodis* Ehrenberg as additional synonyms.

However, eighteen year later, Grunow (in Van Heurck 1881, plate XLIV [44]: fig. 9) illustrated *Fragilaria undata* at the species rank based on material from Marstrand in Sweden (Grunow sample 2145). A short description ('*Les contours varient beaucoup. Tantôt il n'y a pas de rétrécissement, tantôt il y en a un ou plusieurs*' [The outlines vary a lot. Sometimes, there is no constriction, sometimes there is one or several.]) was added. It is, however, remarkable that Grunow's 1862 concept was not followed by later authors; following a thorough literature search, Grunow's names have not been found in any later publication (Van de Vijver, pers. obs.)

Hustedt (1930: 144, fig. 149 A, B) likewise illustrated *Fragilaria undata* but separated the smaller, less constricted valves as a separate variety, *F. undata* var. *quadrata* Hustedt (fig. 149 B, two examples). A year later, in Hustedt (1931: 166), he included his new variety as a synonym for *Fragilaria constricta* f. *stricta* (A.Cleve) Hustedt, a form described by Astrid Cleve as *F. undata* f. *stricta* A.Cleve from Lule Lappmark in Sweden (Cleve-Euler 1895: 35). Although not illustrated in Cleve-Euler (1895), the forma was later documented in Cleve-Euler (1953, fig. 362 n–p). The var. *quadrata* valves illustrated in Simonsen (1987, pl. 190: figs 4–7) and the valves shown in Cleve-Euler (1953) fit entirely within the observed diminution series of *F. undata* observed in the River Mortes sample and therefore these names should now be considered synonyms of *F. undata*. Mayer (1937:53) redescribed Smith's species as *Fragilaria virescens* var. *undatiformis* Mayer, clearly referring to a previous record he made in Mayer (1917, p. 20, plate 1, fig. 2). Inspection of the drawing shows no difference with *F. undata* and therefore the name *F. virescens* var. *undatiformis* should also be considered a heterotypic synonym.

Hustedt (1931) considered *F. undata* to be a synonym of *Fragilaria constricta* Ehrenberg, a species described in 1843 from the Falkland Islands and Mexico (Ehrenberg 1843: 415) and illustrated by Ehrenberg with several line drawings (Ehrenberg 1843: taf. I: 1, fig. 21, taf. III: 6, fig. 10, see Figs 4–5). Ehrenberg (1854, plate XVI [16], I: figs 19, 20 and III [3]: figs 34, 35) identified four valves he observed in the Bergmehl [Mountain Meal, sold as an additive to food in poorer times] from Degernfors and Lillhagsjön in Sweden as *F. constricta* (Figs 6–7). Hustedt (1931) used the European populations identified by Ehrenberg (1854) as a basis for concluding that *F. constricta sensu* Ehrenberg (1854) and *F. undata* are identical making the latter a heterotypic synonym ad keeping all populations under the name *F. constricta* Ehrenberg. Hustedt's concept was later employed by Krammer & Lange-Bertalot (1991: 140) who listed *F. undata* and *F. undata* as a junior synonym. By contrast, Patrick & Reimer (1966:123) treated *F. undata* and *F. undata* var. *quadrata* as synonyms of *F. constricta* f. *stricta*, separating the forma from the nominate *F. constricta*.

In 1988, Williams & Round described the genus *Fragilariforma* with *Fragilariforma virescens* (Ralfs) D.M.Williams & Round as type [$\equiv F.$ virescens W.Smith; see Pottiez & al. 2024 for an analysis of the type of *F. virescens*] and based the morphological features of the genus *Fragilariforma* on that species and a few others. It was clear that *F. undata* (and *F. constricta*), and all varieties and formae, should be transferred to *Fragilariforma*. *Fragilaria constricta* was already transferred in 1988 as *F. constricta* (Ehrenberg) D.M.Williams & Round but it was only in 2017 that Heudre & al. transferred *F. undata* to *Fragilariforma* as *F. undata* (W.Smith) Heudre, C.E.Wetzel & Ector, although the latter authors apparently never examined the original Smith material.

Although the original Ehrenberg material was not examined, the small Ehrenberg drawings (Figs 4– 7) of the original American specimens of F. constricta show differences in valve outline and apices (not protracted, acute versus clearly protracted, rostrate) with the European F. constricta specimens, making conspecificity less likely. Williams & Round (1987: 282) also cast some doubt on the conspecificity of these populations but concluded that at that time the only comparison that can be made was based on the 'uninformative' drawings made by Ehrenberg. The suggestion that the European populations should no longer be identified as F. constricta but that the original Smith name F. undata should be reinstated for these specimens is not acceptable to us. The taxonomic history of F. undata was also discussed by Heudre & al. (2017: 63-64), who considered Hustedt's var. quadrata to be "an illegitimate change of epithet because it is synonym to Fragilaria undata var. undata W.Smith which is the nominal variety of the species." This is not entirely correct as Hustedt (1930: 160) only considered the smaller valves lacking the constriction as the var. quadrata making his name quite legitimate. But the conclusion in Heudre & al. (2017: 264) that all are synonyms of F. undata, is acceptable to us. Of course, it is possible that further analysis of all Ehrenberg type specimens may result in another conclusion. To date, however, Ehrenberg's original F. constricta material from the Falkland Islands/Islas Malvinas cannot be found (Kusber, pers. comm.) and it is likely to be lost.

Since the original Smith material was not examined, all taxonomic analyses done so far, were based on non-type material interpretations. In this contribution, the original William Smith material from River Mortes, Lac Guéry, kept in **BR** (Hoover 1976) was examined using light and scanning electron microscopy observations. This sample is here designated as lectotype for the species.

- *Fragilariforma undata* (W.Smith) Heudre, C.E.Wetzel & Ector (in Heudre & al. 2017: 264) Figs 9–30.
- Basionym: *Fragilaria undata* W.Smith, Annals and Magazine of Natural History, 2nd series, 15: p. 7, pl. 1, fig. 7 (1855)
- Syntype localities: var. y. Mull Deposit; "River Mortes, Lac Guéry, Mont Dore, elev. 4066 ft., June 1854, leg. W.Sm.; near Christiania, Dr. Arnott."
- Lectotype (here designated): slide BR-4845 (Meise Botanic Garden, Belgium), slide made from the original River Mortes Lac Guéry material kept in BR. Fig. 10 represents the lectotype.
- Isolectotypes (here designated): **BM** 621, **BM** 1029, **BM** 22670, **BM** 24059-61, **BM** 28521 and **BM** 50919 (all slides made from Lac Guéry, kept in various sub-collections in **BM**.
- Lectotype locality: River Mortes, Lac [de] Guéry, [Puy-de-Dôme] 4066 ft [1240 m], coll. date 26.vi.1854, leg. W. Smith
- Registration (of lectotype): http://phycobank.org/104604
- Homotypic synonyms: *Fragilaria undata* "var. β" & "var. γ" W.Smith (1856: 24); *Fragilaria virescens* var. β *diatomacea* Grunow (1862: 373); *Fragilaria virescens* var. γ *undata* Grunow (1862: 373)
- Heterotypic synonyms: *Fragilaria undata* f. *stricta* A.Cleve (1895: 35); *Fragilaria undata* var. *quadrata* Hustedt (1930: 144); *Fragilaria constricta* f. *stricta* (A.Cleve) Hustedt (1931: 166); *Fragilariforma constricta* f. *stricta* (A.Cleve) Poulin in Hamilton & al. (1992: 29); *Fragilaria*

quadrata (Hustedt) Lange-Bertalot & Metzeltin (1996: 57); *Fragilaria virescens* var. *undatiformis* A.Mayer (1937: 53, pl. I: figs 17–19); *Fragilariforma quadrata* (Hustedt) Kharitonov (2005: 1702).

- Description: Frustules rectangular in girdle view, solitary. Cingulum composed of up to 6 open, ligulate girdle bands perforated by a single row of small, rounded poroids (Fig. 24). Valves linear in larger specimens with a clear central constriction becoming elliptic-lanceolate in smallest specimens lacking the central constriction (e.g. Figs 20-23). Apices distinctly protracted throughout the entire cell cycle, narrow, rostrate. Capitate apices so far not observed. Valve dimensions of the type population (n=25): valve length 15–35 µm, valve width 10–12 µm. Mantle broad with broad advalvar part bearing long striae and narrow abvalvar hyaline edge with scattered areolae (Fig. 24). Mantle edge lacking mantle plaques (Fig. 24). Valve face flat (Figs 25–27). Continuous series of small, acute spines, irregularly placed on the virgae at the valve face edge (Figs 24–28). Sternum variable in width, usually very narrow. Striae alternating, irregularly spaced, uniseriate, composed of small, rounded areolae, 16–19 in 10 µm, weakly depressed between virgae. Areolae not discernible in LM. Large apical pore fields present on both apices, composed of an irregular pattern of short series of small, rounded poroids, continuing from the valve face onto the mantle. Irregular pattern of low ridges running between the pores. Pore fields not entirely equal in size and shape, giving the valves a slightly heteropolar outlook, only discernible in SEM. One rimoportula per valve, slit-like, present near the smaller apical pore field, replacing some of the areolae in one of the last striae (Figs 28). Internally, sternum clearly visible (Fig. 29). Rimoportula perpendicular to the apical axis (Fig. 30). Valvocopula with fimbriate edge, attached to the valve along the virgae with the row of pores at the pars media (Fig. 29), disappearing at the apices (Fig. 30).
- Notes: In the original William Smith material, the longest valves observed never exceeded 40 μ m in length, but in the literature, longer valves with slightly different valve outlines can be found under different names. Kingston & al. (2001) showed three valves with two identified as *F*. *constricta* (Kingston & al. 2001, figs 76, 77) and one identified as *F*. *constricta* f. *stricta* (Kingston & al. 2001, fig. 78). A few years later, Kingston & al. (2009) concluded, based upon shape analysis, that the formae could not be separated. Analysis of an historic slide present in the Van Heurck collection collected by an unknown collector in the nineteenth century from the Canmore Deposit not far from Aberdeen, Scotland, showed a very large population of *Fragilariforma undata* (Figs 31–49). The observed cell cycle is much larger than in the type material with the longest valves reaching almost 70 μ m with very smoothly rounded undulations. Comparison of the type population and the Canmore population did not show any morphological differences and it can be concluded that the longer valves in the Canmore slide, simply represent the longest valves of this species. In the future, longer series of valves should be depicted to better illustrate valve outline changes throughout the cell cycle.

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Figs 1–23. *Fragilariforma undata* (W.Smith) Heudre, C.E.Wetzel & Ector. LM pictures taken from the lectotype material (BR-4845, River Mortes, Lac Guéry, 4066 ft, coll. date 26.vi.1854, leg. W. Smith). Fig. 1. Reproduction of the original drawing of *Fragilaria undata* from Smith (1855, fig. 7). Fig. 2. Reproduction of the original drawing of *Fragilaria undata* from Smith (1856, fig. 377). Fig. 3. Reproduction of the original drawing of "Remarkable sporangial frustules of *Odontidium tabellariae*" in Gregory (1854: fig. 22). Figs 4 & 5. Reproduction of the original drawings of *Fragilaria constricta* in Ehrenberg (1843, pl. I, I, fig. 22 & pl. IV, V, fig. 10). Figs 6 & 7. Reproduction of the original drawings of *Fragilaria constricta* in Ehrenberg (1843, pl. I, I, figs 19 & 20 and III, 34 & 35). Fig. 8. Scan of the original Smith sample conserved in BR. Figs 9-23. LM views of a size diminution series. Scale bar = 10 μm.

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Figs 24–30. *Fragilariforma undata* (W.Smith) Heudre, C.E. Wetzel & Ector. SEM pictures taken from the lectotype material (BR-4845, River Mortes, Lac Guéry, 4066 ft, coll. date 26.vi.1854, leg. W. Smith). Fig. 24. Frustule in girdle view showing six girdle bands and the acute spines. Fig. 25. SEM external view of an entire valve in oblique view. Figs. 26 & 27. SEM external view of two entire valves with different valve outline. Fig. 28. SEM external detail of a valve apex with slit-like rimoportula and acute spines. Note the vestiges where eroded spines were placed. Fig. 29. SEM internal view of entire valve with the position of the rimoportula. Fig. 30. SEM internal detail of the rimoportula. Scale bar = 10 μm (Figs 24–27), = 1 μm (Figs 28 & 30).

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Figs 31–49. *Fragilariforma undata* (W.Smith) Heudre, C.E.Wetzel & Ector. LM pictures taken from an historic slide (IX-18-A11, Loch Canmor Deposit, Scotland) conserved in BR. Figs 31-49. LM views of a size diminution series. Scale bar = 10 μm.