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Fragilaria subrecapitellata (Fragilariaceae, Bacillariophyta), a new diatom species from Switzerland

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During a biomonitoring assignment in the Swiss canton Ticino, an unknown *Fragilaria* taxon was discovered that could not be identified using the currently available literature. The results of a morphological comparison with the type material of *F. recapitellata*, based on light and scanning electron microscopy, showed that the new Swiss taxon has sufficient differences to be separated as a new species: *Fragilaria subrecapitellata* sp. nov. The new species can be separated by its lanceolate to elliptic-lanceolate valve outline with convex valve margins, and its smaller valves compared to *F. recapitellata*. The distribution and iconography of *F. recapitellata* in literature data is analysed. As a result of this analysis, *Fragilaria deformis* is appointed as the correct name for the taxon generally known as *F. candidagilae* or *F. capucina* var. *capitellata* (Grunow) Lange-Bertalot in Krammer & Lange-Bertalot.

Keywords: *Europe,* Fragilaria*, morphology, new species, type material*

Introduction

In 2008, Tuji & Williams discussed several *Fragilaria* taxa in the '*F. pectinalis-capitellata*' complex, based on the analysis of the type material of *Fragilaria perminuta* (Grunow) Lange-Bertalot, *Fragilaria gloiophila* (Grunow) Van de Vijver et al., *Fragilaria socia* (J.H.Wallace) Lange-Bertalot, *Fragilaria pectinalis* (O.F.Müller) Lyngbye, *Fragilaria capitellata* (Grunow) J.B.Petersen, *Synedra capitellata* var. *cymbelloides* Grunow and *Synedra capitellata* f. *striis-distantioribus* Grunow. However, their concept of *F. capitellata* was rather broad and included both capitate and non-capitate forms. *Fragilaria capitellata* later proved to be a younger homonym of *F. capitellata* Lauby (1910), which was corrected by Lange-Bertalot & Metzeltin (in Metzeltin et al. 2009) by renaming *Fragilaria capitellata* as *F. recapitellata* Lange-Bertalot & Metzeltin.

The observation of an unidentified *Fragilaria* taxon in some rivers in Switzerland showing some resemblance to *F. recapitellata*, urged the reanalysis of the (unmounted) type material of *Synedra capitellata* Grunow to determine a possible conspecificity. In 1991, Hürlimann & Straub already reported on the presence in Switzerland of a taxon they grouped as 'Sippe 2' showing some similarities with *F. recapitellata* but with sufficient differences to separate it. In an attempt to find additional populations of *F. recapitellata*, it turned out that the latter is a very rare species in Europe, as only one population from North Macedonia could be identified as *F. recapitellata* s.s. The latter population has been added to the comparison analysis in the present paper.

Delgado et al. (2015) reanalysed the type slide of *F. recapitellata*, splitting off a new species, *F. candidagilae* S.F.P.Almeida et al. that was often incorrectly identified as *F. recapitellata* (see for instance Lange-Bertalot et al. 2017: 274). They also slightly modified the description provided for *F. recapitellata* in Tuji & Williams (2008). Van de Vijver et al. (2020a) already noted that there is high similarity between *F. candidagilae* and *F. deformis* (W.Smith) Van de Vijver et al., a forgotten taxon described in the nineteenth century, and suggested possible conspecificity. During the analysis of an historic sample from the

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Grunow collection (W, Vienna, Austria) labelled *Synedra truncata* (Greville) Ralfs, a large population of *F. deformis* was found, resulting in a better interpretation of the *F. deformis/candidagilae* enigma. The conclusions from this analysis are discussed in this paper.

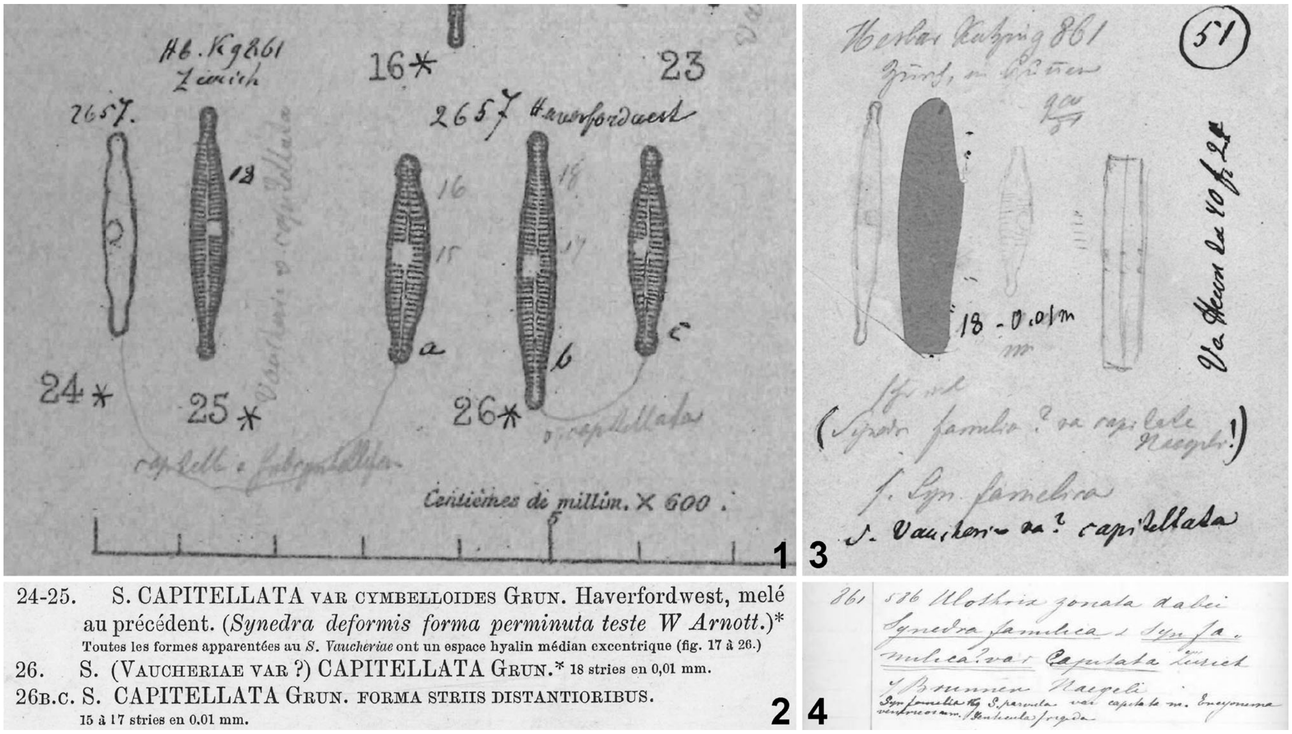
The morphology of *F. subrecapitellata* is compared to that of known taxa worldwide. Brief notes on its ecology and accompanying diatom flora are added.

Material and methods

In the Grunow collection in the *Naturhistorisches Museum* in Vienna (W, Austria), an annotated copy of Van Heurck's Atlas (1880–1885) is kept. Each figure on the plates showing the *Synedra* Ehrenberg and *Fragilaria* Lyngbye taxa is annotated with the number and origin of the sample from which it was drawn (Figs 1–2). In the same collection, all the original line drawings Grunow made of the diatoms he observed are conserved. Each drawing is completed by extra information such as slide numbers, type locality and stria density (Fig. 3). This copy, together with Tuji & Williams (2008), was used to track down the original material Grunow used to describe *S. capitellata*. In Van Heurck (1881), *S. capitellata* is represented on plate XL [40], fig. 26, although on the annotated copy, most likely a pre-published version, the taxon is numbered as fig. 25 (whereas the figure caption already indicates 26).

Synedra capitellata was observed in a sample Grunow used from the Kützing herbarium (Kützing 861, *Ulothrix zonata*, Zürich Brunnen, leg. Nägeli) (Fig. 4), although it is unclear whether Grunow used material from the Natural History Museum in London (BM, UK) or the Van Heurck collection, at that time housed in the *Natuurwetenschappelijk Museum* in Antwerp (AWH, Belgium), the latter being transferred in 2006 to the Meise Botanic Garden (BR, Belgium). Both institutes (BM, BR) possess part of the Kützing collection, with duplicates for most samples. As Grunow was a close collaborator to Henri Van Heurck, spending some time in his workplace in Antwerp, it is most likely he used material from Antwerp. Tuji & Williams (2008) studied the material kept in BM whereas in the present study, unmounted material from BR is used.

An additional population of *F. recapitellata* was found in sample Levkov 4757 (coll. date 07/06/2010) from the river Boshava in the Republic of North Macedonia, a small, karstic, lowland, mesotrophic river with a bottom composed of large stones and pebbles, overgrown during summer by large quantities of *Cladophora* and aquatic mosses, such as *Rhyncostegium* sp. The sample itself was taken from aquatic mosses near the shore at 20–25 cm water depth.



24-25. S. CAPITELLATA VAR CYMBELLOIDES GRUN. Haverfordwest, melé au précédent. (*Synedra deformis forma perminuta teste W Arnott.*)*
Toutes les formes apparentées au *S. Vaucheriae* ont un espace hyalin médian excentrique (fig. 17 à 26.)
26. S. (VAUCHERIAE VAR ?) CAPITELLATA GRUN.* 18 stries en 0,01 mm.
26B.C. S. CAPITELLATA GRUN. FORMA STRIIS DISTANTIORIBUS.
15 à 17 stries en 0.01 mm.

861 586 Ulothrix zonata dabei Synedra familica & Syn fa-
milica? var Capitata Zürich
/ Brunnen Naegeli
Syn familica Kg S. parvula var capitata m. Encyonema ventricosum. Denticula frigida

Figs 1–4. Original drawings of *Synedra vaucheriae* var. *capitellata*. Fig. 1. Scan of the annotated copy of Van Heurck (1881) plate XL, figs 24–26 kept in the Grunow collection (W). Note that the numbering of figs 25 and 26 have been switched in the pre-published copy. Fig. 2. Scan of the original figure caption in Van Heurck (1881) for plate XL, figs 24–26. Fig. 3. Scan of the original drawing in the Grunow drawing collection (W) representing the valves drawn by Grunow from sample Kützing 861. The cut-out drawing is used in Van Heurck (1881) for plate XL, fig. 26. Fig. 4. Scan of sample 861 in the original Kützing catalogue kept in Meise Botanic Garden (BR).

The unknown Swiss *Fragilaria* taxon was observed in several samples collected from the Maggia river system, a 56 km long, shallow (depth < 0.5 m, often shallow, but very high discharges can occur during heavy rain), fast-flowing river in the canton Ticino in southwestern Switzerland that ends its course near the city of Locarno in the Lago Maggiore. The entire river catchment area is situated in a silicate-rich region. The upper part of the river system is formed by the Lavizzara river whereas one of the main tributaries is the Melezza river (Centovalli Valley).

Three samples containing populations of the unknown *Fragilaria* taxon were used in this study.

- Hürlimann 6664: Lavizzara river (46°23″10.96′N/8°39″51.39′E, alt. 694 m), coll. date 7.VII.2020, sampled by Mrs C. Gufler.
- Hürlimann 6667: Maggia river (46°13″32.21′N/8°43″56.66′E, alt. 292 m), coll. date 7.VII.2020, sampled by Mrs C. Gufler.
- Hürlimann 6671: Melezza river (46°10″50.66′N/8°42″45.45′E, alt. 244 m), coll. date 7.VII.2020, sampled by Mrs C. Gufler.

To evaluate the possible conspecificity between *F. deformis* and *F. candidagilae*, published images in Delgado et al. (2015, *F. candidagilae*) and Van de Vijver et al. (2020a, *F. deformis* and *F. candidagilae*) were compared with the *Fragilaria* population in Grunow sample 118 (Nadelburg, Austria, March 1856, W1901-24307), labelled '*Synedra truncata* Ralfs', which was retrieved from the *Naturhistorisches Museum* (W) in Vienna (Austria).

Subsamples of the historical material were prepared for light (LM) and scanning electron microscopy (SEM) observations following the method described in van der Werff (1955). Small volumes of the samples were cleaned by adding 37% H_2O_2 and heating to 80°C for about 1 h. The reaction was completed by addition of saturated $KMnO_4$. Following digestion and centrifugation (three times for 10 min at 3700 rpm), the resulting cleaned material was diluted with distilled water to avoid excessive concentrations of diatom valves on the slides. The Swiss samples were prepared first with HCL, washed and filtered using Teflonfilters. The resulting material was then boiled in hot H_2SO_4 with the addition of $KMnO_4$ and finally washing by filtering with Teflonfilters. Cleaned diatom material was mounted in Naphrax. The resulting slides were analysed using an Olympus BX53 microscope at 1000 × magnification (N.A. 1.30), equipped with Differential Interference Contrast (Nomarski) optics and the Olympus UC30 Imaging System, connected to the Cell Sense Standard program. For each taxon, the number of specimens, measured at random on the type slide, is indicated ($n = X$).

For scanning electron microscopy (SEM), part of the suspension was filtered through 3-μm Isopore™ polycarbonate membrane filters (Merck Millipore), pieces of which were fixed on aluminium stubs after air-drying and coated with platinum (15 nm film thickness) using a Leica sputter coater EM ACE600 (Leica Microsystems GmbH, Wetzlar, Germany). Stubs were observed using an ultra-high-resolution analytical field emission (FE) scanning electron microscope, Hitachi SU-70 electron microscope (Hitachi High-Tech Corporation, Tokyo, Japan) at 5 kV and 10 mm working distance (LIST, Luxembourg) and a JEOL-JSM-7100 F field emission scanning electron microscope (JEOL Europe bv, Leuven, Belgium) at 2 kV and 4 mm working distance (Meise Botanic Garden, Belgium). Slides and stubs are stored at the BR-collection (Meise Botanic Garden, Belgium) and LIST (Luxembourg Institute of Science and Technology, Luxembourg). Plates were prepared using Photoshop CS5.

Terminology used in the description of the various structures of the siliceous cell wall is based on Ross et al. (1979, areola structure), Cox & Ross (1981, stria structure), Williams & Round (1987, generic features for *Fragilaria*) and Tuji & Williams (2006, generic features for *Fragilaria*). For taxonomic comparison, the following papers were consulted: Krammer & Lange-Bertalot (1991), Flower et al. (2004), Tuji & Williams (2006, 2008), Van de Vijver et al. (2012, 2020a, 2020b), Delgado et al. (2015), Heudre et al. (2018), Novais et al. (2019), Van de Vijver & Ector (2020).

For the typification of the new species, we chose to use the entire slide as the holotype following Article 8.2 of the International Code for Botanical Nomenclature (Turland et al. 2018). Diatoms show broad variability over their cell cycle making the choice for the entire population on the slide more obvious.

Results

***Fragilaria subrecapitellata* Van de Vijver, J.Hürlimann, D.M.Williams, C.E.Wetzel & Ector, sp. nov.** (Figs 5–47)

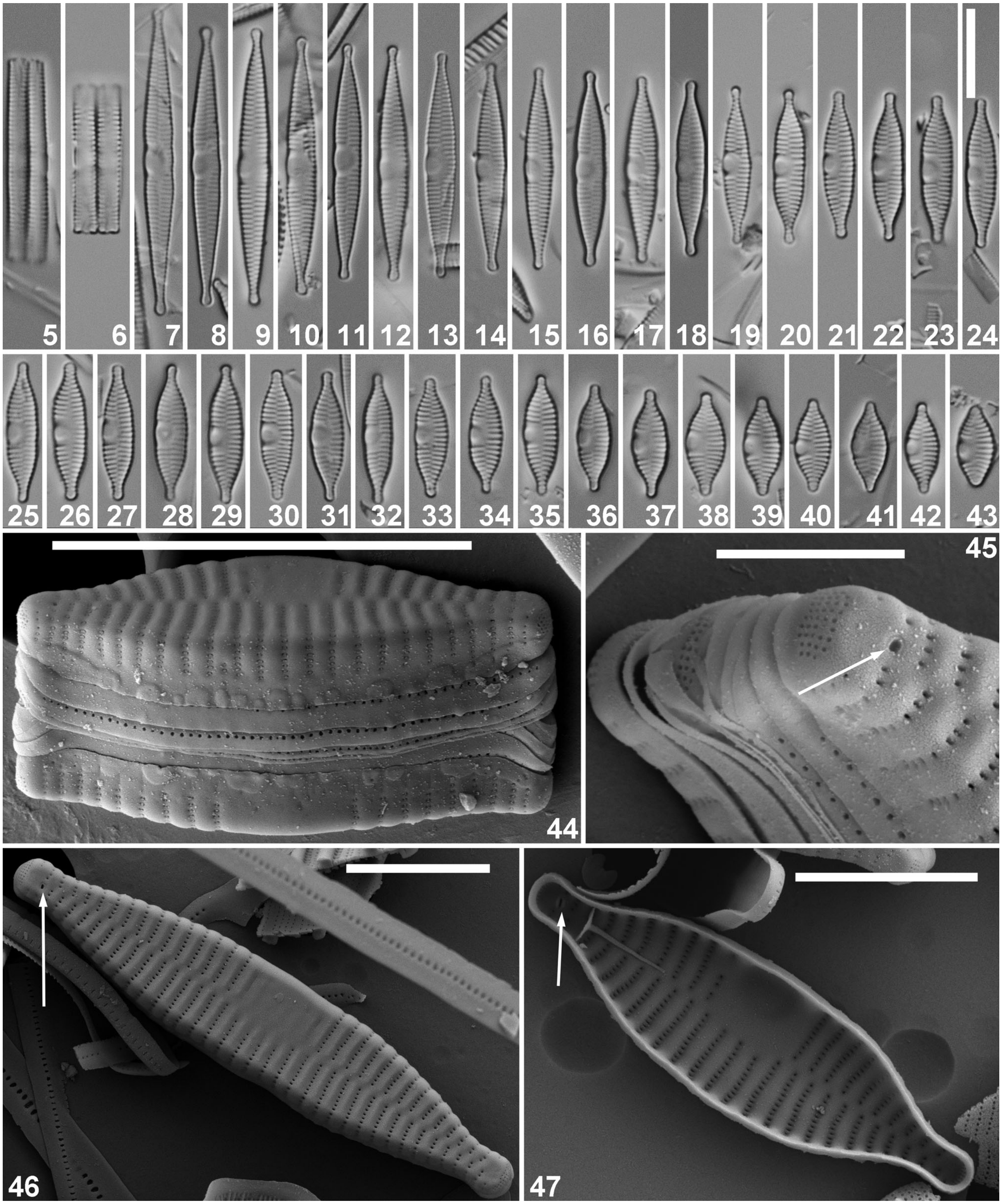
Holotype: BR-4662 (Meise Botanic Garden, Belgium)

Isotype: PLP-390 (University of Antwerp, Belgium)

Type locality: Lavizzara river, canton Ticino, Switzerland, sample Hürlimann 6664 (coll. date 7.VII.2020, leg. J. Hürlimann).

Etymology: The specific epithet *subrecapitellata* refers to the similarity with *F. recapitellata,* emphasizing the lower valve dimensions.

Light microscopy (Figs 5–43): Frustules in girdle view rectangular, solitary or two frustules attached to each other (Figs 5, 6). Ribbon-like colonies not observed. Larger valves lanceolate with clearly convex, never parallel margins, gradually narrowing from central area towards apices. Smaller valves elliptic-lanceolate with very convex margins. Apices clearly elongated, following a distinct constriction, capitate throughout entire valve diminution series



Figs 5–47. *Fragilaria subrecapitellata* sp. nov. LM and SEM images taken from the type population (BR-4662, Lavizzara river, canton Ticino, Switzerland, sample Hürlimann 6664). Figs 5–6. (LM) Frustules in girdle view. Figs 7–43. (LM) Size diminution series of the type population showing the slight change in valve outline. Fig. 44. (SEM) External view of an entire frustule. Note the mantle plaques on the abvalvar edge of the mantle and the open girdle bands. Fig. 45. (SEM) External detail of the valve apex showing the rimoportula (arrow) and the apical pore field. Fig. 46. (SEM) External view of an entire valve showing the position of the rimoportula (arrow), the swollen central area and the ghost striae. Fig. 47. (SEM) Internal view of an entire valve with the position and shape of the rimoportula (arrow). Scale bars represent 10 µm except for Fig. 45 where scale bars = 2 µm and Figs 46 & 47 where scale bars = 5 µm.

with smallest valves usually showing short, rostrate apices. Valve dimensions ($n = 50$): valve length 9–35 µm, width 3.5–4.5 µm. Sternum very narrow, almost non-existent, linear, very slightly widening towards central area. Central area clearly asymmetrical, one side depressed, clearly buttressed, lacking striae, opposite side with occasionally slightly shortened striae (see for instance Fig. 28). Ghost striae not observed in LM. Striae parallel in larger valves, becoming weakly radiate towards apices, 18–20 in 10 µm. In smaller valves, striae clearly radiate (Figs 36–43). Areolae not discernible in LM.

Scanning electron microscopy (Figs 44–47): Girdle composed of several (4-5) open copulae, diminishing in size away from valve, advalvar side bearing a row of rounded perforations (Figs 44, 45). Abvalvar edge of valve mantle showing large, siliceous mantle plaques (Fig. 44). Advalvar part of mantle with uniseriate striae, continuing without interruption onto valve face (Fig. 44). Marginal spines absent (Figs 44, 46). Virgae raised from valve surface with vimines occurring within depression (Fig. 46). Striae uniseriate, composed of small, rounded to apically very slightly elongated areolae (Fig. 45). Areolae externally covered by individual vela (Fig. 44). Ghost striae visible in central area (Fig. 46). Apical pore field well developed, composed of five rows of small, round to squarish pores (Fig. 45). Rimoportula large, present at each apex, replacing vimines of final virga (Figs 45, 46, arrows). Internally, depressed central area clearly visible (Fig. 47). Rimoportula transapically elongated, clearly oblique (Fig. 47).

Ecology and associated diatom flora: *Fragilaria subrecapitellata* was observed in several samples from the Maggia river system characterized by a silicate catchment area, rather low conductivities (60–80 µS/cm) and a high water quality. The index value DI-CH (= diatom index of Switzerland, BAFU 2007) classifies the sites as very clean (DI-CH from 1.4–2). All samples were characterized by high oxygen (about 100% saturation) and low conductivity levels (60–80 $\mu S\ cm^{-1}$). In 2018 further chemical analyses of these rivers showed low PO_4-P and NO_3-N levels (< 1.8 and 500 $\mu g\ L^{-1}$ respectively) and a pH of 7.3–7.5 (UPAAI 2018).

Apart from *F. subrecapitellata*, the holotype sample is dominated by *Achnanthidium gracillimum* (F.Meister) Lange-Bertalot, *A. lineare* W.Smith, *A.* cf. *jackii* Rabenhorst, *Odontidium mesodon* (Kützing) Kützing, *Hannaea arcus* (Ehrenberg) R.M.Patrick, *Fragilaria austriaca* (Grunow) Lange-Bertalot, *Diatoma ehrenbergii* Kützing and *Encyonema silesiacum* (Bleisch) D.G.Mann.

Verification of samples of the Maggia river from earlier years (March 2012, March 2015) showed that the species was already present, identified either as *Fragilaria capucina* var. *perminuta* (Grunow) Lange-Bertalot or *F. capucina* var. *vaucheriae* (Grunow) Lange-Bertalot (J. Hürlimann, pers. obs.).

***Fragilaria recapitellata* Lange-Bertalot & Metzeltin** (Figs 48–76)

Basionym: *Synedra capitellata* Grunow in Van Heurck 1881, pl. 40, fig. 26 (as *Synedra vaucheriae* var.? *capitellata*)

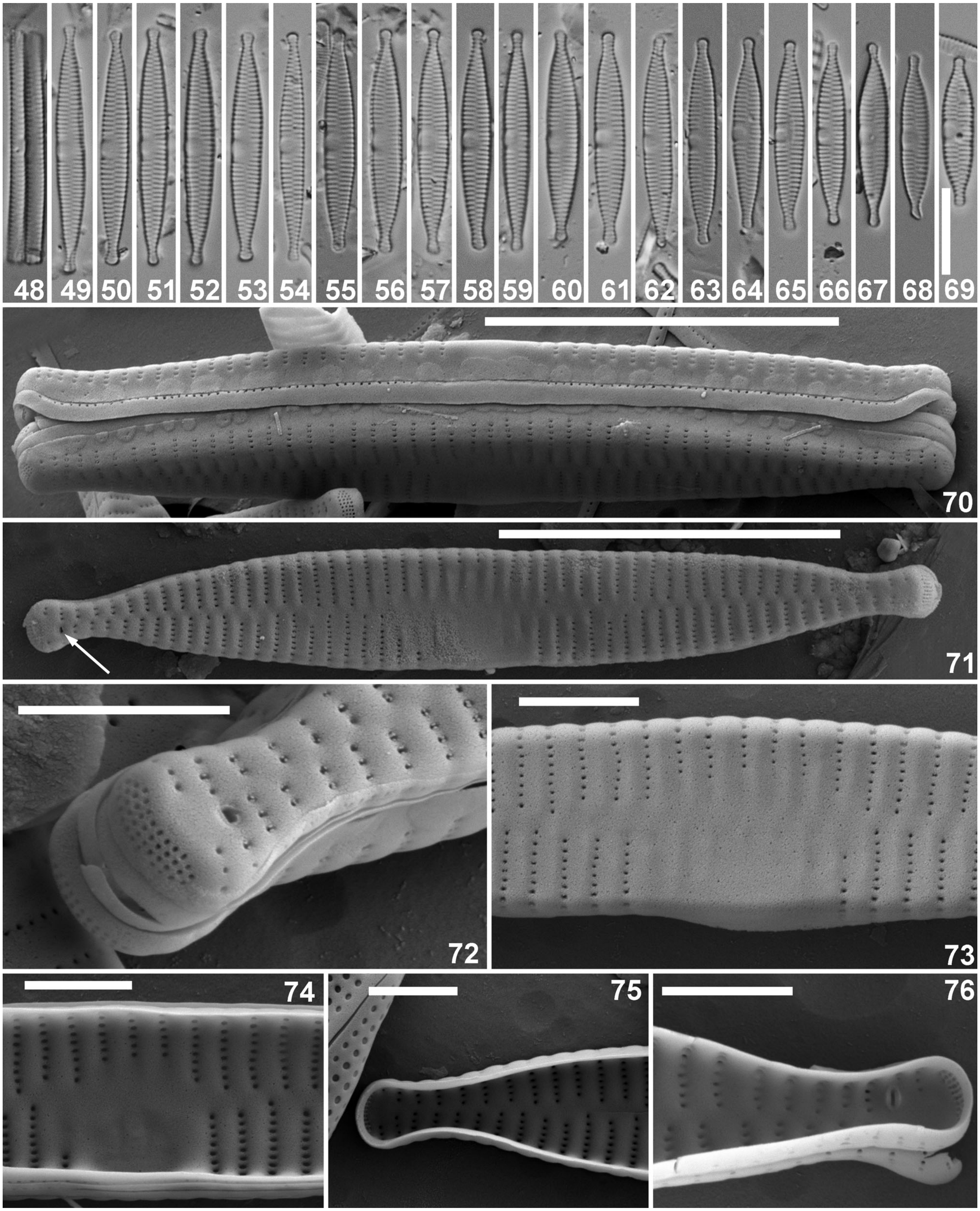
Material examined: Kützing sample 861 (Zürich, Switzerland) (BR!)

Light microscopy (Type population, Figs 48–69): Frustules in girdle view rectangular, solitary or two frustules attached to each other, never forming ribbon-like colonies (Fig. 48). Valves lanceolate to linear-lanceolate with almost parallel to weakly convex margins, only narrowing near apices. Apices clearly protracted, broadly capitate throughout entire valve diminution series. Valve dimensions ($n = 100$): valve length 17–25 µm, width 3.0–4.0 µm. Sternum very narrow, linear, very slightly widening towards central area. Central area asymmetrical with one side clearly swollen, often depressed, hyaline, entirely lacking striae, with opposite side showing normal striation pattern with occasionally several weakly shortened striae. Ghost striae rarely present. Striae parallel to very weakly radiate throughout, alternating, becoming slightly more radiate near apices, 18–20 in 10 µm. Areolae not discernible in LM.

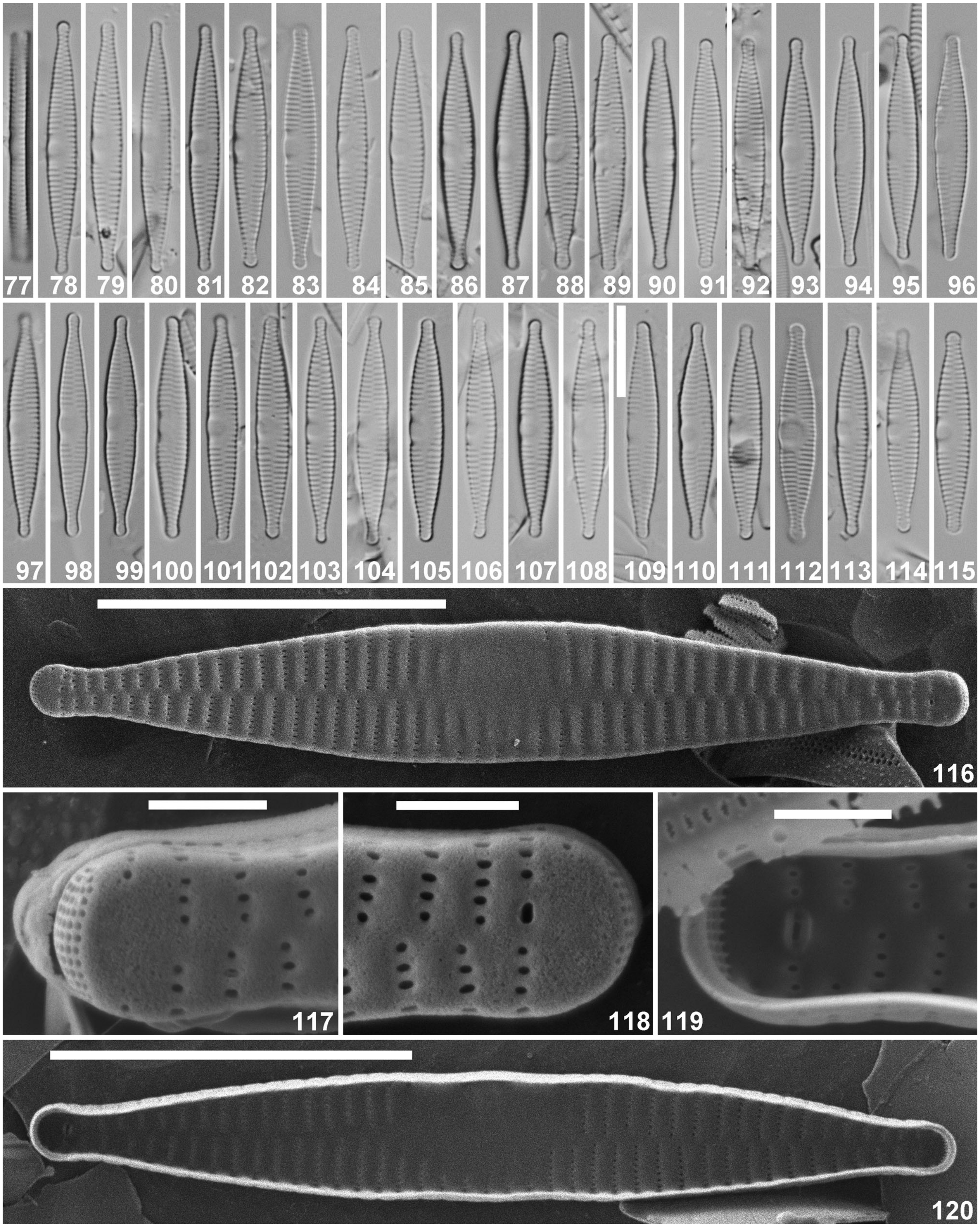
Scanning electron microscopy (Figs 70–76): Girdle composed of several (possibly two) open copulae, the advalvar side bearing one row of rounded perforations (Fig. 70). Abvalvar edge of valve mantle showing large, siliceous mantle plaques. Advalvar part of mantle bearing uniseriate striae, continuing without interruption onto valve face (Fig. 71). Marginal spines absent (Figs 70, 71). Virgae raised from valve surface with vimines occurring within depression. Striae uniseriate, composed of small, rounded to apically elongated areolae. Areolae externally covered by individual vela (Fig. 72). Central area clearly swollen, asymmetrical (Figs 71, 73). Ghost striae visible (Fig. 73). Apical pore field well developed, composed of at least four rows of small, squarish pores (Fig. 72). Rimoportula large, present at one apex per valve (Figs 71, arrow, 72). Internally, depressed central area clearly visible (Fig. 74). Apical pore fields clearly visible internally (Figs 75, 76). Rimoportula transapically elongated, almost straight (Fig. 76).

Remarks: The *F. recapitellata* population from the Republic of Northern Macedonia (Figs 77–120) shows very similar morphological characteristics confirming the typical valve morphology of this species. The valves are more lanceolate compared to the type population but the apices are of similar size and shape.

Associated diatom flora: Sample Kützing 861 is dominated by *F. recapitellata* (almost 25% of all counted valves) together with *Fragilaria* cf. *gracilis* Østrup (25%), *Denticula tenuis* Kützing (8%), *Achnanthidium*



Figs 48–76. *Fragilaria recapitellata* Metzeltin & Lange-Bertalot. LM and SEM images taken from the type population (Kützing sample 861, material kept in Meise Botanic Garden, BR). Fig. 48. (LM) Frustules in girdle view. Figs 49–69. (LM) Size diminution series of the type population showing the slight change in valve outline. Fig. 70. (SEM) External view of an entire frustule. Note the mantle plaques on the abvalvar edge of the mantle and the open girdle bands. Fig. 71. (SEM) External view of an entire valve showing the position of the rimoportula (arrow), the swollen central area and the ghost striae. Fig. 72. (SEM) External detail of the valve apex showing the rimoportula and the apical pore field. Fig. 73. (SEM) External detail of the swollen central area with faint ghost striae. Fig. 74. (SEM) Internal detail of the depressed central area. Fig. 75. (SEM) Internal detail of the valve apex without rimoportula. Fig. 76. (SEM) Internal detail of the valve apex with a rimoportula. Scale bars represent 10 μm except for Figs 72–76 where scale bars = 2 μm.



Figs 77–120. *Fragilaria recapitellata* Metzeltin & Lange-Bertalot. LM and SEM images taken from the Boshava river in the Republic of North Macedonia (sample Levkov 4757). Figs 77–115. (LM) Size diminution series of the population showing the slight change in valve outline and dimensions. Fig. 77 represents a frustule in girdle view. Fig. 116. (SEM) External view of an entire valve lacking spines. Fig. 117. (SEM) External view of the apex without rimoportula, showing the apical pore field. Fig. 118. (SEM) External detail of the apex with rimoportula. Fig. 119. (SEM) Internal detail of the valve apex with rimoportula. Fig. 120. (SEM) Internal view of the entire valve. Scale bars represent 10 μm except for figs 117–119 where scale bars = 1 μm.

cf. *microcephalum* Kützing (8%), *Encyonema ventricosum* (C.Agardh) Grunow (5%) and *Gomphonema micropus* Kützing (5%). The Macedonian sample was dominated by *A. microcephalum* (20% of all counted valves), *Diatoma ehrenbergii* Kützing (17%), *Nitzschia dissipata* (Kützing) Grunow (12%), *Nitzschia supralitorea* Lange-Bertalot (12%), *Achnanthidium pyrenaicum* (Hustedt) H.Kobayasi (4%) and *Sellaphora seminulum* (Grunow) D.G.Mann (4%).

According to van Dam et al. (1994), *F. recapitellata* (as *F. vaucheriae* var. *capitellata*) prefers alpha-mesosaprobic, eutrophic waters. Similarly, Lange-Bertalot et al. (2017) classified the species as living in eutrophic conditions tolerating high saprobic levels (up to the alpha-mesosaprobic level). It should be noted, however, that the latter data most likely refer to *F. deformis* and not to *F. recapitellata* (see Discussion).

***Fragilaria deformis* (W.Smith) Van de Vijver & Ector** in Van de Vijver et al. (2020a) (Figs 121–157)

Basionym: *Synedra deformis* W.Smith, 1856, Synopsis of British Diatomaceae, p. 98.

Heterotypic synonym: *Fragilaria candidagilae* Almeida, Delgado, Novais & S.Blanco in Delgado et al. (2015).

Material examined: Grunow sample 118 (Nadelburg, Austria, coll. date March 1856) (W!)

Light microscopy (Figs 121–154): Frustules in girdle view rectangular, solitary or two frustules attached to each other (Figs 121, 122). Ribbon-shaped colonies not observed. Larger valves linear with parallel margins, giving the valves a rectangular outline. Smaller valves more elliptic-lanceolate to almost elliptical with convex margins. Apices always protracted, rostrate in smaller valves to capitate in larger valves, with clearly developed shoulders. Valve dimensions ($n = 50$): valve length 11–25 µm, valve width 4.5–5.5 µm. Axial area narrow but distinct, linear, only widening slightly near the central area. Central area unilateral, asymmetrical due to absence of striae on one side. Ghost striae observed. Striae parallel near central area becoming radiate at the apices, 14–16 in 10 µm, often irregularly spaced. Areolae not discernible in LM.

Scanning electron microscopy (Figs 155–157): External rimoportula opening small, situated on the last stria before the apices (Figs 155, 156). Apical pore field rather large, composed of more than five rows of small pores (Fig. 156). Internally, rimoportula very large (Fig. 157).

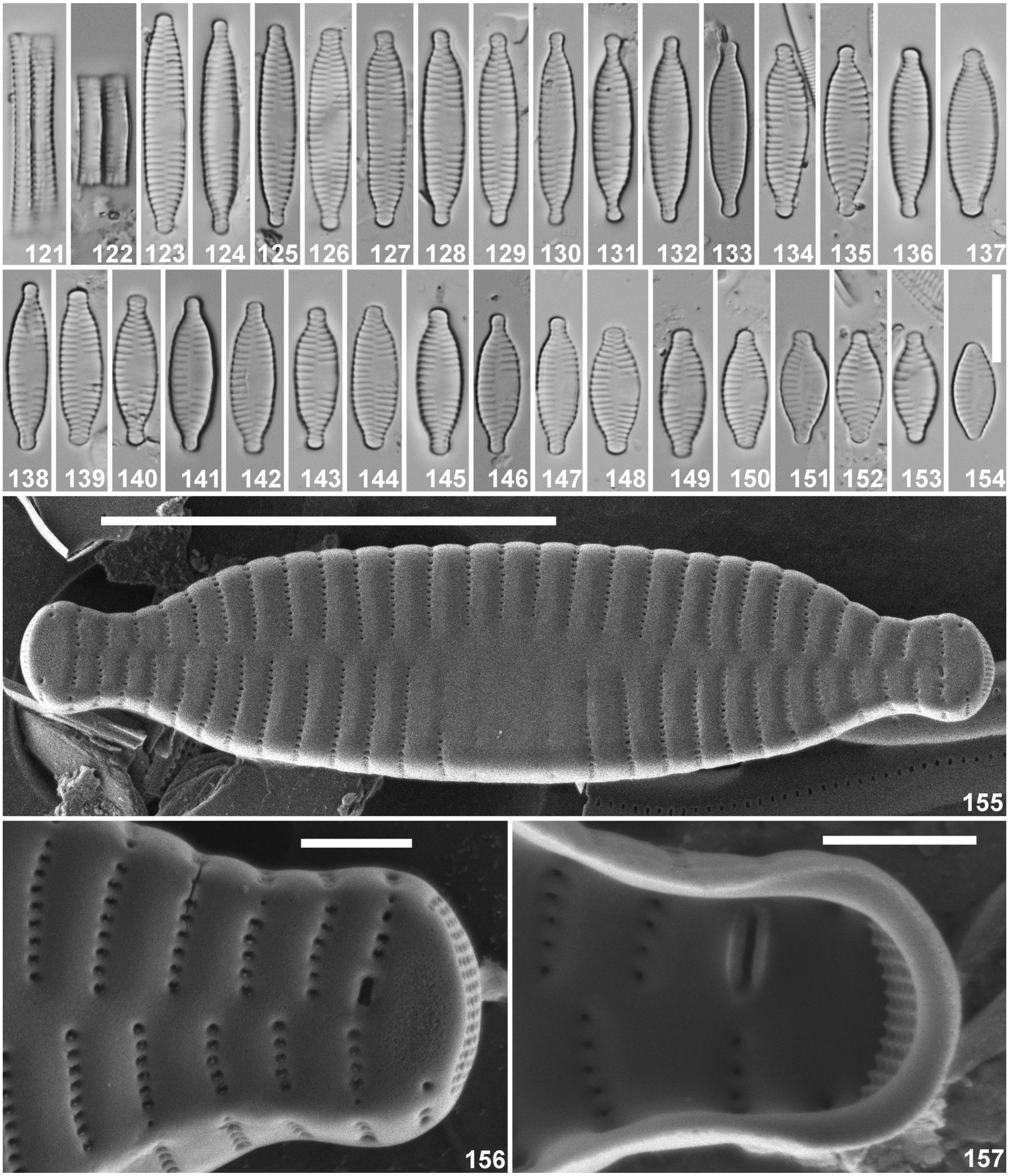
Remarks: The original Grunow identification of these valves as *Synedra truncata* is not correct. The latter taxon was originally described as *Exilaria fasciculata* var. *truncata* by Greville in 1823 (pl. 16, fig. 4). Analysis of the type material of the latter shows that the taxon is more closely related to *F. vaucheriae* (Kützing) J.B.Petersen and has nothing to do with *F. deformis* (Van de Vijver & Williams, unpubl. res.).

Discussion

The first two taxa discussed in this paper (*F. subrecapitellata* and *F. recapitellata*) are most likely related to each other, although molecular data to confirm this hypothesis are not available. Morphologically this small complex is characterized by the presence of an asymmetrical, swollen central area, a relatively high stria density (17–20 in 10 µm) and a lanceolate to linear-lanceolate valve outline with distinctly protracted, capitate to rostrate apices. Although they share these common features, it is still possible to separate the two species based on a combination of morphological characteristics.

Table 1 shows a comparison between the two species discussed alongside several other species presenting some similarities with the *F. recapitellata* group: *F. drouotiana* Heudre et al., *F. goeyersiana* Van de Vijver & Ector, *F. sandellii* Van de Vijver & Jarlman, *F. misarelensis* S.F.P.Almeida et al. and *F. austriaca* (Van de Vijver et al. 2012, 2020b, Heudre et al. 2018, Novais et al. 2019, Van de Vijver & Ector 2020).

Fragilaria subrecapitellata can be separated from *F. recapitellata* based on differences in valve outline, in the shape of the apices, in the position of the rimoportula and in the observed length range. There is a clear overlap in length range between both taxa with the range observed in the type material of *F. recapitellata* within the range for *F. subrecapitellata*. However, all populations of *F. subrecapitellata* analysed in this study, show a much wider length range (9–35 µm) compared to *F. recapitellata* (17–25 µm). The majority (> 60% of all measured specimens) of the observed valves of the new species is composed of short valves (< 12 µm) whereas in the verified populations of *F. recapitellata*, at present no valves shorter than 17 µm have been observed. Although relatively large, the analysed population from the Republic of North Macedonia had a rather narrow length range of 21–26 µm (Figs 77–115), lacking valves shorter than 20 µm. Longer valves are also present in *F. subrecapitellata* but occur only rarely (< 5% of all measured valves), although very occasionally valves > 30 µm long were observed. However, in both analysed populations of *F. recapitellata*, valves above 26 µm long have not been observed. Tuji & Williams (2008) reported a maximum valve length of 39 µm for *F. recapitellata* although analysis of their published images showed that the longer valves belong to a different species, related to the *F. gracilis* complex. Their fig. 43 lacks an inflated central area and the typical capitate apices and should therefore not be identified as *F. recapitellata*. Delgado et al. (2015) indicated 21.4–30.4 µm as the valve length range, but this could not be confirmed in our study after a thorough analysis of more than 100 valves of the type material. *Fragilaria subrecapitellata* usually also has slightly wider valves, although there is a considerable overlap (3.0–4.0 µm in *F. recapitellata* versus 3.5–4.5 µm in *F. subrecapitellata*). There seems to be no difference in stria



Figs 121–157. *Fragilaria deformis* Van de Vijver & Ector. LM and SEM images taken from Nadelburg, Austria (sample Grunow 118). Figs 121–154. (LM) Size diminution series of the population showing the clear change in valve outline and dimensions. Figs 121 and 122 represent frustules in girdle view. Fig. 155. (SEM) External view of an entire (larger) valve lacking spines. Fig. 156. (SEM) External view of the valve apex with rimoportula. Fig. 157. (SEM) Internal detail of the valve apex with rimoportula. Scale bars represent 10 µm except for Figs 156–157 where scale bars = 1 µm.

Table 1. Comparison table of *Fragilaria* taxa, similar to *F. subrecapitellata.*

	Fragilaria subrecapitellata	*Fragilaria recapitellata*	*Fragilaria lanceolata-baikali*	*Fragilaria goeyersiana*	*Fragilaria drouotiana*	*Fragilaria misarelensis*	*Fragilaria austriaca*
reference	this paper	this paper	Van de Vijver et al. (2021)	Van de Vijver & Ector (2020)	Heudre et al. (2018)	Novais et al. (2019)	Van de Vijver et al. (2020b)
length (µm)	9–35	17–25	10–45	10–28	15–28	10–32	25–70
width (µm)	3.5–4.5	3.0–4.0	4.0–5.5	2.5–3.0	2.5–3.0	3.0–5.0	3.0–3.5
valve outline	larger valves lanceolate with clearly convex margins, gradually narrowing from central area towards apices, smaller valves elliptic-lanceolate	lanceolate to linear-lanceolate with almost parallel to weakly convex margins, only narrowing near apices	strictly lanceolate in larger specimens becoming more elliptic-lanceolate in smaller valves	strictly narrowly lanceolate, with convex margins gradually tapering from the central area to the apices	narrow, rhombic-lanceolate, never elliptic-lanceolate	lanceolate, occasionally with central swelling	narrow, linear-lanceolate with weakly inflated central part, gradually tapering towards the apices
apices	clearly protracted, elongated, always capitate	clearly protracted, capitate	protracted, sub-capitate to rostrate	protracted, capitate to rostrate	rostrate to subcapitate	capitate	protracted, clearly capitate
stria density (in 10 µm)	18–20	18–20	17–20	22–24	17–22	15–18	13–14
spines	absent	absent	sometimes present	Absent	absent	absent	present

density and striation pattern. A second important difference between both taxa is the shape of the apices. Both taxa possess the typical asymmetrically swollen central area. However, almost all observed valves of the type population of *F. recapitellata* possess parallel to very weakly convex margins, with the valves only narrowing very close to the apices. Valves with strongly convex margins, gradually narrowing from the central area to the apices, have not been observed. The Macedonian population had more convex margins that are somewhat comparable to the type population of *F. subrecapitellata*. At present, all observed valves in the different populations of *F. subrecapitellata* show typically convex margins, always gradually narrowing from the central area to the apices. This gradually narrowing also gives the impression that in *F. subrecapitellata* the valve apices are more elongated and protracted, with a more distinct constriction before the apices. Both species possess clearly protracted, capitate apices, but the apices in *F. subrecapitellata* are always narrower, more acutely rounded than the apices of *F. recapitellata* that are broader. As these differences in valve outline have been observed consistently in all analysed populations, we believe that conspecificity can be excluded and therefore the description of *F. subrecapitellata* based on morphological features is justified.

Fragilaria drouotiana and *F. goeyersiana* show some similarities in valve outline but differ in a lower valve width (2.5–3.0 µm vs. 3.5–4.5 µm) and a slightly lower valve length (maximum 32 µm). Both species also possess a higher stria density (up to 24 in 10 µm, vs. 17–20 in 10 µm for *F. subrecapitellata*). Their valve outline lacks the typically convex margins but instead they have more lanceolate-rhombic outlines with straight margins (Heudre et al. 2018, Van de Vijver & Ector 2020). The specimens originally described as *F. sandellii* were considered to have only short valves with a maximum length of 22 µm (Van de Vijver et al. 2012), although recent analyses showed that the valve length can reach 70 µm (Van de Vijver et al. submitted). The much higher valve width (4.5–6.0 µm), lower stria density (16–18 in 10 µm) and less protracted, subrostrate, bluntly rounded apices exclude conspecificity from the three species illustrated and discussed in this paper. Another species showing some similarity is *F. misarelensis*, described in 2019 from Portugal. This species is slightly wider (up to 5.2 µm) but has a lower stria density (15–18 in 10 µm) and larger, capitate apices (Novais et al. 2019) making it sufficiently different. Based on valve outline, *Fragilaria sublanceolata-baikali* (Flower & D.M.Williams) Novais, C.Delgado & S.Blanco, described in 2004 from Lake Baikal (Flower et al. 2004, Novais et al. 2019, Van de Vijver et al. 2021) shows an almost similar valve outline, but can be separated from both *F. recapitellata* and *F. subrecapitellata* because the taxon from Lake Baikal lacks the typically swollen asymmetrical central area and the clearly protracted, capitate valve apices. Moreover, *F. sublanceolata-baikali* usually has broader valves (4.0–5.5 µm vs. 3.0–4.5 µm for both other taxa). The presence of short, conical spines has never been observed in *F. recapitellata* and *F. subrecapitellata,* which are entirely devoid of spines. Conspecificity or an infraspecific relationship with *F. recapitellata* and *F. subrecapitellata* can therefore be excluded. Finally, *F. austriaca* is a larger species with well-developed, triangular spines, a linear-lanceolate valve outline, an inconspicuous central area and much lower stria density (13–14 in 10 µm) (Van de Vijver et al. 2020b).

Taxa belonging to the *F. recapitellata* group are rare with only a few confirmed records worldwide. Grunow originally described *S. capitellata* based on specimens from a Kützing sample (Zürich, Switzerland). Cleve (1883) reported the species from a freshwater sample collected near Cape Sabine on the Canadian Arctic Ellesmere Island. Ross (1947) recorded the taxon from some of the same material Cleve examined (BM 29145), confirming its identity and transferring it to *Fragilaria vaucheriae* var. *capitellata* (Grunow in Van Heurck) Ross (1947, p. 184 and p. 314). The species has been observed in samples from North Macedonia and northern Italy (B. Van de Vijver, pers. obs.). Delgado et al. (2015) investigated the epitype slide of *F. recapitellata* and gave a list of recent illustrated references, unfortunately without verifying these records. Metzeltin et al. (2009) renamed the species to *F. recapitellata* but the published illustration (pl. 8, fig. 13) clearly represents a taxon belonging to the *F. pectinalis* group (B. Van de Vijver, unpub.) and cannot be identified as *F. recapitellata*. In Japan, several papers report the presence of *F. recapitellata* but a careful analysis of the published illustrations shows that none of these records are conspecific with the type of *F. recapitellata* and thus represent other species (Shiono & Jordan 1995: pl. 2, fig. 9, Ohtsuka 2002: figs 64–66, Ohtsuka et al. 2007: fig. 55, Hirota & Ohtsuka 2009: figs 62–64, Takano et al. 2009: fig. 14). The same applies for Lee et al. (1994: pl. 1, figs 15 & 16) reporting *F. recapitellata* (*F. vaucheriae* var. *capitellata*) from the Kwang river in South Korea. The illustrated valves show some affinity to *F. recapitellata* but are broader with less capitate apices and therefore most likely belong to a different species. Pictured valves in Gasse (1980, pl. 34, figs 2 & 3), Makarova & Achmetova (1987, pl. 1, fig. 1) and Vyverman (1991, pl. 7, fig. 3) represent different taxa and should not be identified as *F. recapitellata*. In South America, several papers reported the presence of *F. recapitellata* (as *F. vaucheriae* var. *capitellata*). Silva et al. (2010) illustrated two valves observed in the eutrophic Iraí river (State of Paraná, Brazil) showing some resemblance to *F. recapitellata* but with a lower stria density (maximum 16 in 10 µm) and a less swollen central area. It is unlikely that these valves, found in eutrophic circumstances, are conspecific with the type of *F. recapitellata*.

Published records are largely obscure due to confusion with illustrations of a taxon originally identified as *F. capucina* var. *capitellata* (Grunow) Lange-Bertalot in

Krammer & Lange-Bertalot (1991, pl. 109, figs 25–28), but later proved to belong to a different taxon, described in 2015 as *F. candidagilae* by Delgado et al. (2015). However, analysis of the type material of *F. candidagilae* and *F. deformis* (Van de Vijver et al. 2020a) already raised the possibility that they are conspecific, giving priority to *F. deformis*, originally described in 1856 from a small pool near Lewes, UK (Smith 1856). The observation of a large population of *F. deformis* in the historic Grunow sample 188 confirmed that all valves described as *F. candidagilae* from the type material show no morphological differences with *F. deformis*. Therefore, the correct name for this taxon (following the principle of priority, Turland et al. 2018, art. 11.4) is *F. deformis* with *F. candidagilae* as heterotypic synonym. Several of the above-mentioned publications actually illustrated *F. deformis* (e.g. Takano et al. 2009: fig. 14, Falasco et al. 2009: figs 85, 86). Since recent, widely used literature, such as Lange-Bertalot et al. (2017, pl. 9, figs 41–46) still identify valves clearly belonging to *F. deformis*, as *F. recapitellata*, it will be impossible to determine the distribution and ecological preferences of *F. recapitellata* based on (non-illustrated) literature data.

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No potential conflict of interest was reported by the authors.

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