

Analysis of the *Fragilaria rumpens* complex (Fragilariaceae, Bacillariophyta) with the description of two new species

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Abstract: The former *Synedra rumpens* complex has long puzzled diatom taxonomists. In the nineteenth century, many infraspecific taxa were described as varieties or forms of *S. rumpens*. In the present study, type material of *Synedra rumpens* and several infraspecific taxa such as *S. rumpens* var. *fragilarioides* and *S. familiaris* f. *parva* and f. *major* was investigated using LM and SEM observations. For comparison, the original material of several other relevant diatom taxa (such as *Fragilaria perdulicatissima*, *F. spinaspeciosa*, *Synedra campyla*, *S. vaucheriae* var. *distans*) was also analysed. The results based on these comparisons show that all infraspecific taxa should be split from *Fragilaria rumpens*. *Fragilaria campyla* is a new combination within the genus *Fragilaria* with *F. parva* and *S. (rumpens* var.?) *familiaris* f. *major* as synonyms. *Fragilaria scotica* is likewise a new combination in *Fragilaria*. *Fragilaria metcalfeana* is proposed as new name for *Synedra familiaris* var. *neogena*. The analysis of *F. distans* and *F. fragilarioides* confirmed their conspecificity, with *F. fragilarioides* having priority as name. Finally, two new species, *F. pseudofamiliaris* Van de Vijver, T.M.Schuster, Kusber et D.M.Williams sp. nov. and *F. bahlsiana* Van de Vijver, C.E.Wetzel et Ector sp. nov. are described. Using an analysis of the associated diatom flora, the ecological preferences of each taxon are briefly discussed.

Key words: Europe, *Fragilaria*, morphology, new species, *Synedra rumpens* complex, type analysis

INTRODUCTION

KÜTZING (1844) originally described *Synedra rumpens* Kützing from a brackish sample collected at the Oldenburgische Küste (coastal region around Bremen, Germany). The species was later transferred to the genus *Fragilaria* by CARLSON (1913) as *F. rumpens* (Kützing) G.W.F.Carlson. Its taxonomic identity remained obscure for a long time, not least due to incorrect interpretations by subsequent authors of the drawing KÜTZING (1844, pl. 16, fig. VI 4–5) added to his short description. Grunow in VAN HEURCK (1881, pl. XL, fig. 14) was one of the first to illustrate one valve he identified as *Synedra rumpens* Kützing ‘*genuina*’ based on Kützing’s type material (sample 194, TUJI & WILLIAMS 2006a), which

is evident by the ‘*vidi*’ (!) he added to the drawing. Grunow’s drawing in VAN HEURCK (1881) distinctly showed a clear hyaline central area. Subsequently, the central area was interpreted as being very large and, in most cases, even slightly swollen (see for instance HUSTEDT 1930, fig. 175 or PATRICK & REIMER 1966, pl. 5, fig. 19), taxonomically broadening the original species concept. In addition to drawing the actual type, as indicated by the annotation ‘*genuina*’ (VAN HEURCK 1881, pl. XL, fig. 14), Grunow in VAN HEURCK (1881, pl. XL, figs 11–13, 15 & 16) also described a broad array of varieties, however, doubting this rank by adding a ‘?’ in every name: *Synedra rumpens* var. ? *scotica* Grunow (fig. 11), *Synedra rumpens* var. ? *fragilarioides* Grunow (fig. 12), *Synedra rumpens* var. ? *meneghiniana* Grunow

(fig. 13) and *Synedra* (*rumpens* var.?) *familiaris* Kützing forma *parva* (fig. 15) and forma *major* (fig. 16). The taxonomic identity of var. *meneghiniana* has recently been investigated and the taxon proved to be conspecific with *Fragilaria pararumpens* Lange–Bertalot et al. (VAN DE VIJVER et al. 2021a). Based on his analysis of Neogene sediments from Slovakia, GRUNOW (1882) described another taxon in this complex: *Synedra familiaris* var. *neogena* Grunow. MAYER (1917), elevated var. *scotica* to species level as *Synedra scotica* Ant.Mayer, and split it into two varieties [var. *genuina* and var. *undulata* (Grunow) Ant.Mayer]. The drawings in his publication, however, do not correspond to those of *S. rumpens* var. *scotica* in VAN HEURCK (1881).

HUSTEDT (1930, pp. 156–157 and 1931, pp. 207–208) lists all of Grunow's varieties as synonyms of *Synedra rumpens*. In addition, HUSTEDT (1931, p. 207) synonymised several other taxa, such as *S. campyla* Hilse and *S. scotica*, with *S. rumpens*, but rather surprisingly excluded the original concept of *S. rumpens* var. *scotica* Grunow that he considered an independent variety of *S. rumpens*. CLEVE–EULER (1953) shared Hustedt's ideas on the *S. rumpens* complex recognising the same varieties. LANGE–BERTALOT (1980) was the first to show LM photographs of the type of *Synedra rumpens* (1980, pl. II, figs 39–41) discussing the complex of taxa associated with it. LANGE–BERTALOT (1980, p. 747) considered all these taxa (including var. *familiaris* and var. *scotica*) as synonyms of *Fragilaria capucina* Desmazières, a hypothesis later rejected in KRAMMER & LANGE–BERTALOT (1991) when *Synedra rumpens* was split from *F. capucina* as 'rumpens–Sippe'. The combination *F. capucina* var. *rumpens* Lange–Bertalot (KRAMMER & LANGE–BERTALOT 1991) was invalidly proposed, as no basionym was indicated, a situation corrected by BUKHTIYAROVA (1995). Later, LANGE–BERTALOT (1993) transferred *Synedra rumpens* to the *F. capucina* complex as a subspecies: *F. capucina* ssp. *rumpens* Lange–Bertalot. Most infraspecific *S. rumpens* taxa were not included in the synonymy of the *rumpens* complex, but instead were added to the list of synonyms of the *gracilis* complex (KRAMMER & LANGE–BERTALOT 1991, p. 123). In the most recent monographs on the European diatom flora (e.g. LANGE–BERTALOT et al. 2017) none of the former infraspecific *S. rumpens* taxa were included, apart from *Fragilaria familiaris* sensu Krasske (LANGE–BERTALOT et al. 2017, p. 271).

Synedra familiaris Kützing has also been the subject of a long debate regarding its taxonomic identity. TUJI & WILLIAMS (2008) discussed its taxonomic history, but concluded that the generally accepted idea of it being a *Fragilaria* species should be maintained. Recently, however, VAN DE VIJVER et al. (2020a) studied all the historical material related to this species and reached a different conclusion. It was impossible to unambiguously identify what KÜTZING had in mind in 1844 when he described *S. familiaris*, since original (type) material from Saint Lô (Normandy, France) could not be found,

the original drawing offered by KÜTZING (1844, pl. 15, fig. XII) is not sufficiently detailed to discriminate the species (and even the genus), and the material LANGE–BERTALOT (1980) used cannot be considered the lectotype as it was not original material, but from a different place in Normandy. Only the lectotypification in TUJI & WILLIAMS (2008) was generally accepted and all other populations formerly (and historically) identified as *S. familiaris* were described as a new species in the genus *Tabularia*: *T. neofamiliaris* Van de Vijver et D.M. Williams (VAN DE VIJVER et al. 2020a).

Following a careful analysis of all historical literature, it was clear that much confusion still remains regarding the *rumpens* complex, and that a revision of the original material of all these taxa was necessary. In the present paper, we analyse all original type materials for the species in the *Synedra rumpens* complex that could be found (see Table S1). Only the original type slide for *S. familiaris* var. *major* (=Grunow sample 970) could not be re-examined due to logistic constraints. Illustrations for the latter were published in TUJI & WILLIAMS (2008, figs 29–33) and these images are used for comparison in the current paper. The type material for *Fragilaria spinospeciosa* Lange–Bertalot et Cantonati in CANTONATI et al. (2019), *Synedra delicatissima* W. Smith, *S. vaucheriae* var. *distans* Grunow in VAN HEURCK (1881), and *S. campyla* Hilse in RABENHORST (1861) are also investigated in the present paper as these taxa showed some resemblance to the *S. rumpens* complex. In addition, several historic samples retrieved from the Van Heurck collection (BR, Meise Botanic Garden, Belgium) containing populations belonging to the *Synedra rumpens* complex or one of its varieties were also analysed by light (LM) and scanning electron microscopy (SEM). This results in the description of two new species: *Fragilaria bahlsiana* Van de Vijver, C.E. Wetzel et Ector sp. nov. and *F. pseudofamiliaris* Van de Vijver, T.M. Schuster, Kusber et D.M. Williams sp. nov. Several *Synedra* taxa are transferred to the genus *Fragilaria*: *Fragilaria campyla* (Hilse) Van de Vijver, Kusber et D.M. Williams comb. nov., *F. metcalfeana* (Grunow) Van de Vijver, D.M. Williams, Kusber et T.M. Schuster nom. nov., and *F. scotica* (Grunow) Van de Vijver, C.E. Wetzel et Ector comb. nov. et stat. nov. *Fragilaria distans* (Grunow) Bukhtiyarova is added as a synonym for *Fragilaria fragilaroides* (Grunow) Cholnoky based on the priority of Cholnoky's combination at species level (see TURLAND et al. 2018, art. 11).

MATERIAL AND METHODS

Table S1 lists all samples used in this study. Most samples are type material retrieved from the Grunow collection (W, Naturhistorisches Museum, Vienna, Austria) and the Van Heurck collection (BR, Meise Botanic Garden, Belgium).

Sub-samples of the selected material were prepared for LM and SEM observations following the method described in VAN DER WERFF (1955). Small quantities of the sub-samples were cleaned by adding 37% H₂O₂ 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 10 minutes at 3700× rpm), the resulting cleaned material was diluted with distilled water to avoid excessive concentrations of diatom valves on the slides and mounted in Naphrax®. The diatom 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. On the type slide for each taxon, the number of specimens was measured at random and is shown as n=X.

For SEM, a few drops of the oxidized suspensions were run through a 5- μm Isopore™ polycarbonate membrane filter (Merck Millipore). The SEM stubs with affixed pieces of membrane were sputter-coated with a platinum layer of 10 nm and studied using a JEOL–JSM–7100F field emission scanning electron microscope operated at 1 kV and 4 mm working distance (Meise Botanic Garden, Belgium) and an ultra-high-resolution Hitachi SU–70 analytical field emission (FE) scanning electron microscope (Hitachi High–Technologies, Europe, GmbH), operated at 5 kV and 10 mm working distance (LIST, Luxembourg). Slides and stubs analysed in this study are stored at BR (Meise Botanic Garden, Belgium). Plates were prepared using Photoshop CS5.

Terminology used in the description of the various structures of the siliceous cell wall is based on ROSS et al. (1979, areola structure), COX & ROSS (1981, stria structure), WILLIAMS & ROUND (1987, genus features for *Fragilaria*), and TUJI & WILLIAMS (2006b, genus features for *Fragilaria*). Note that the terms ‘sternum’ for the axial area (ROUND 1979) and ‘ocellulimbus’ for the inset apical pore field (WILLIAMS 1986) are used. For taxonomic comparisons, the following papers were used: VAN HEURCK (1881), PATRICK & REIMER (1966), LANGE–BERTALOT (1980), KRAMMER & LANGE–BERTALOT (1991), TUJI (2004, 2007), TUJI & HOUKI (2004), TUJI & WILLIAMS (2006a, 2008), LINARES–CUESTA & SÁNCHEZ–CASTILLO (2007), LANGE–BERTALOT & ULRICH (2014), LANGE–BERTALOT et al. (2017), CANTONATI et al. (2019), VAN DE VIJVER et al. (2020a, b, 2021a, b).

RESULTS AND DISCUSSION

The results of the present study demonstrate that the *Fragilaria rumpens* complex is more diverse than currently recognized in the literature. This is primarily due to broadly defined taxa, such as *Fragilaria capucina* var. *rumpens*. For example, HUSTEDT (1931) placed many named taxa into synonymy with *Synedra rumpens*, such as *S. campyla* and *S. scotica*, while including others as varieties of *S. rumpens*. These concepts were followed by PATRICK & REIMER (1966) and LANGE–BERTALOT (1980). The latter included almost all infraspecific taxa from the *S. rumpens* complex in synonymy with *Fragilaria capucina*, but abandoned these concepts later (see for instance KRAMMER & LANGE–BERTALOT 1991).

In the present paper, the original material of eleven taxa in the *Synedra rumpens* complex has been investigated. Based on the results, some of its infraspecific taxa should be merged, as they represent the same species, while others should be recognised as distinct species. This has important consequences for the taxonomy of

the *Fragilaria rumpens* group occurring in Europe.

The following species are discussed, grouping the different taxa under their proposed accepted name:

Fragilaria rumpens (Kützing) G.W.F. Carlson

Fragilaria campyla (Hilse) Van de Vijver, Kusber et D.M. Williams comb. nov.

Fragilaria scotica (Grunow) Van de Vijver, C.E. Wetzel et Ector comb. nov. stat. nov.

Fragilaria pseudofamiliaris Van de Vijver, T.M. Schuster, Kusber et D.M. Williams sp. nov.

Fragilaria bahlsiana Van de Vijver, C.E. Wetzel et Ector sp. nov.

Fragilaria metcalfeana Van de Vijver, D.M. Williams, Kusber et T.M. Schuster, nov. nom.

Fragilaria fragilarioides (Grunow) Cholnoky

Two additional species were also analysed as they are easily confused with species in the *Synedra rumpens* complex:

Fragilaria perdelicatissima Lange–Bertalot et Van de Vijver

Fragilaria spinaspeciosa Lange–Bertalot et Cantonati

Fragilaria rumpens (Kützing) G.W.F. Carlson 1913

One of the main distinguishing features in the *Fragilaria rumpens*–group is the ability to form colonies. *Fragilaria rumpens* forms extremely long, ribbon-like colonies often containing several tens of valves. This feature of *F. rumpens* is shared with *F. capucina* (VAN DE VIJVER et al. 2021b). An important difference between the two is the presence of two rimoportulae per valve in *F. capucina*, whereas *F. rumpens* has only one (HEUDRE et al. 2019; VAN DE VIJVER et al. 2021b), excluding all possible synonyms. These species can also be distinguished based on their valve dimensions, with *F. capucina* having a slightly larger valve width than *F. rumpens* (3.5–4 μm vs. 3.0–3.5 μm) and a lower stria density (15–16 vs. 19–20 in 10 μm).

Fragilaria rumpens (Kützing) G.W.F. Carlson 1913 (Figs 1–35)

Basionym: *Synedra rumpens* Kützing 1844, KÜTZING (1844), Die kieselschaligen Bacillarien oder Diatomeen: 69, pl. 15, fig. VI 4 & 5.

≡ *Fragilaria capucina* ssp. *rumpens* (Kützing) Lange–Bertalot 1993.

≡ *Fragilaria capucina* var. *rumpens* (Kützing) Lange–Bertalot ex Bukhtiyarova 1995.

≡ *Desmogonium kuetzingii* Rabenhorst 1864, nom. illeg.

Description

LM (Figs 1–28): Frustules in girdle view rectangular, linked forming long, ribbon-like colonies (Figs 3–9). Valves linear to linear–lanceolate with almost straight to very weakly convex margins. Longer valves often curved or undulating. Apices distinctly protracted, rostrate to often capitate. Valve dimensions (n=25): length 20–80 μm , width 3.0–3.5 μm . Sternum very narrow, linear, gradually widening towards central area. Central area forming a large, rectangular hyaline area, spanning entire valve width. Occasionally central area appearing weakly swollen (Figs 15, 16, 24) or unilateral (Fig. 28), latter bordered by shortened striae. Striae alternating parallel to slightly radiate throughout entire valve, 19–20 in 10 μm . Areolae not discernible in LM.

SEM (Figs 29–35): Frustules linked using strongly

entwined, well developed linking spines (Figs 29, 30, 34). Linking spines irregularly shaped and bifurcated at the valve center, becoming conical at apices (Fig. 29). Mantle plaques distinct, present at mantle edge (Fig. 30). Valve face flat with only weakly raised virgae (Figs 31, 33). Ghost striae usually present in the central area (Fig. 31) although sometimes absent (Fig. 35). Apical pore fields of the ocellulimbus type, well developed, composed of several rows of small poroids (Fig. 32). External rimoportula opening rimmed, obliquely positioned between last stria and valve apex (Fig. 33). Striae composed of externally occluded, rounded areolae (Fig. 33). Internal opening of the rimoportula small, obliquely positioned (Fig. 35; arrow). Girdle composed of epicingulum and hypocingulum, each of three, open bands (Figs 29, 30). Third band considerably thinner than previous two (Figs 29, 30); all barely ligulate, opening at valve pole. Each band with irregularly spaced granules at abvalvar edge, two rows of pores (Figs 29, 30), only one row visible internally (Fig. 35).

Analysed material: Kützing, Oldenburgische Küste, sample 194 (type material) archived at BR! as BR-4677. **Lectotype:** BM 18357 (Natural History Museum, London, UK), designated in KRAMMER & LANGE-BERTALOT (1991, p. 446).

Associated diatom flora: The type material is dominated by *Fragilaria rumpens*. Other relatively frequent taxa in the sample include *Tabellaria flocculosa* (Roth) Kützing and *Meridion constrictum* Ralfs, both indicative of electrolyte poor, oligo- to mesotrophic, soft, running waters (CANTONATI et al. 2012; LANGE-BERTALOT et al. 2017).

The taxon identified by VAN HEURCK, in his Types du Synopsis de Diatomées de Belgique (1882–1885), as *Synedra rumpens* var. *familiaris* Kützing (Types n° 296) shows no difference to the type population of *Fragilaria rumpens* and is therefore considered a synonym. Valve dimensions including stria density, colony type, shape of the central area and shape of the apices do not differ from the type of *F. rumpens* (Table S2).

***Synedra rumpens* var. *familiaris* Kützing sensu Van Heurck 1885 (Figs 36–54)**

LM (Figs 36–54): Frustules in girdle view rectangular forming long, ribbon-like colonies (Figs 36, 37). Valves elongated, linear-lanceolate with parallel margins, gradually tapering towards apices throughout entire cell diminution series. Apices distinctly protracted, subcapitate to capitate, in both smaller and longer specimens. Valve dimensions (n=30): length 40–70 µm, width 2.5–3.0 µm. Sternum narrow, linear, gradually weakly widening near central area. Central area forming rectangular, weakly swollen, hyaline zone, spanning entire valve width. Ghost striae always present (Figs 40, 43, 48). Striae alternating, parallel throughout entire valve, only weakly more radiate at apices, 19–20 in 10 µm. Areolae not discernible in LM.

Scanning electron microscopy observations were not possible. Only a handful of historic slides were

conserved in the Van Heurck collection and it was not possible to destructively sample any for SEM analysis. The vial containing the original material used to make Type n° 296 is missing from the collection.

Analysed material: Slide IX-44-C5, Van Heurck, Types du Synopsis de Belgique, n° 296, Holstein, Schleswig-Holstein, Germany, kept in BR.

Associated diatom flora: The accompanying notes for Van Heurck's Type du Synopsis, no. 296 (295 according to the label), provided by Grunow, lists the following taxa as present: *Synedra rumpens* var. *familiaris*, *Synedra vaucheriae* var.? (or *Staurosira intermedia*), *Achnanthes lanceolata*, *Gomphonema parvulum*, *G. subclavatum*, *G. angustatum* var., *Meridion circulare*, and *Eunotia lunaris* (VAN HEURCK 1882–1885). Analysis of the slide showed that the dominant species include *Eunotia bilunaris* (Ehrenberg) Schaarschmidt, *Fragilaria rumpens*, *Fragilaria* cf. *pectinalis* (O.F.Müller) Lyngbye, *Gomphonema parvulum* Kützing, *G. subclavatum* (Grunow) Grunow, *G. angustatum* (Kützing) Rabenhorst, *Meridion circulare* (Greville) C. Agardh, and *Tabellaria flocculosa* (Roth) Kützing. Based on the ecological information provided in LANGE-BERTALOT et al. (2017) this composition points to mesotrophic, moderately electrolyte-rich, circumneutral conditions.

***Fragilaria campyla* (Hilse) Van de Vijver, Kusber et D.M. Williams comb. nov.**

Analysis of the type material of *Synedra campyla* Hilse, here transferred to the genus *Fragilaria* as *Fragilaria campyla* (Hilse) Van de Vijver, Kusber et D.M. Williams comb. nov., showed that most of the valves in the type population of this species are deformed, showing bent, undulating or twisted valves. *Fragilaria* taxa often exhibit these kinds of deformations, sometimes due to heavy metal or pesticides enrichment or pollution (MCFARLAND et al. 1997; FALASCO et al. 2009), but several more or less typical valves were also observed. It is, however, also quite unlikely that pesticides would have caused the deformation in 1860 when the sample Hilse used was collected. Valve dimensions, shape of the central area, valve outline and stria density are almost identical to *F. parva* (Grunow) Tuji et D.M. Williams, especially when both the lectotype specimens of *F. campyla* and the Brébisson specimens from Falaise representing *F. parva* are considered. *Synedra* (*rumpens* var.?) *familiaris* f. *parva* Grunow was raised to species level by TUJI & WILLIAMS (2008) as *Fragilaria parva*. In the same paper, another Grunow taxon, *Synedra* (*rumpens* var.?) *familiaris* f. *major* was also investigated but not raised to species level as it was thought to be a synonym of *F. parva* and representing the longer valves of the cell diminution series (TUJI & WILLIAMS 2008, p. 29). GRUNOW in VAN HEURCK (1881, pl. XL, figs 16a–c) illustrated two valves under the name f. *parva*, originating from different localities. One of these, Grunow sample 2654, was based on material from Walker Arnott's sample S 701 that originated from Glen Cove, Long Island (USA, leg. M. Edwards s.n.) and was assigned as lectotype by TUJI & WILLIAMS (2008, p.

29, fig. 14) (Fig. 80). The other was a sample collected by Brébisson from Falaise (Fig. 81). The material for the latter sample was retrieved from BR under the name *Synedra vaucheriae* Kützing. The longest valves in this population are conspecific with the valves depicted in TUJI & WILLIAMS (2008, figs 29–33) representing *f. major*. Since the Falaise population showed a clear continuum of valves identified as *f. parva* and valves identified as *f. major*, we concur with TUJI & WILLIAMS (2008) that both forms are conspecific and belong to *Fragilaria parva* (Table S2). The name *Synedra (rumpens var.?) familiaris f. major* is therefore a synonym of *F. parva*. A possible relationship with *Synedra familiaris* Kützing has been rejected by VAN DE VIJVER et al. (2020a), who showed that *Synedra familiaris* belongs to the genus *Tabularia*. As *Synedra campyla* was described at species rank in 1860, prior to the description of *Synedra (rumpens var.?) familiaris f. parva* in 1881, the former has priority according to ICN art. 11 (TURLAND et al. 2018) and the correct name for these specimens is *Fragilaria campyla*. The lectotypes *Fragilaria campyla* and *Fragilaria parva* are ambiguous regarding teratologies and missing morphological information for taxon identification, including their conspecificity. These ambiguities can be overcome by the Brébisson sample from Falaise, and thus, it is here proposed as the epitype to the lectotype designated for *F. campyla* in accordance with ICN Art. 9.9 (TURLAND et al. 2018).

Three materials are discussed here: *Fragilaria campyla* (Rabenhorst material), *F. parva* (Walker Arnott material), and a sample from BRÉBISSON labelled *Synedra vaucheriae*.

KAHLERT et al. (2019) analysed several species in *Fragilaria* based on molecular data, and some of their illustrated valves show a similarity with *F. campyla* and might be considered conspecific with it. However, one was identified as *F. tenera* (KAHLERT et al. 2019, fig. 8), although the depicted valves strongly differ from the type population of *F. tenera* (see LANGE–BERTALOT & ULRICH 2014; ALMEIDA et al. 2016). Further morphological analysis of the specimens in KAHLERT et al. (2019) is therefore required.

***Fragilaria campyla* (Hilse) Van de Vijver, Kusber et D.M. Williams comb. nov. (Figs 55–79)**

Basionym: *Synedra campyla* Hilse in Rabenhorst, HILSE in RABENHORST (1861), Alg. Eur. Dec.: 103/104, n° 1024.

Additional information: description by HILSE (1861), Jahres–Bericht der Schlesischen Gesellschaft für Vaterländische Cultur 38: 84.
≡ *Synedra lunaris* var. *campyla* (Hilse ex Rabenhorst) Kirchner 1878.
≡ *Eunotia lunaris* var. *campyla* (Hilse in Rabenhorst) F.Meister 1912.
≡ *Eunotia curvata* var. *campyla* (Hilse in Rabenhorst) Woodhead et Tweed 1960.

Registration: <http://phycobank.org/102747>

LM (Figs 55–73): Frustules in girdle view rectangular, solitary or with two cells together. Aggregates of multiple frustules grouped together occasionally observed. Ribbon–like colonies not observed. Valves elongated, linear to linear–lanceolate. Teratological forms with

irregularly undulating or bent valve outlines often observed (Figs 69–73). Apices protracted, capitate throughout entire cell diminution series. Valve dimensions (n=25): length 35–45 µm, width 2.5–3.0 µm. Sternum distinct but narrow, gradually widening towards central area. Central area forming large, rectangular hyaline zone, spanning entire valve width. Ghost striae clearly present in almost all valves. Striae alternating, parallel, only weakly radiate near apices, 19–20 in 10 µm. Areolae not discernible in LM.

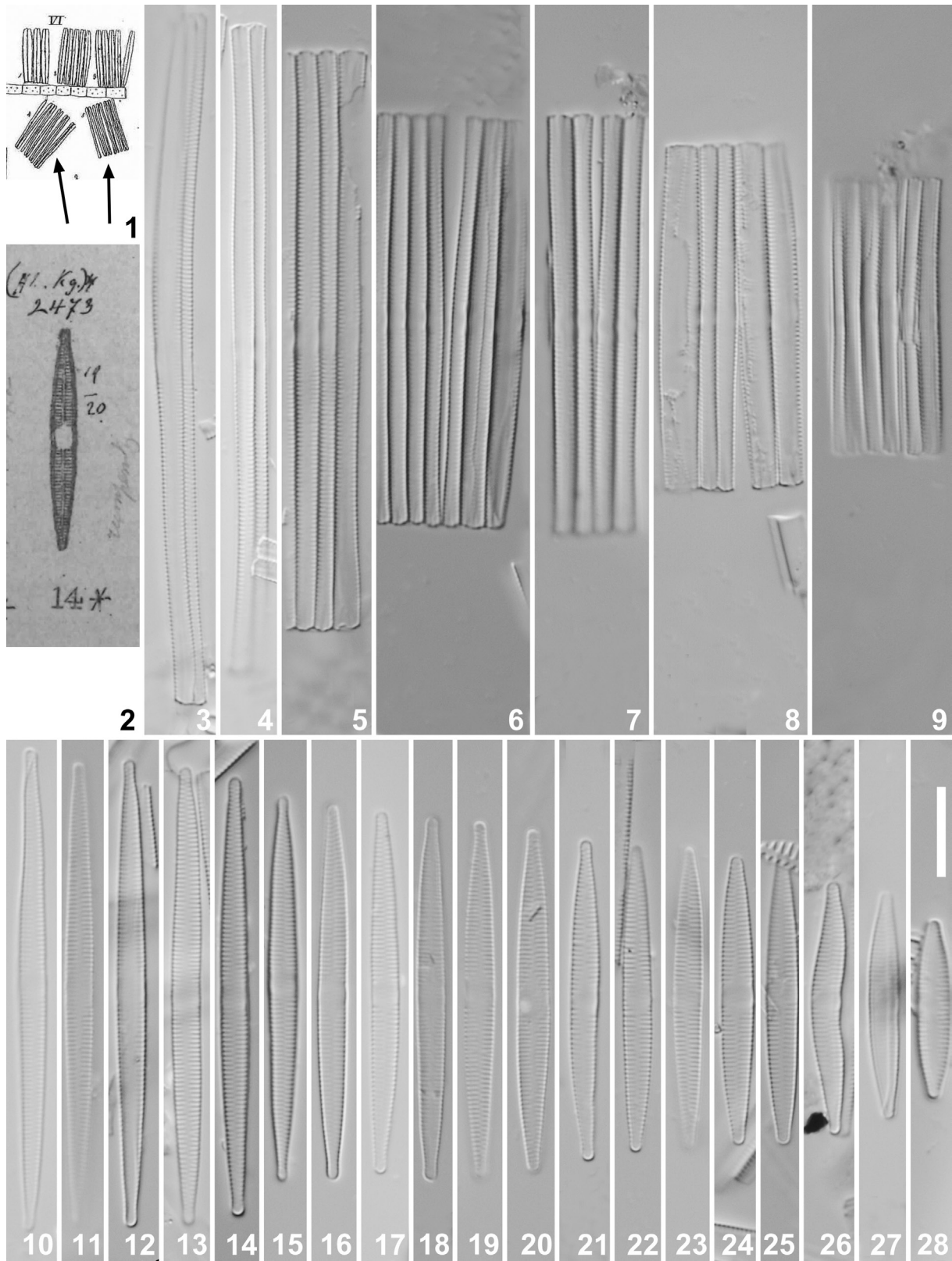
SEM (Figs 74–79): Valve face flat with weakly raised virgae (Figs 74, 75). Sternum large, clearly widening towards the central area (Figs 75, 79). Small, acute to shark tooth–shaped spines in continuous series at the valve margins, running from apex to apex, almost always aligned with a virga (Fig. 75). Several spines present at the apices (Fig. 77). Large mantle plaques present at the mantle edge (Fig. 76). Central area with distinct ghost striae, visible as long, shallow grooves (Figs 74, 75). Striae uniseriate, composed of small, rounded areolae (Fig. 75). Apical pore field of the ocellulimbus type, well developed, composed of several rows of small, rounded poroids (Figs 77, 78). Externally, rimoportula opening small, rounded, rimmed, located at apices, in centre of final stria (Fig. 77, arrow). Internally, rimoportula opening located close to valve margin, eccentric (Figs 78, 79, arrow). Girdle composed of epi– and hypo–cingulum, each of four open bands (Figs 74, 76). Fourth band considerably thinner than previous three (Figs 74, 76), ligulate, tapering and opening at valve pole. Each band with one row of pores (Figs 74, 76), visible internally (Fig. 79) and externally (Figs 74, 76, but these may be displaced by processing of material).

Lectotype (here designated): slide BR–4667 (Meise Botanic Garden, Belgium), slide made from original material for RABENHORST (1861) Algen Europa’s n° 1024, kept at BR.

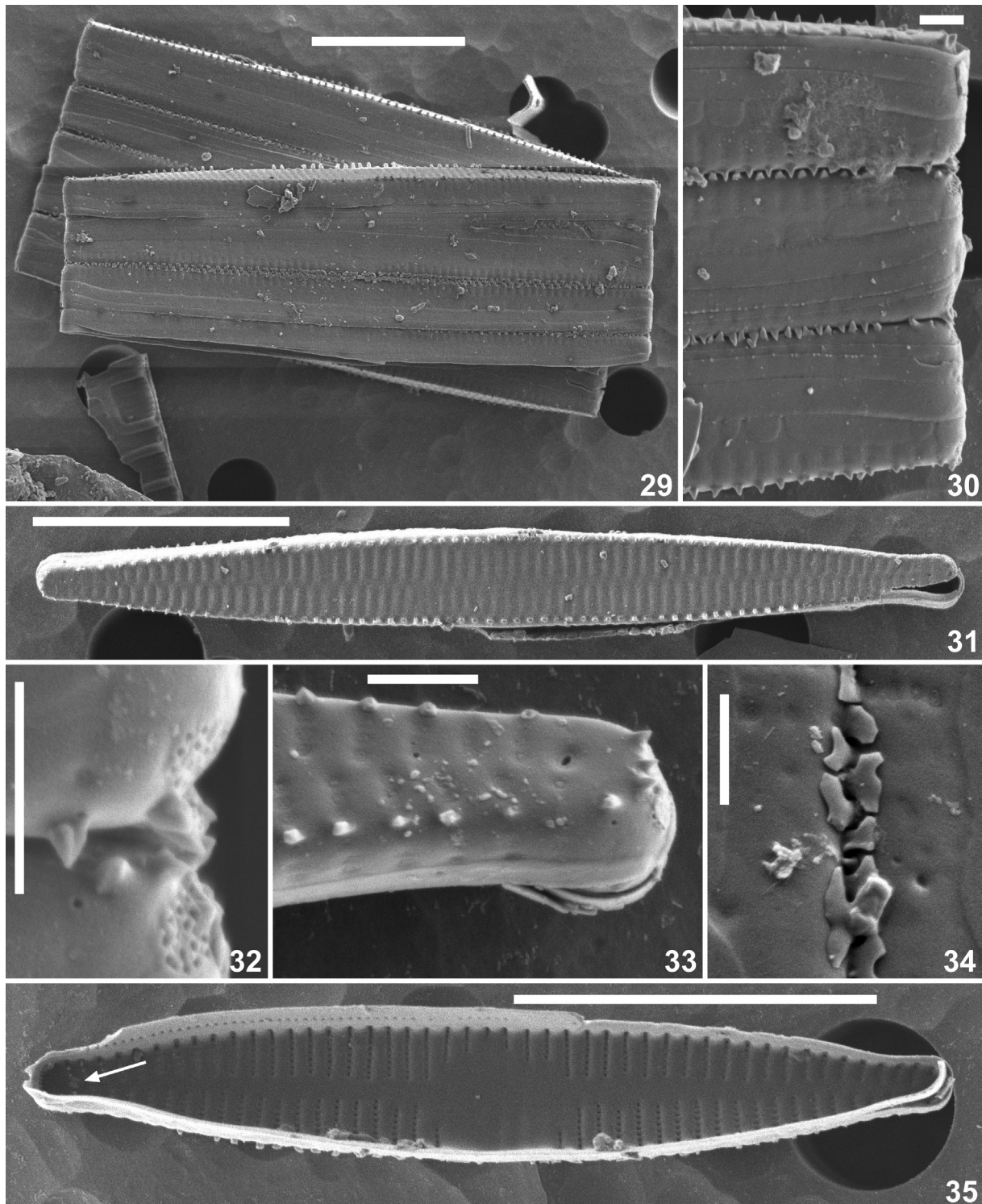
Epitype (here designated for the above lectotype of *Synedra campyla* Hilse): slide BR–4668, prepared from Brébisson material of *Synedra vaucheriae* Falaise (France), material archived in the Van Heurck collection (BR) (see above).

Analysed material: BR–4667, RABENHORST (1861), Algen Europa’s, exsiccata n° 1024, in einem Brunnenabfluss von Katschwitz bei Strehlen (Poland, leg. F.W.HILSE s.n.), material kept in BR.

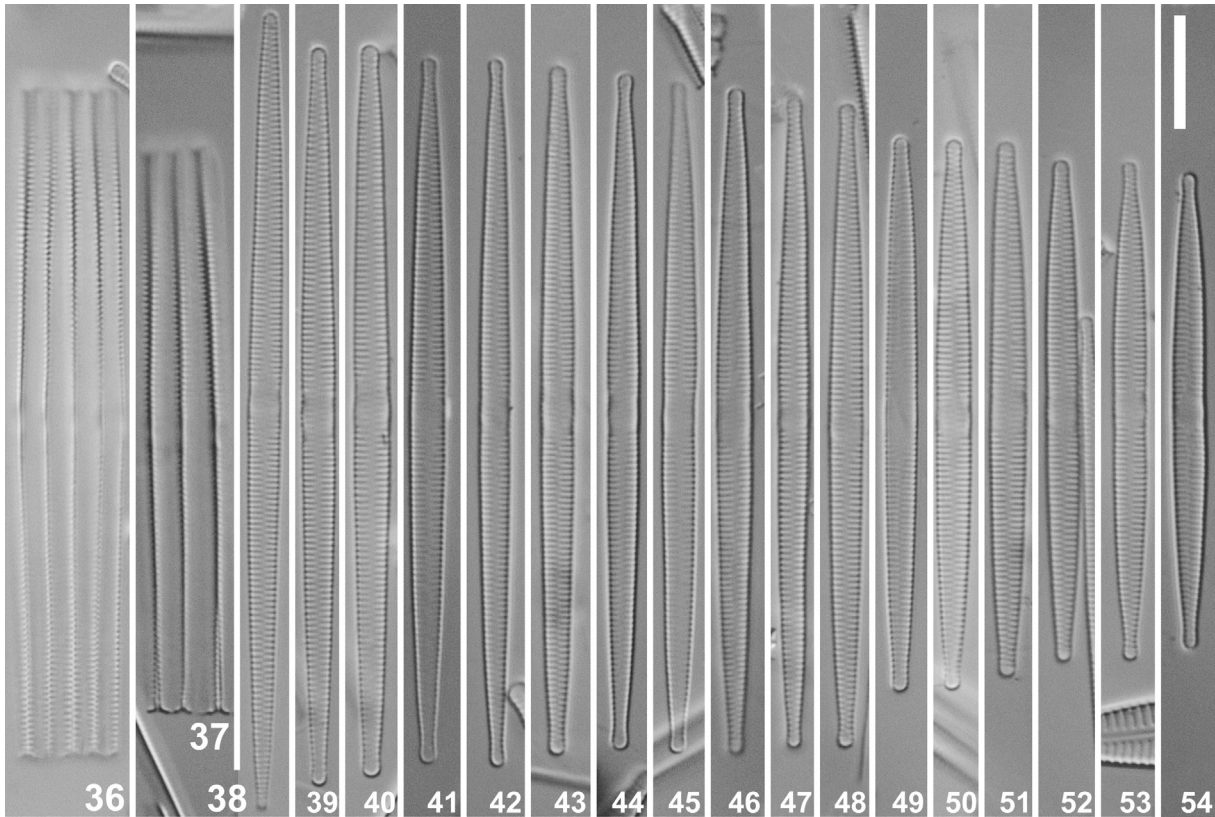
Associated diatom flora: The sample is dominated (in decreasing order of abundance) by *Planothidium lanceolatum* (Brébisson ex Kützing) Lange–Bertalot, *P. frequentissimum* (Lange–Bertalot) Lange–Bertalot, *Sellaphora atomoides* (Grunow) C.E.Wetzel et Van de Vijver, *Fragilaria campyla*, *Gomphonema exilissimum* (Kützing) Kützing, and *Meridion circulare* (Greville) C.Agardh. This species composition indicates higher nutrient levels and α–mesosaprobic, circumneutral to alkaline conditions (LANGE–BERTALOT et al. 2017).



Figs 1–28. *Fragilaria rumpens* (Kützing) G.W.F. Carlson. LM images taken from the type material (KÜTZING sample 194, BR–4677): (1) original drawing from KÜTZING (1844, pl. 15, fig. VI 4 & 5). The arrows indicate *F. rumpens* frustules. (2) annotated drawing by GRUNOW (sample 2473) in VAN HEURCK (1881, pl. XL, fig. 14); (3–9) views of several frustules in girdle view, connected to form a ribbon-like colony; (10–28) LM views of the population arranged in decreasing length. Scale bar represents 10 μm.



Figs 29–35. *Fragilaria rumpens* (Kützing) G.W.F. Carlson. SEM images taken from the type material (KÜTZING sample 194, BR-4677): (29) SEM external view of several frustules connected by linking spines; (30) detail of apices of three frustules linked to each other. Note the mantle plaques and linking spines. (31) external view of an entire valve showing the marginal series of spines; (32) SEM external detail of valve apex in girdle view showing apical pore field and small spines at apices; (33) SEM external detail of valve apex showing rimoportula; (34) SEM detail of linking spines; (35) SEM internal view of an entire valve showing rimoportula (arrow) at the apex. Scale bars represent 10 µm (29, 31, 35) and 1 µm (30, 32–34).



Figs 36–54. *Synedra rumpens* var. *familiaris* Kützing sensu Van Heurck. LM images taken from slide IX–44–C5, VAN HEURCK, Types du Synopsis de Belgique, n° 296 (Holstein, Schleswig–Holstein, Germany). LM views of population arranged in decreasing length. (36, 37) represent frustules in girdle view. Scale bar represents 10 μ m.

Fragilaria parva (Grunow) Tuji et D.M. Williams 2008 (Figs 80–117)

Basionym: *Synedra* (*rumpens* var.?) *familiaris* f. *parva* Grunow in Van Heurck, GRUNOW in VAN HEURCK (1881), Synopsis des Diatomées de Belgique, pl. XL, fig. 15.

= *Synedra* (*rumpens* var.?) *familiaris* f. *major* Grunow in VAN HEURCK 1881.

– *Synedra scotica* (Grunow) Ant. Mayer 1917 sensu MAYER (1917) exclusive of the type.

To exclude from synonymy: *Synedra rumpens* var. *scotica* Grunow in VAN HEURCK (1881).

LM (Figs 80–111): Frustules in girdle view rectangular, single or with two cells together (Figs 82, 83). Ribbon-like colonies not observed. Valves linear to linear-lanceolate with parallel to only very weakly convex margins, throughout entire cell diminution series. Apices distinctly protracted, capitate to rostrate in smaller specimens. Valve dimensions (n=40): length 20–40 μ m, width 3.0–3.5 μ m. Sternum narrow but distinct, linear, gradually widening towards the central area. Central area swollen, forming a large hyaline rectangular zone. Ghost striae clearly visible. Striae alternating, parallel to weakly radiate throughout the entire valve, more radiate near the apices, 19–21 in 10 μ m. Areolae not discernible in LM.

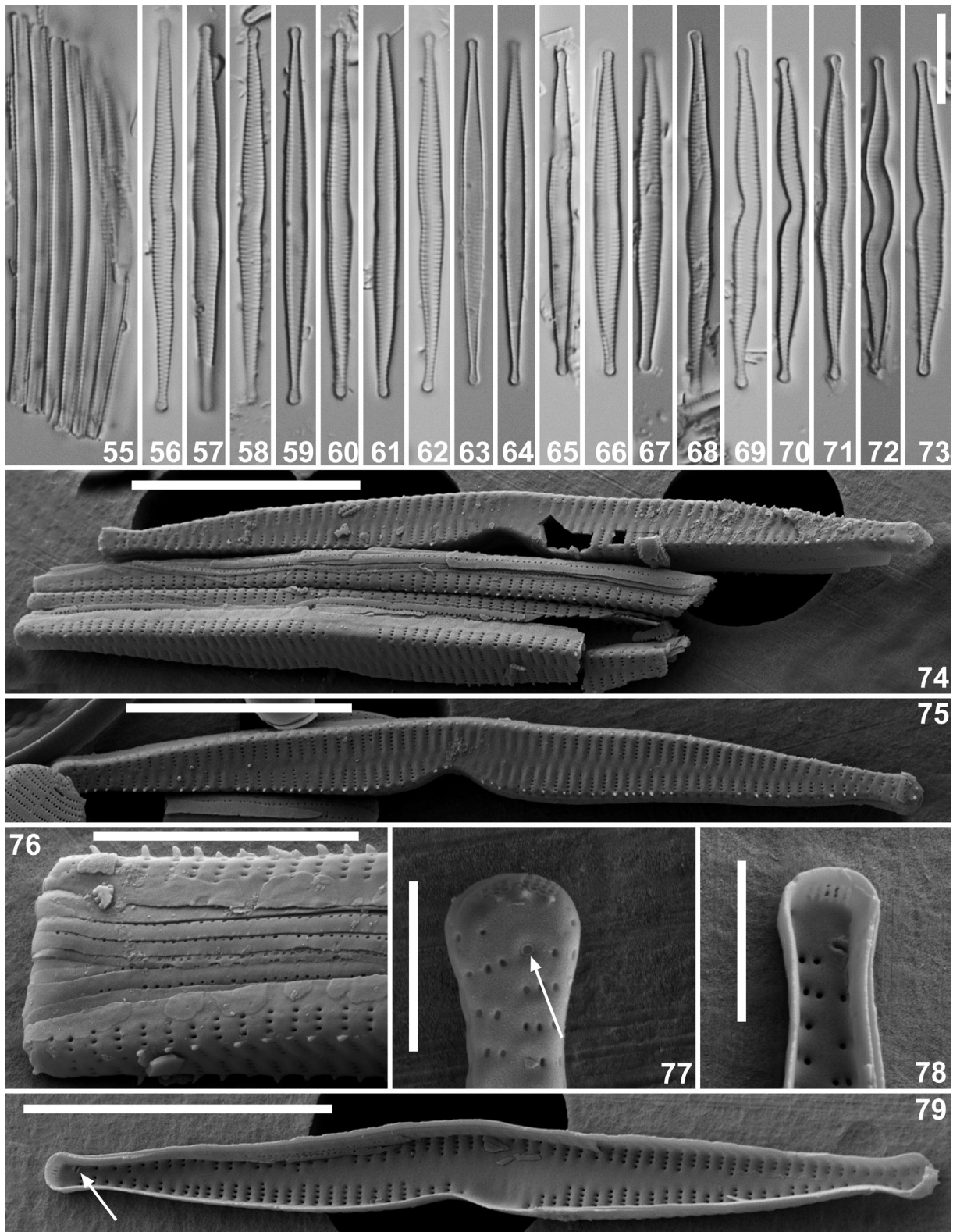
SEM (Figs 112–117): Valve face flat (Fig. 112). Striae uniseriate, composed of several small, rounded to weakly apically elongated areolae (Figs 114–116). Small transapical slits present near the sternum at end of each stria (Fig. 115, arrow), absent near apices. Ghost striae in

central area very distinct, visible as shallow, transapically elongated grooves (Fig. 113). Marginal spines present forming continuous series from apex to apex, non-linking, mostly shark tooth shaped (Figs 112–115), (most) situated between virgae in place of vimen (Figs 112–115). Several (often broken) spines present at apices (Figs 114, 115). External rimoportula opening small, rimmed, rounded, located at one apex in last stria (Fig. 115). Apical pore field of the ocellulimbus type, rectangular, well delimited, composed of 4 rows of relatively large rectangular poroids (Fig. 114). Internally, central area very distinct, shallowly depressed. Virgae clearly raised (Fig. 117). Internal rimoportula opening with paired lips, almost straight, positioned at one apex within virga (Fig. 117). Girdle composed of epi- and hypo-cingulum, each of three open bands (Figs 112, 113). Ligulate, tapering and opening at valve pole. Each band with one row of pores (Figs 113, 116), visible externally (Fig. 113, but may be displaced by processing of material).

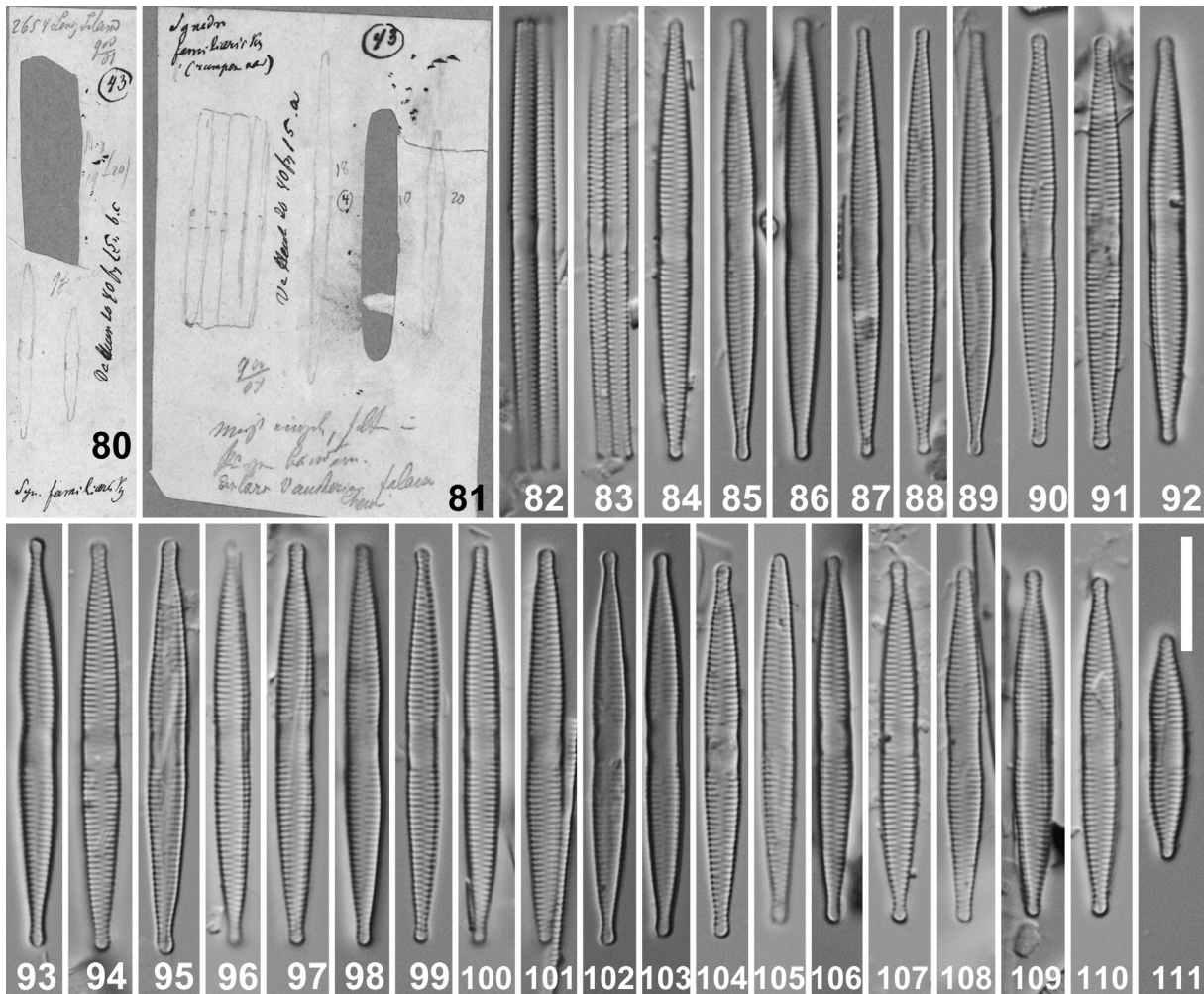
Lectotype: W0164811 Grunow sample 2654, designated in TUJI & WILLIAMS (2008) archived in W.

Analysed material: BR–4669, WALKER ARNOTT sample S 701 (Glen Cove Long Island, USA, leg. M. EDWARDS) = Grunow sample 2654 illustrated in VAN HEURCK (1881, pl. XL, Fig. 15b, c) (Fig. 80).

Associated diatom flora: The type material is dominated (in decreasing abundance) by *Melosira varians* C. Agardh,



Figs 55–79. *Fragilaria campyla* (Hilse) Van de Vijver, Kusber et D.M. Williams comb. nov. LM and SEM images taken from the lectotype material (BR-4667, RABENHORST exsiccata no. 1024a, Strehlen, Poland): (55–73) LM views of population arranged in decreasing length. Fig. 55 represents an aggregation of frustules. (74) SEM external view of several aggregated frustules; (75) external view of an entire valve showing marginal series of spines and ghost striae; (76) SEM external detail of valve apex in girdle view showing mantle plaques, girdle bands, and small spines; (77) SEM external detail of valve apex showing rimoportula (arrow); (78) SEM internal detail of valve apex showing rimoportula; (79) SEM internal view of an entire valve showing rimoportula (arrow) at the apex rimoportula (arrow). Scale bars represent 10 µm (55–76, 79) and 1 µm (77, 78).



Figs 80–111. *Fragilaria parva* (Grunow) Tuji et D.M. Williams. Drawings and LM images taken from the type material (BR-4669, WALKER ARNOTT S 701): (80) cut-out remainder of original drawing from the Grunow collection at W used for VAN HEURCK (1881, pl. XL, fig. 16b&c); (81) cut-out remainder of the original drawing from the Grunow collection used for VAN HEURCK (1881, pl. XL, fig. 16a); (82–111) LM views of population arranged in decreasing length, (82, 83) represent frustules in girdle view. Scale bar represents 10 μ m.

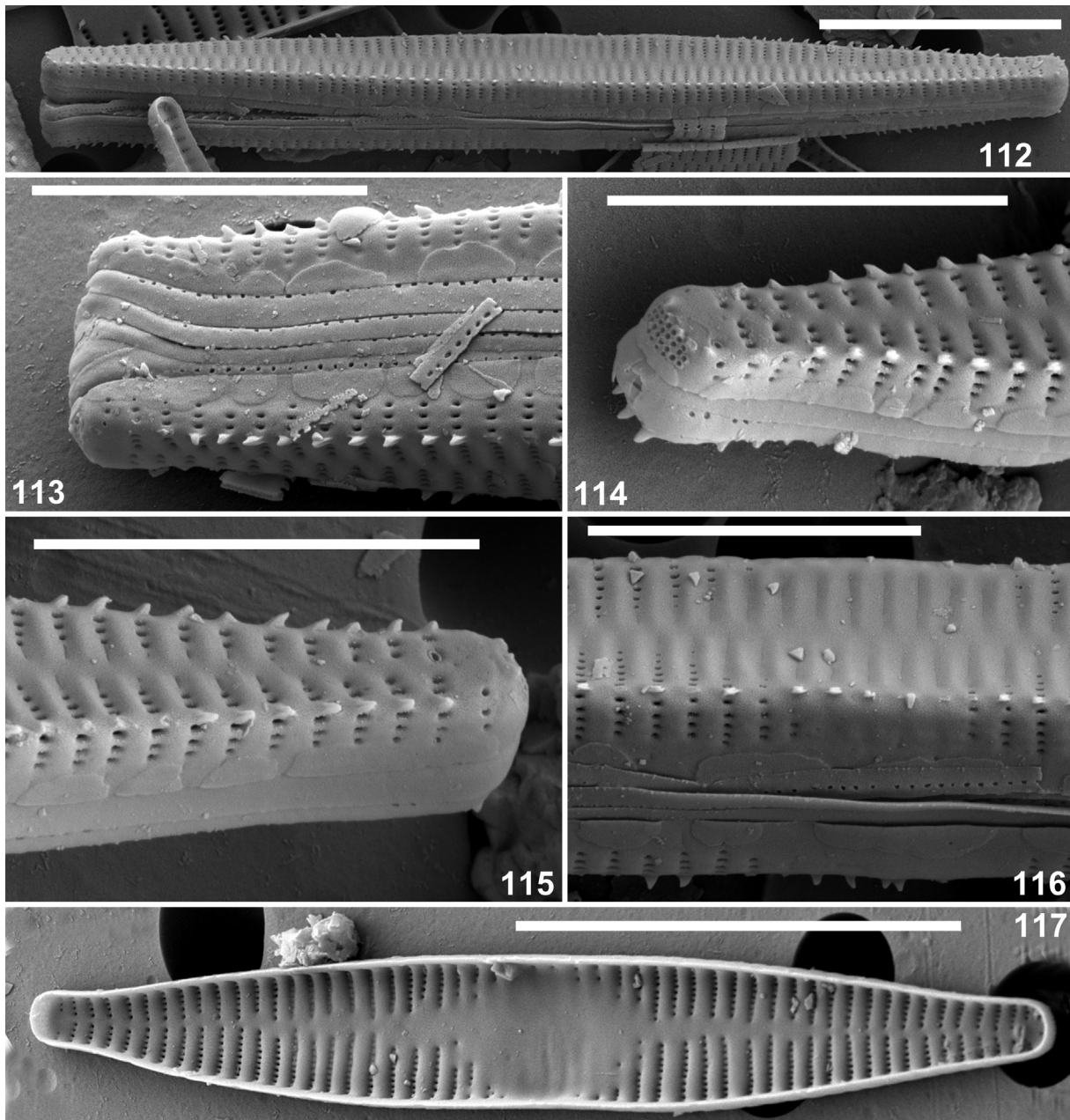
Fragilaria parva, *Gomphonema parvulum*, *Planothidium frequentissimum*, *Ulnaria oxyrhynchus* (Kützing) Aboal, *Surirella angusta* Kützing, and *Navicula cryptocephala* Kützing. Infrequent taxa include *Frustulia vulgaris* (Thwaites) De Toni, *Navicula gregaria* Donkin, *Nitzschia* cf. *perminuta* (Grunow) M. Peragallo, and *Surirella minuta* Brébisson. According to LANGE-BERTALOT et al. (2017), this species composition points to moderately to strongly electrolyte rich, eutrophic, circumneutral to alkaline running waters.

***Synedra vaucheriae* Kützing sensu Brébisson (Figs 118–161)**

LM (Figs 118–154): Frustules in girdle view rectangular, usually two cells together (Figs 118–122). Ribbon-like colonies not observed in the raw, untreated material. Valves linear to linear-lanceolate with gradually narrowing valve margins. Apices distinctly protracted, capitate to rostrate throughout entire cell diminution series. Valve

dimensions (n=60): length 20–70 μ m, width 3.0–3.5 μ m. Sternum narrow, but distinct, linear, near central area slightly expanding. Central area distinctly swollen, forming well-delimited large hyaline rectangular zone. Ghost striae usually clearly visible in central area. Striae alternating, almost parallel to weakly radiate throughout entire valve, more radiate near apices, 19–21 in 10 μ m. Areolae not discernible in LM.

SEM (Figs 155–161): Usually two frustules connected to each other (Fig. 157). Small conical, non-linking spines present forming continuous series at valve face margin extending from apex to apex (Figs 155–157); irregular sizes, shapes and, predominantly, aligned with vimines (Figs 155–157). Mantle plaques large, clearly present at mantle edge (Fig. 157). Mantle striae composed of several small areolae (Fig. 157). Valve face flat (Figs 156, 158), but with distinctly raised virgae. Several spines (often broken) present at apices (Fig. 159). Striae uniseriate, composed of several small, rounded to weakly apically elongated areolae (Fig. 158). Ghost striae in central area



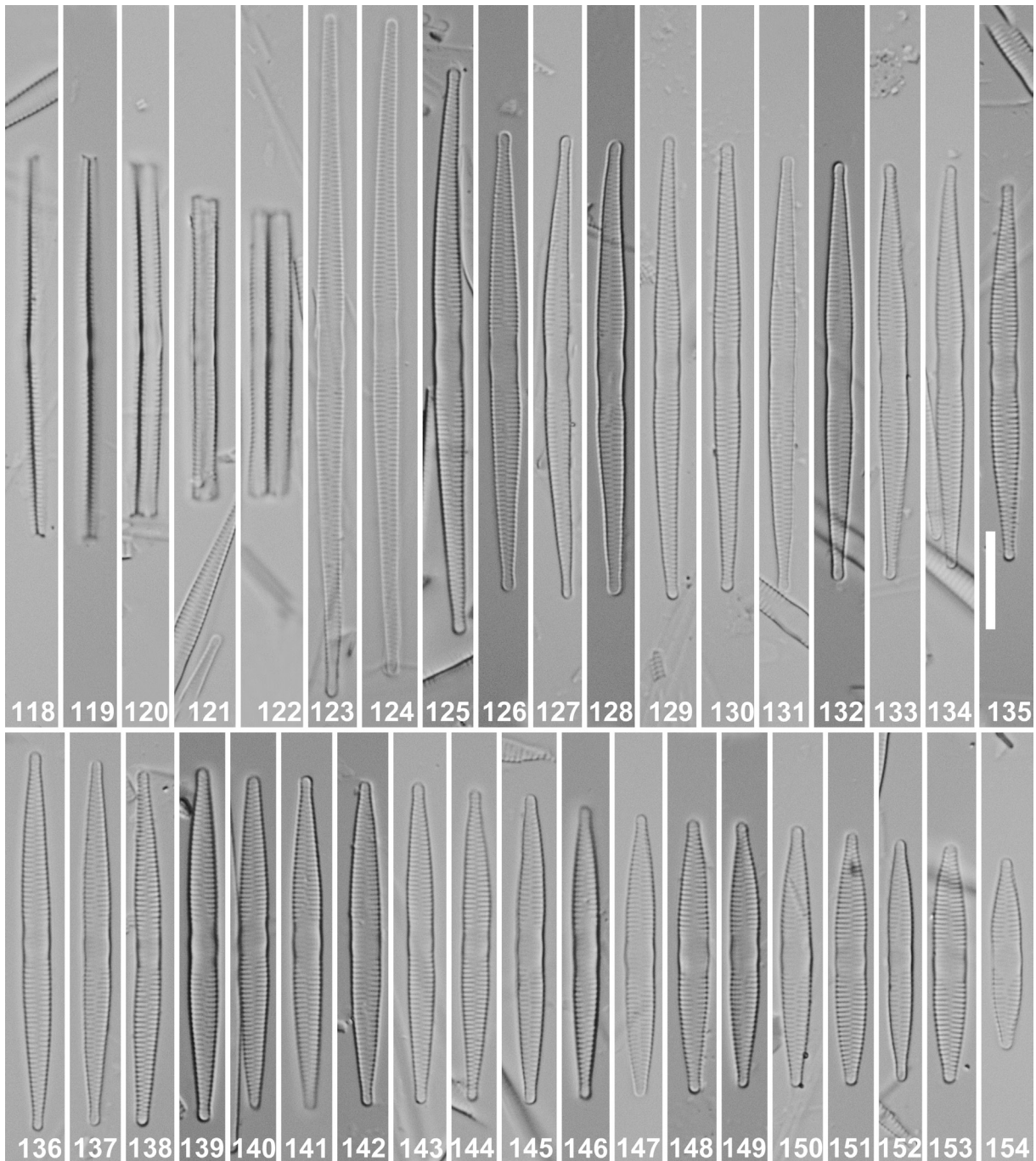
Figs 112–117. *Fragilaria parva* (Grunow) Tuji et D.M.Williams. SEM images taken from the type material (BR–4669, WALKER ARNOTT S 701): (112) external view of an entire frustule showing valve face and marginal series of spines; (113) SEM external detail of valve apex in girdle view showing mantle plaques and small spines; (114) SEM external detail of valve apex showing apical pore field; (115) SEM detail of valve apex showing slit-like areolae near the sternum and rimoportula; (116) SEM external detail of central area with ghost striae; (117) SEM internal view of an entire valve. Scale bars represent 10 μm (112, 117) and 5 μm (113–116).

very distinctly present, visible as shallow, transapically elongated grooves (Fig. 158). Small, rounded, rimmed external rimoportula opening located in last stria at one apex (Fig. 159). Apical pore field of the ocellulimbus type, rectangular, well delimited, composed of 4 rows of relatively large rectangular poroids (Fig. 159). Internal rimoportula opening as paired lips, obliquely positioned at one apex (Fig. 160). Internally, central area very distinct, shallowly depressed. Virgae clearly raised (Fig. 161).

Analysed material: BR–4668, Brébisson sample under

the name *Synedra vaucheriae* (Falaise, Normandy, France) illustrated in VAN HEURCK (1881, pl. XL, fig. 15a) (Fig. 80).

Associated diatom flora: The investigated sample is entirely dominated by *Synedra vaucheriae* sensu Brébisson. Less frequent taxa include *Brachysira brebissonii* R.Ross, *Eunotia bilunaris* (Ehrenberg) Schaarschmidt, *Gomphonema* cf. *parvulum*, *Tabellaria flocculosa* and several *Pinnularia* and other *Eunotia* species. This species composition points to more mesotrophic, weakly acid conditions (LANGE–BERTALOT et al. 2017).

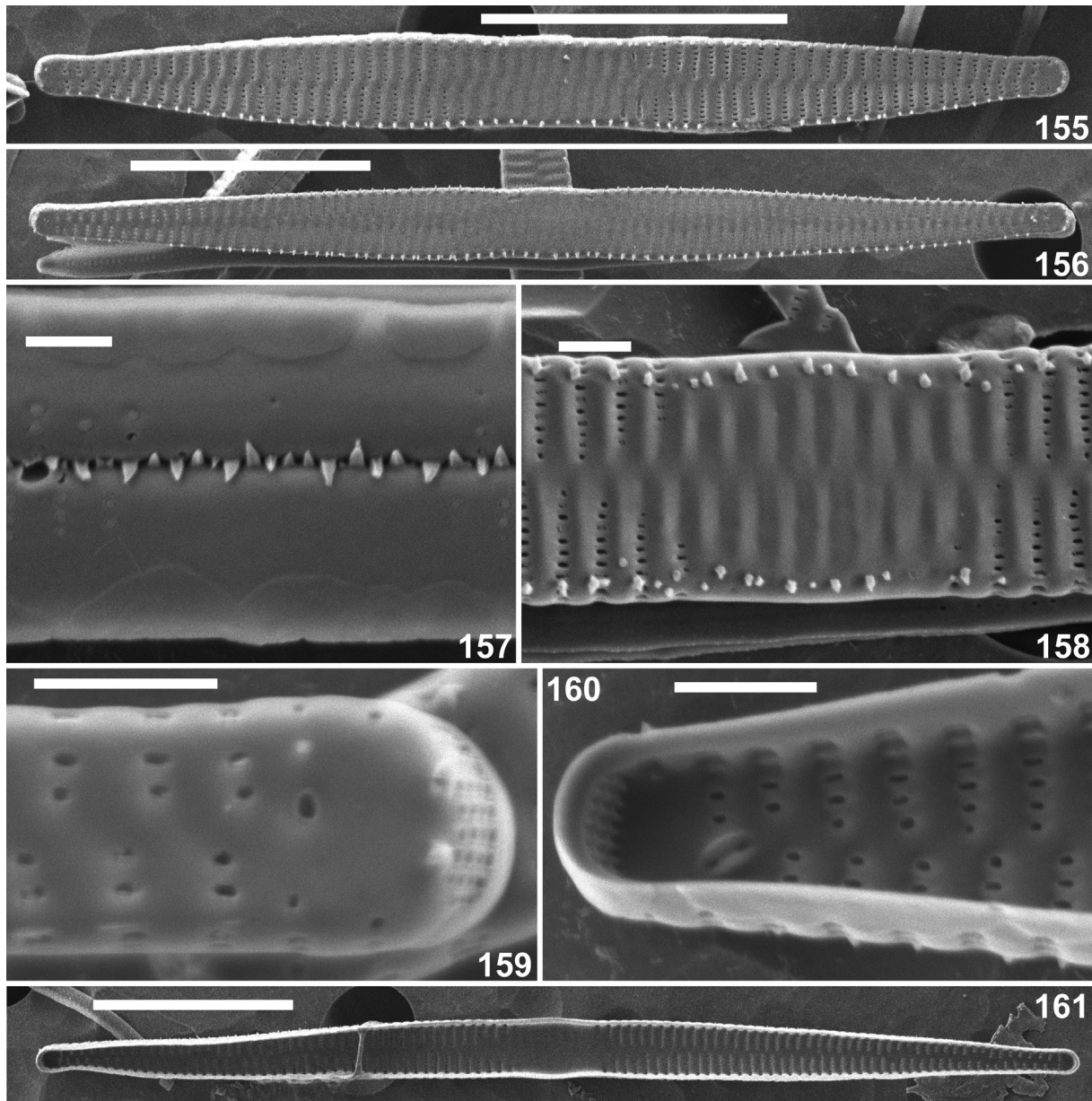


Figs 118–154. *Synedra vaucheriae* Kützing sensu Brébisson. LM images taken from the Falaise material (BR-4668, epitype for *F. campyla*). LM views of population arranged in decreasing length. (118–122) represent frustules in girdle view. Scale bar represents 10 μm .

***Fragilaria scotica* (Grunow) Van de Vijver, C.E.Wetzel et Ector comb. nov. et stat. nov.**

Synedra rumpens var. *scotica* Grunow [now transferred to *Fragilaria scotica* (Grunow) Van de Vijver, C.E.Wetzel et Ector comb. nov. et stat. nov.] has to be excluded as synonym for *F. campyla* since the only observed specimen showing sufficient similarity to the drawing in VAN HEURCK (1881, pl. XL, fig. 11) differs markedly in having a larger valve width (4 μm versus 2.5–3 μm in *F. campyla*) and a lower stria density (15 versus 19–20 in 10 μm for *F. campyla*), giving the species a more

sturdy, coarser appearance. More analyses of similar populations will be necessary to establish its taxonomic identity. Analysis of further samples taken from Loch Leven near Kinross (Scotland) in Walker Arnott's collection did not yield more specimens (VAN DE VIJVER, pers. obs.). Nevertheless, the observed valve and the drawing provide sufficient evidence for transferring these specimens and recognition as a distinct species, *Fragilaria scotica*. The two varieties of *Synedra scotica* (var. *genuina* and var. *undulata*) in MAYER (1917) present all features of *F. parva* and these names should therefore



Figs 155–161. *Synedra vaucheriae* Kützing sensu Brébisson, SEM images taken from the Falaise material (BR-4668, epitype for *F. campyla*): (155, 156) external view of two entire valves showing the marginal series of spines and the ghost striae in the central area; (157) SEM external detail of the spines; (158) SEM external detail of the central area with the ghost striae; (159) SEM detail of the valve apex showing the rimoportula and the apical pore field; (160) SEM internal detail of apex with the rimoportula; (161) SEM internal view of an entire valve. Scale bars represent 10 μm (155, 156, 161) and 1 μm (157–160).

be considered as synonyms of the latter.

***Fragilaria scotica* (Grunow) Van de Vijver, C.E. Wetzel et Ector comb. nov. et stat. nov. (Figs 162–164)**

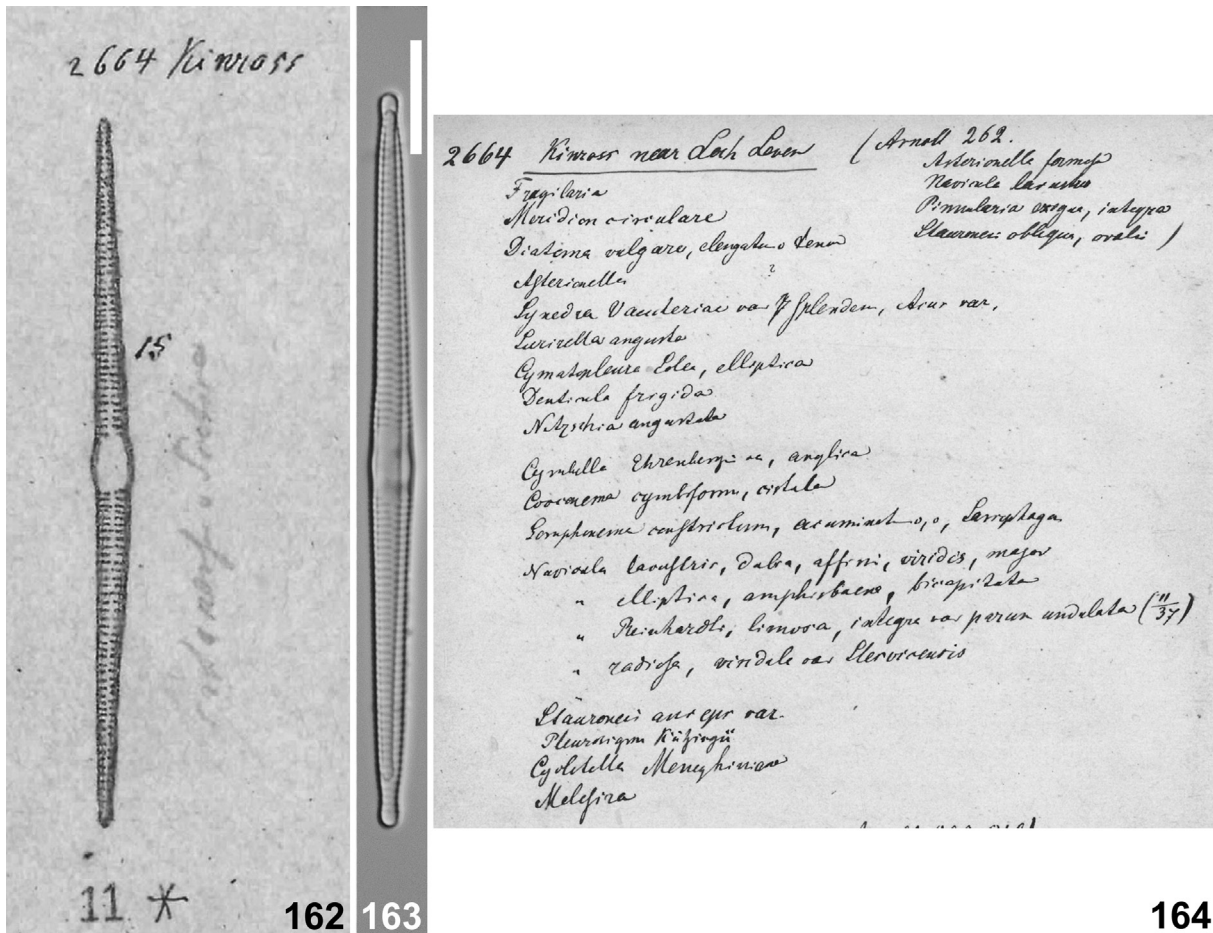
Basionym: *Synedra rumpens* var. *scotica* Grunow in Van Heurck, GRUNOW in VAN HEURCK (1881), Synopsis des Diatomées de Belgique, Atlas fasc. 3, pl. XL, fig. 11.

Registration: <http://phycobank.org/102749>

To exclude from synonymy: *Synedra scotica* (Grunow) Ant. Mayer 1917 sensu MAYER (1917) exclusive of the type. After scanning three slides made from the type material (Grunow sample 2664 = Walker Arnott sample 262) from Kinross (UK), only one valve could be found that showed a clear resemblance to the drawing Grunow

published in VAN HEURCK (1881, pl. XL, fig. 11) (Fig. 162). The LM photographs of Grunow sample 2664 in LANGE-BERTALOT (1980, figs 53–57) belong to different species present in sample 2664. The valve depicted here (Fig. 163) has a length of 65 μm and a width of 4 μm . Its outline is linear-lanceolate with gradually narrowing margins and protracted, rostrate apices. The central area is clearly inflated and well delimited. Striae are alternating and almost parallel becoming weakly radiate near the apices, 15 in 10 μm .

Lectotype: W0164807, Grunow sample 2664, designated in LANGE-BERTALOT (1980) archived in W.



Figs 162–164. *Fragilaria scotica* (Grunow) Van de Vijver, C.E. Wetzel et Ector comb. nov. Drawing and LM image taken from the lectotype material (BR-4670, WALKER ARNOTT sample 262, Loch Leven, Kinross, Scotland): (162) annotated drawing in Van Heurck (1881, pl. XL, fig. 11) kept at W, (163) LM view of a single valve observed in the type material; (164) scan of the original Grunow notes in the annotation books archived at W, for Grunow sample 2664. Scale bar represents 10 μm .

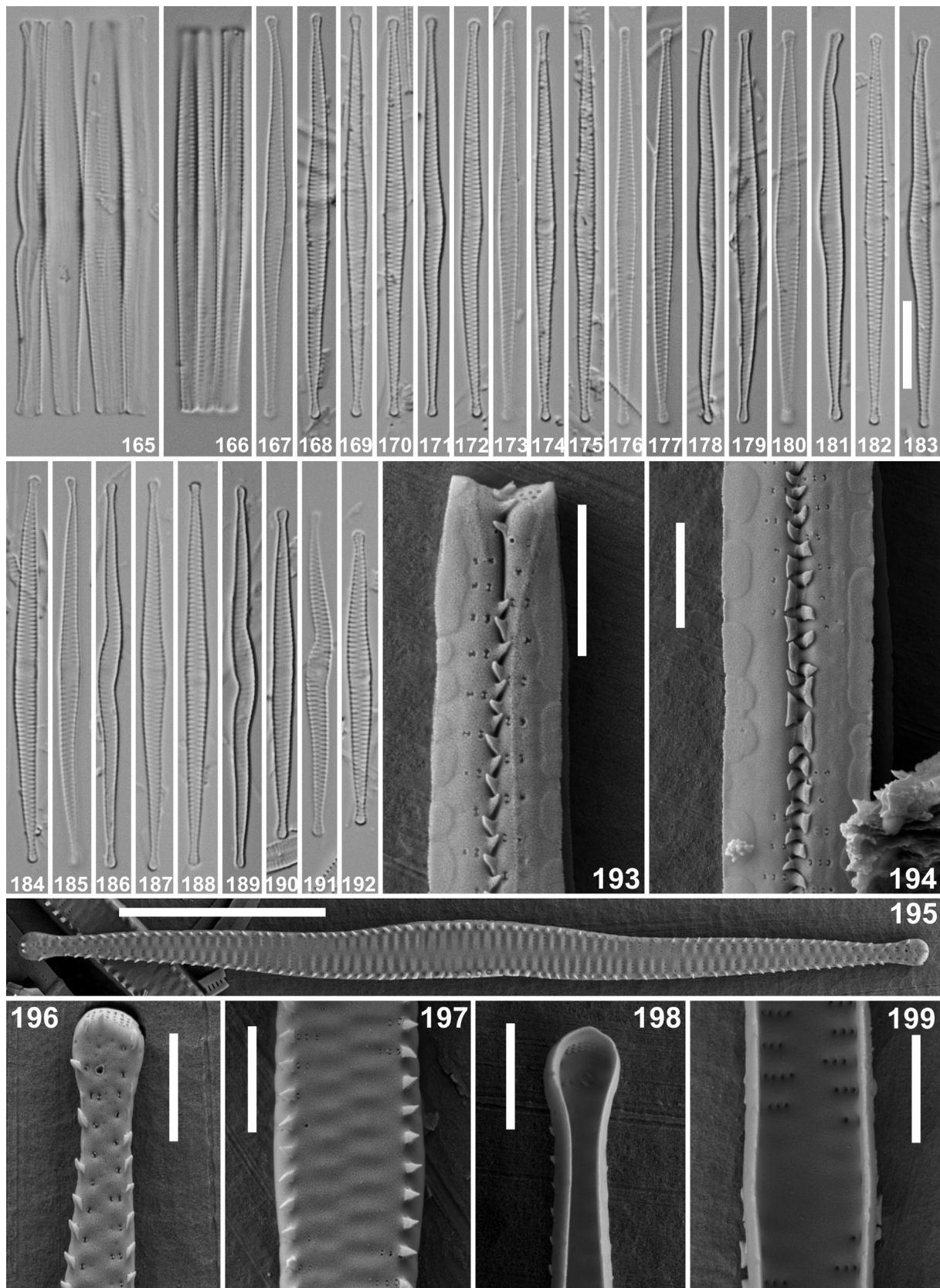
Analysed material: BR-4670, Walker Arnott sample 262 (Kinross near Loch Leven, Scotland, UK) (= Grunow sample 2664 according to Grunow's accession books kept at W, Fig. 164).

Associated diatom flora: Grunow's notes in his accession books on sample 2664 do not mention the presence of *Synedra rumpens* var. *scotica*, despite the presence of a large number of reported diatom taxa (Fig. 164). This already indicates the rarity of this taxon. As can be seen from his reported species list, the diatom composition points to alkaline, meso- to slightly eutrophic, electrolyte-rich conditions (LANGE-BERTALOT et al. 2017). Given the extreme rarity of the taxon, it is unclear whether these conditions should be attributed to *F. scotica*.

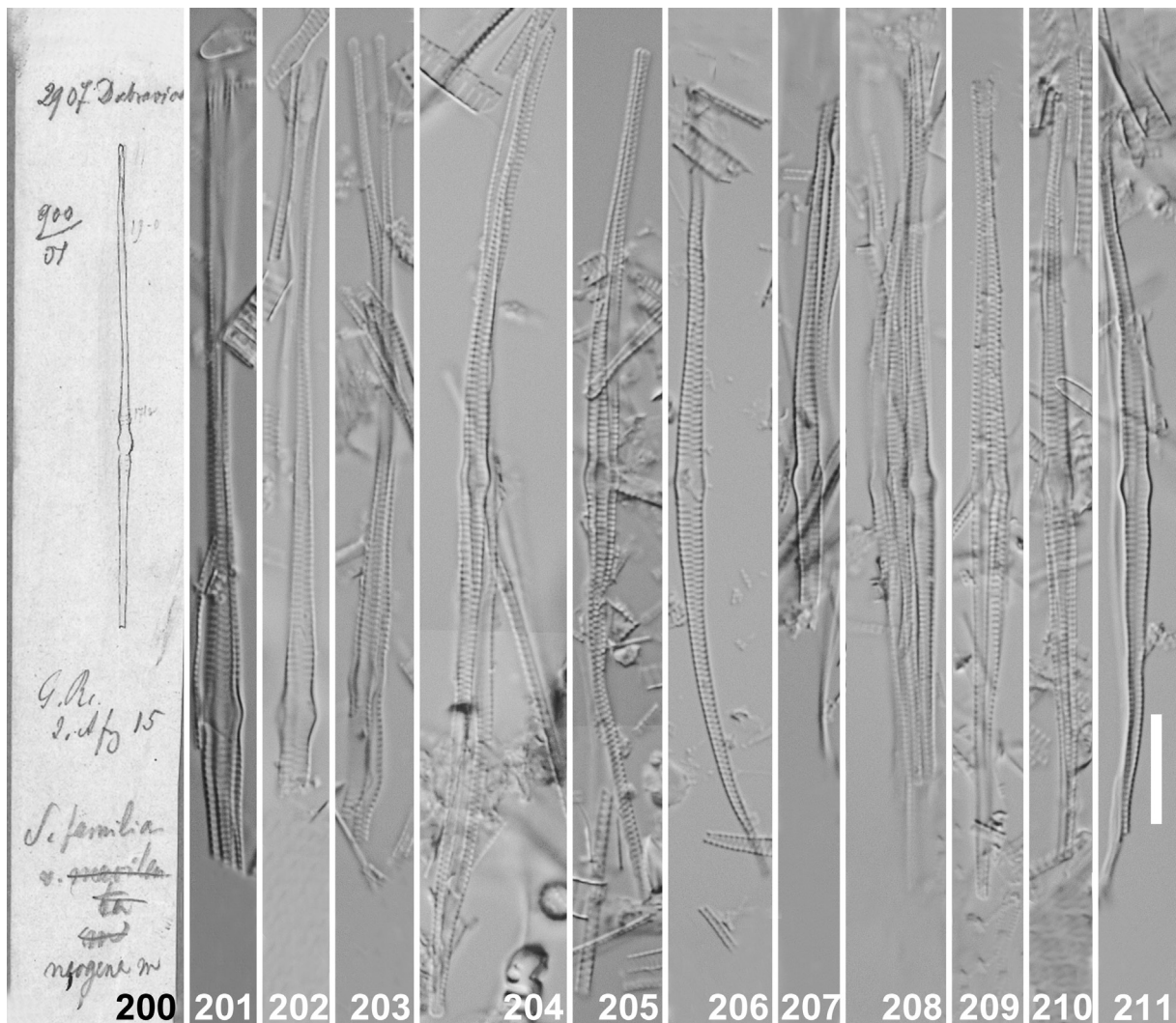
***Fragilaria pseudofamiliaris* Van de Vijver, T.M. Schuster, Kusber et D.M. Williams sp. nov.**

Synedra rumpens var. *familiaris* Kützing, as depicted by Hauck & Richter in their exsiccata set *Phykotheke universalis* (n° 300, Dresden in HAUCK & RICHTER 1889), is here described as the new species *Fragilaria pseudofamiliaris*. Contrary to the other forms described

by Grunow (f. *parva* and f. *major*), *F. pseudofamiliaris* produces long, ribbon-like colonies. Since VAN DE VIJVER et al. (2020a) have already established that *Synedra familiaris* Kützing belongs to the genus *Tabularia*, and the name *Fragilaria familiaris* (Kützing) Hustedt was already taken (HUSTEDT 1957), the specimens provided by Hauck & Richter require a different name under *Fragilaria*. Analysis of this population revealed some distinct features, justifying its description as a new species. The ribbon-like colonies are characterized by a clear gap between the apices, a feature so far only seen in *Fragilaria pararumpens* Lange-Bertalot et al. (see for instance LANGE-BERTALOT et al. 2017, pl. 9, figs 9–14), *F. crotonensis* Kitton (e.g. LANGE-BERTALOT & ULRICH 2014, pl. 19, figs 1–2), and *F. prolongata* (Grunow) Van de Vijver et al., the latter belonging to the *F. crotonensis* Kitton complex (see VAN DE VIJVER et al. 2020b, fig. 4). However, these three species differ from *F. pseudofamiliaris* morphologically otherwise excluding any conspecificity. Observations of a similar gap in colonies of *Fragilaria rumpens* have not been observed up until now. Moreover, *F. pseudofamiliaris*



Figs 165–199. *Fragilaria pseudofamiliaris* Van de Vijver, T.M.Schuster, Kusber et D.M.Williams sp. nov., LM and SEM images taken from the holotype material (BR–4671, Artesischer Brunnen, Dresden, Germany, Exsiccatae series HAUCK & RICHTER, Phykotheke universalis n° 300): (165–192) LM views of population arranged in decreasing length; (165, 166) represent ribbon-like colonies. Note the gap between apices. (193) SEM external detail of two frustules connected via their apices; note acute non-linking spines; (194) SEM external detail of central area in girdle view. Two valves connected to each other via their linking spines; (195) external view of an entire valve showing marginal series of spines and ghost striae; (196) SEM external detail of valve apex showing rimoportula and apical pore field; (197) SEM external detail of central area showing ghost striae; (198) SEM internal detail of valve apex showing rimoportula; (199) SEM internal detail of central area. Scale bars represent 10 μ m (165–192, 195) and 1 μ m (193, 194, 196–199).



Figs 200–211. *Fragilaria metcalfeana* Van de Vijver, D.M.Williams, Kusber et T.M.Schuster nom. nov., drawing and LM images taken from the lectotype slide [BR-4672, Grunow sample 2907, Klebschiefer von Dubravica (= Besztercebánya, Slovakia, formerly Neusohl, Hungary)]: (200) original drawing in the Grunow drawing collection kept at W; (201–211) LM views of population arranged in decreasing length. Scale bar represents 10 μ m.

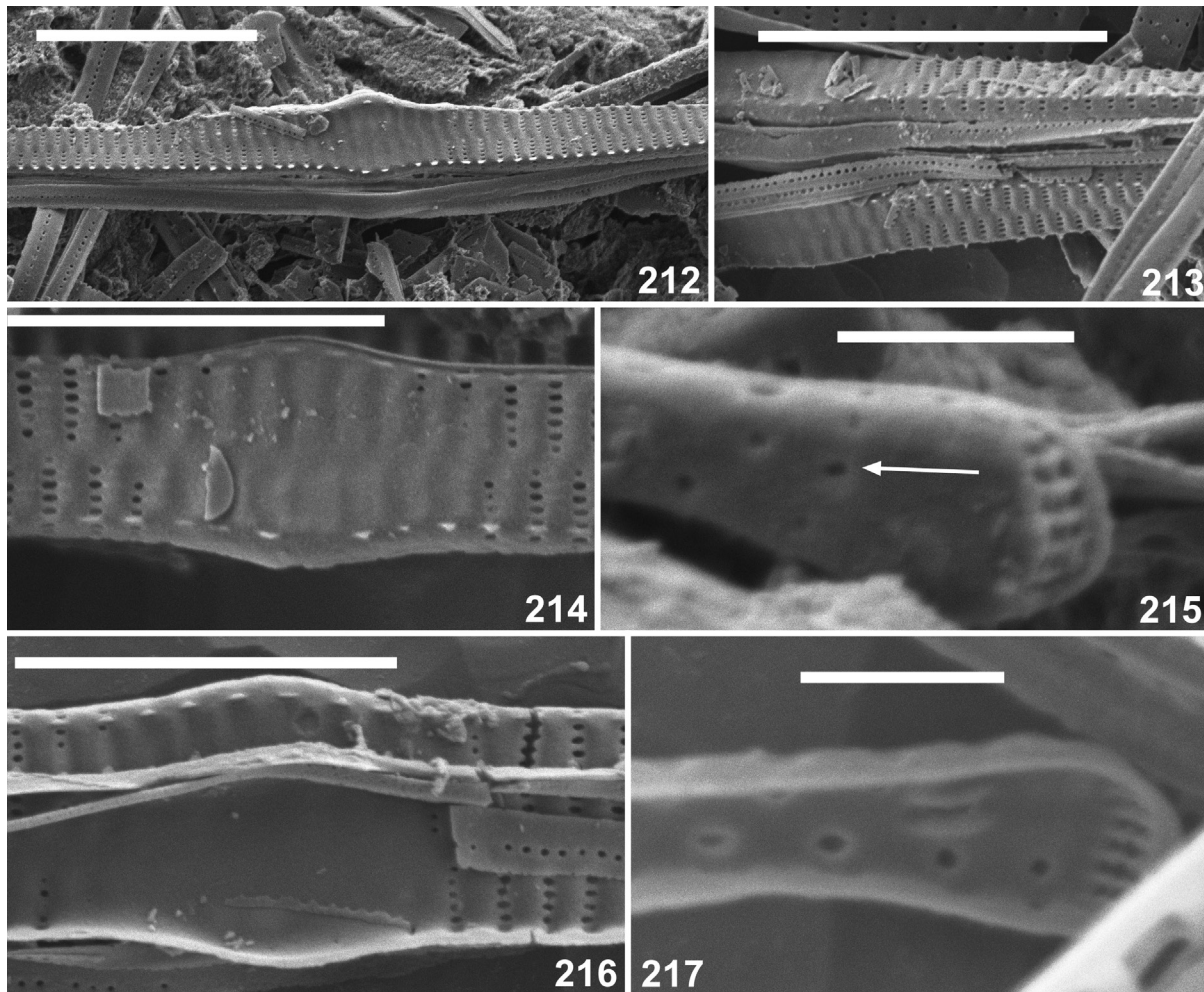
has a very small central area, a lower valve width than *F. rumpens* (2–3 vs. 3–3.5 μ m) and a more elongated, lanceolate valve outline. Colony formation separates this species from *Fragilaria campyla*. LANGE–BERTALOT & ULRICH (2014, pl. 8, figs 8–14) illustrated a population of *F. pseudofamiliaris* from Lake Olbersdorf in Saxony (Germany) identified as *F. perdelicatissima*. Analysis of the type material of *F. perdelicatissima* (see below) clearly showed sufficient differences to contradict the identification in LANGE–BERTALOT & ULRICH (2014) of the Saxonian population as *F. perdelicatissima*. The type locality of *F. pseudofamiliaris* is Dresden, the capital of the German state of Saxony (Lake Olbersdorf is located about 70 km east of Dresden). The striae in *F. perdelicatissima* are short and almost marginal forming a large sternum. Moreover, *F. perdelicatissima* does not produce ribbon-like colonies, lacks spines and has a longer length range (up to 100 μ m) compared to *F. pseudofamiliaris* (Table S2).

***Fragilaria pseudofamiliaris* Van de Vijver, T.M.Schuster, Kusber et D.M.Williams sp. nov. (Figs 165–199)**

– *Synedra familiaris* Kützing f. *major* Grunow in HAUCK & RICHTER (Oct. 1889), *Phykotheke universalis*, fasc. VI, n° 300 [RICHTER, *Hedwigia* 29(6), p. 357, 1890].

Registration: <http://phycobank.org/102750>

LM (Figs 165–192): Frustules in girdle view rectangular, forming long, ribbon-like colonies, linked at valve centre (Figs 165, 166). Valves elongated, narrowly lanceolate, margins gradually tapering towards apices throughout entire cell diminution series. Apices distinctly protracted, subcapitate to capitate, in specimens of all sizes. Teratological valves with twisted, bent or undulated valve outline (Figs 171, 181, 186, 189). Valve dimensions (n=50): length 30–50 μ m, width 2.0–3.0 μ m. Sternum narrow but distinct, linear, gradually widening towards the central area. Central area forming small, rectangular, hyaline zone (occasionally absent, e.g., Fig. 169), spanning entire valve width. Ghost striae occasionally present (Figs 189, 190). Striae alternating, parallel throughout



Figs 212–217. *Fragilaria metcalfeana* Van de Vijver, D.M.Williams, Kusber et T.M.Schuster nom. nov., SEM images taken from the lectotype material [BR-4672, GRUNOW sample 2907, Klebschiefer von Dubravica (= Besztercebánya, Slovakia, formerly Neusohl, Hungary)]: (212) SEM external detail of central area in girdle view showing inflated central area and marginal spines; (213) SEM external detail of central area showing girdle bands; (214) SEM external detail of central area showing ghost striae; (215) SEM detail of valve apex showing rimoportula (arrow) and apical pore field; (216) SEM internal detail of central area (lower part of the figure). Upper part of the figure is part of an external view with marginal spines; (217) SEM internal detail of the apex with rimoportula. Scale bars represent 10 μm (213, 214, 216) and 1 μm (215–217).

entire valve, becoming more radiate at apices, 18–19 in 10 μm . Areolae not discernible in LM.

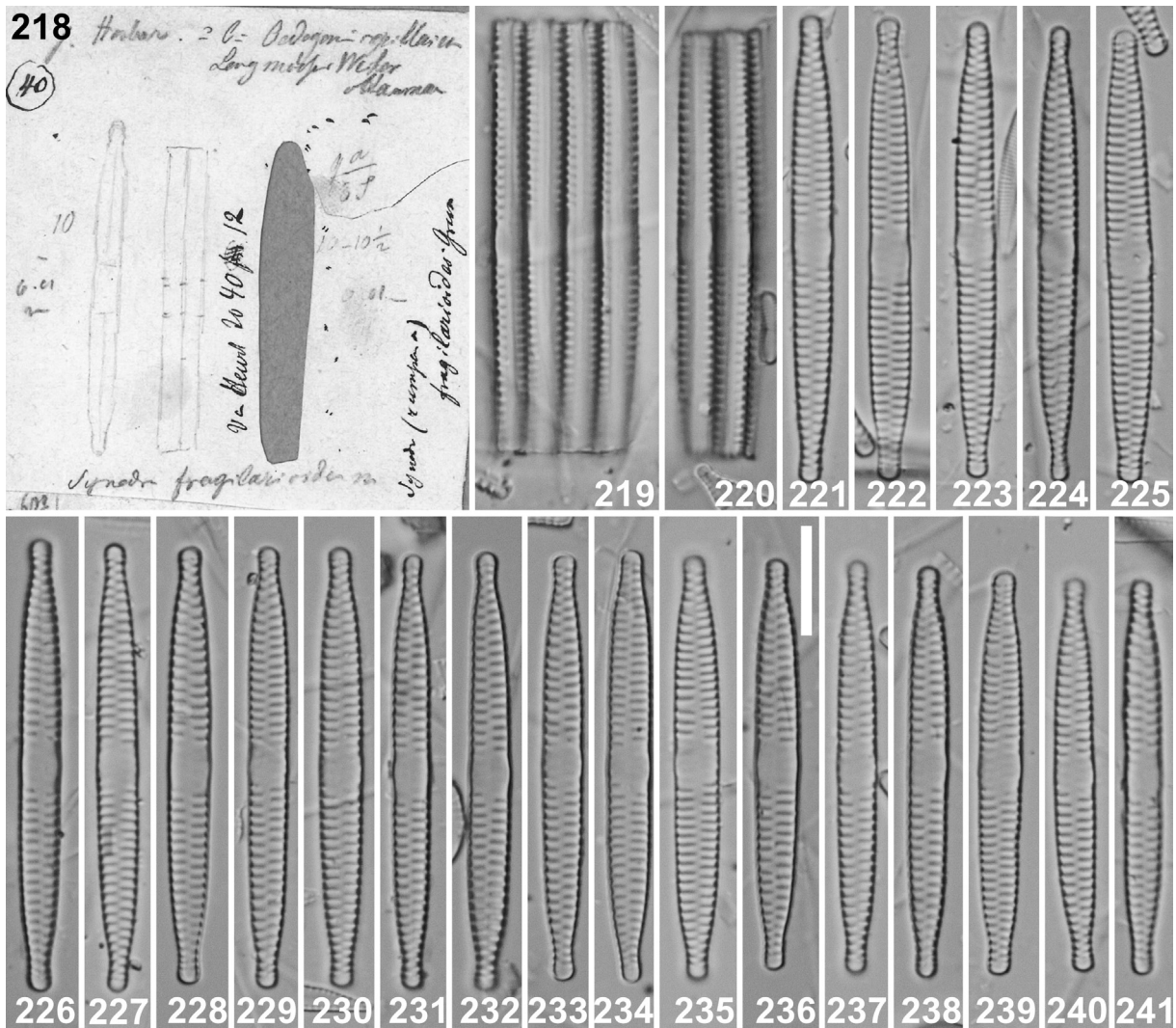
SEM (Figs 193–199): Frustules connected to each other via well developed, bifurcating, broad linking spines at the central area (Fig. 194). At apices, occasionally near central area, spines acute, shark tooth-like (Figs 193, 194). Spines forming continuous series at valve margins, corresponding to a vimen (Fig. 195). Several spines present at apices (Figs 195, 196). Valve face flat with slightly raised virgae (Figs 195–197). Central area with distinct ghost striae (Fig. 197). Striae uniseriate, composed of several small, rounded areolae (Figs 195–197). Apical pore field of the ocellulimbus type, well developed, composed of at least four rows of small, rounded poroids (Fig. 196). External rimoportula opening large, rounded, rimmed, located midway between last two striae at one apex (Fig. 196). Internally, rimoportula obliquely positioned (Fig. 198). Central area relatively flat, small (Fig. 199).

Holotype: BR-4671 (Meise Botanic Garden, Belgium), slide prepared from material of Hauck & Richter, Phytotheka universalis n° 300, conserved in BR.

Isotypes: PLP-391 (University of Antwerp, Belgium), W0164806 (W, Natural History Museum Vienna, Austria).

Type locality: Artesischer Brunnen, Dresden, Germany (coll. date V.1888, leg. C. SCHILLER s.n.), Collection Hauck & Richter, Phytotheka universalis n° 300, material kept in W.

Associated diatom flora: The dominant diatom species in the type material is *F. pseudofamiliaris*. Other taxa in the sample include *Achnanidium exile* (Kützing) Heiberg, *A. cf. microcephalum* Kützing, *Brachysira neoexilis* Lange–Bertalot, *Cymbella affinis* Kützing, *Diatoma tenuis* C.Agardh, *Encyonopsis subminuta* Krammer, and *Fragilaria goeyersiana* Van de Vijver et Ector. Most of these species are typical for calcium bicarbonate enriched, meso- to eutrophic, medium electrolyte-rich lakes (LANGE–BERTALOT et al. 2017).



Figs 218–241. *Fragilaria fragilarioides* (Grunow) Cholnoky, drawings and LM images taken from the lectotype material (BR–4673, Grunow sample 30484, Lengmooser Weiher, Longomoso, South Tyrol, Italy): (218) cut-out remainder of original drawing from the Grunow collection used for VAN HEURCK (1881, pl. XL, fig. 12); (219–241) LM views of population arranged in decreasing length; (219, 220) represent frustules in girdle view. Scale bar represents 10 μ m.

***Fragilaria metcalfeana* Van de Vijver, D.M. Williams, Kusber et T.M. Schuster nom. nov.**

Synedra familiaris var. *neogena* Grunow, now transferred to the genus *Fragilaria* as *F. metcalfeana* Van de Vijver, D.M. Williams, Kusber et T.M. Schuster nom. nov., was added to this study to complete the analysis of all former infraspecific taxa named in the *rumpens*–*familiaris* complex. Although specimens in the Neogene type material were highly fragmented, the observations made clear that this taxon cannot be maintained in this complex and represents a distinct species. Since PANTOCSEK (1913) already described a *Fragilaria neogena* Pantocsek, a new name was necessary for a transfer to *Fragilaria*. *Fragilaria metcalfeana* can be distinguished from all other taxa discussed in the current paper and from other longer *Fragilaria* taxa based on the very distinctly swollen central area justifying its species status (LANGE–BERTALOT & ULRICH 2014).

***Fragilaria metcalfeana* Van de Vijver, D.M. Williams, Kusber et T.M. Schuster nom. nov. (Figs 200–217)**

Replaced synonym: *Synedra familiaris* var. *neogena* Grunow 1882, GRUNOW (1882, p. 139, pl. XXIX, fig. 15)

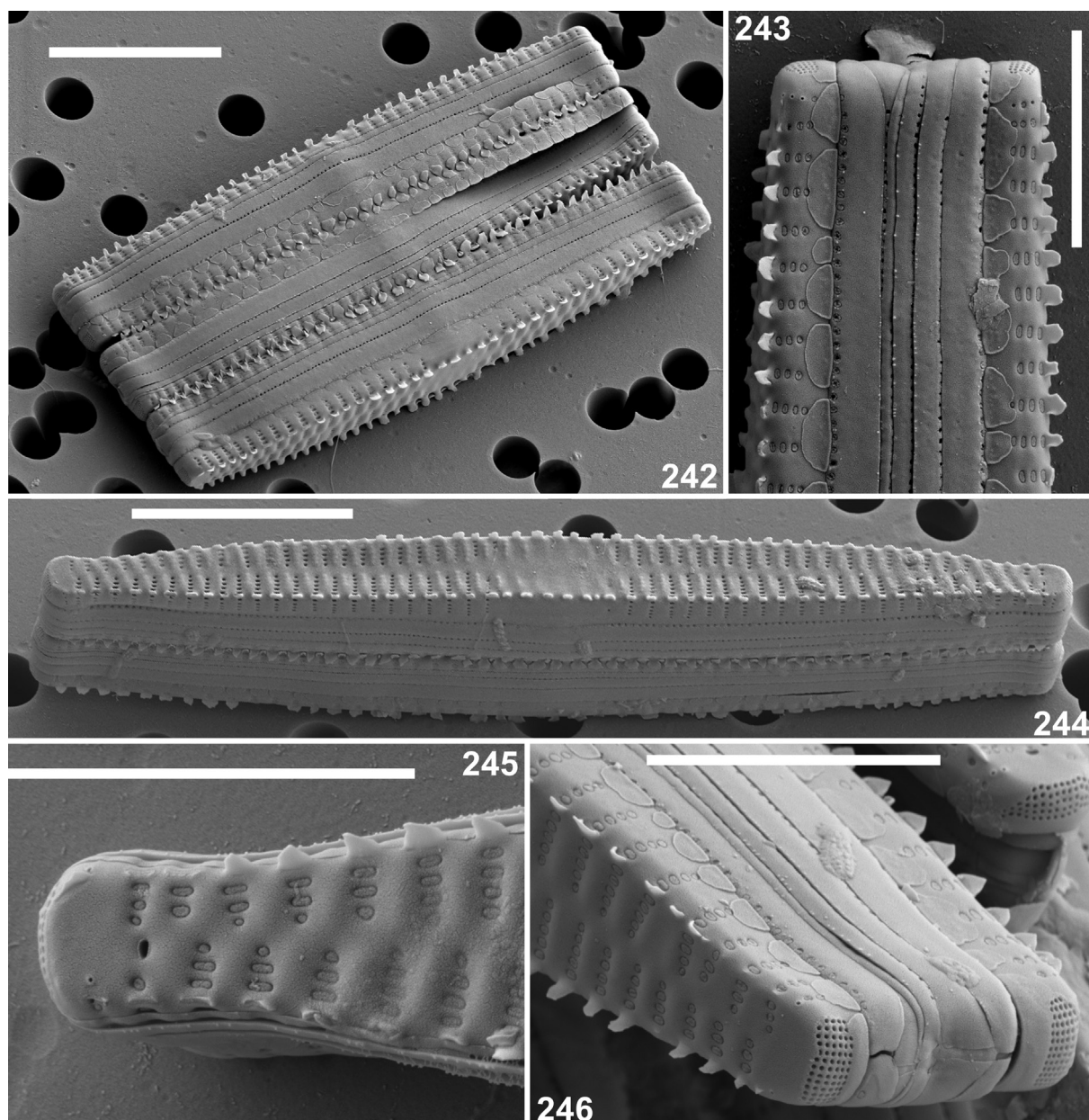
≡ *Synedra rumpens* var. *neogena* (Grunow) Hustedt 1937

≡ *Synedra acus* var. *neogena* (Grunow) S. Metcalfe 1988 nom. inval.

Registration: <http://phycobank.org/102751>

The original drawing made by Grunow for the illustration in GRUNOW (1882, p. 139, pl. XXIX, fig. 15) was retrieved from the Grunow collection in W (Fig. 200). The drawing was annotated with the sample number Grunow used to describe the specimens for his new taxon (sample 2907, Dubravica). The longer valves in the type material are fragmented making it almost impossible to find entire valves or frustules and the following description is therefore based on fragments.

METCALFE (1988) invalidly combined the taxon as a variety of *Synedra acus* Kützing based on a number of features such as the presumed presence of closed girdle bands, the presence of rimoportulae and apical pore

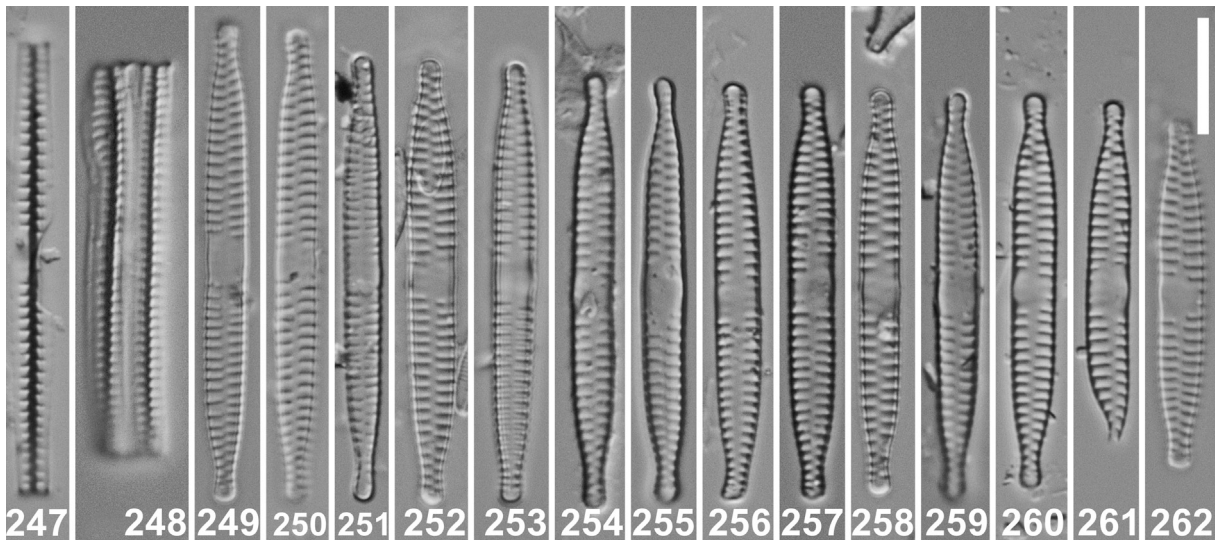


Figs 242–246. *Fragilaria fragilarioides* (Grunow) Chohnoky, SEM images taken from the lectotype material (BR-4673, Grunow sample 30484, Lengmooser Weiher, Longomoso, South Tyrol, Italy): (242) SEM external view of two entire frustules connected via linking spines forming a ribbon-like colony; (243) SEM external detail of apices with mantle plaques and girdle bands; (244) SEM external view of an entire valve in girdle view showing marginal series of spines, ghost striae, and raised virgae; (245) SEM detail of the valve apex showing rimoportula; (246) SEM detail of valve apex showing apical pore field. Scale bars represent 10 μm (242, 244) and 5 μm (243, 245, 246).

fields, and the absence of spines. Some of these features are contradicted by the observations in the present paper suggesting that the valves METCALFE (1988) observed and the type material of *F. metcalfeana* are most likely not conspecific. HUBER–PESTALOZZI (1942) briefly discussed this taxon mentioning its important role in the tropical plankton as HUSTEDT (1937) mentioned the taxon from southeast Asia. The depicted valves in HUSTEDT (1937), however, clearly represent a different species raising doubts about the distribution of *F. metcalfeana* in tropical regions. The analysis of the material METCALFE (1988) observed will be necessary to clarify their identity.

LM (Figs 201–2011): Valves strongly elongated, very thin, linear with distinctly inflated central part. Apices protracted, slightly capitate. Valve dimensions ($n=15$): length 60–120 μm , width 1.0–1.5 μm , width (central area) 2.5–3.5 μm . Sternum very narrow, partly invisible, not broadening at central area. Central area inflated, hyaline, well delimited, ghost striae present. Striae alternating, parallel throughout entire valve, ca. 18 in 10 μm . Areolae not discernible in LM.

SEM (Figs 212–217): Series of marginal spines present, situated within a vimen and occurring more or less evenly from apex to apex (Figs 212, 213). Valve face



Figs 247–262. *Fragilaria distans* (Grunow) Bukhtiyarova, LM images taken from the lectotype material (BR–4674, Grunow sample 440, Bozen (=Bolzano), South Tyrol, Italy), LM views of population arranged in decreasing length: (247, 248) represent frustules in girdle view. Scale bar represents 10 μm .

flat with weakly raised virgae (Figs 212, 213). Ghost striae distinct in central area (Fig. 214). Striae uniseriate, composed of apically elongated areolae (Fig. 241). Apical pore field of the ocellulimbus type, large, composed of at least 2–3 rows of relatively large poroids (Fig. 215). External rimoportula opening small, rounded, almost not distinguishable from areolae (Fig. 215, arrow), internally ghost striae not visible in central area (Fig. 216). Internal rimoportula opening apically elongated (Fig. 217). Girdle only fragments, of thin bands with single row of poroids, possibly 3 (Figs 212, 213, 216).

Lectotype (here designated): BR–4672 (Meise Botanic Garden, Belgium), slide prepared from Grunow sample 2907 (leg. J. KLEMENS s.n.), conserved at BR.

Isolectotype (here designated): W0164804 (W, Natural History Museum Vienna, Austria).

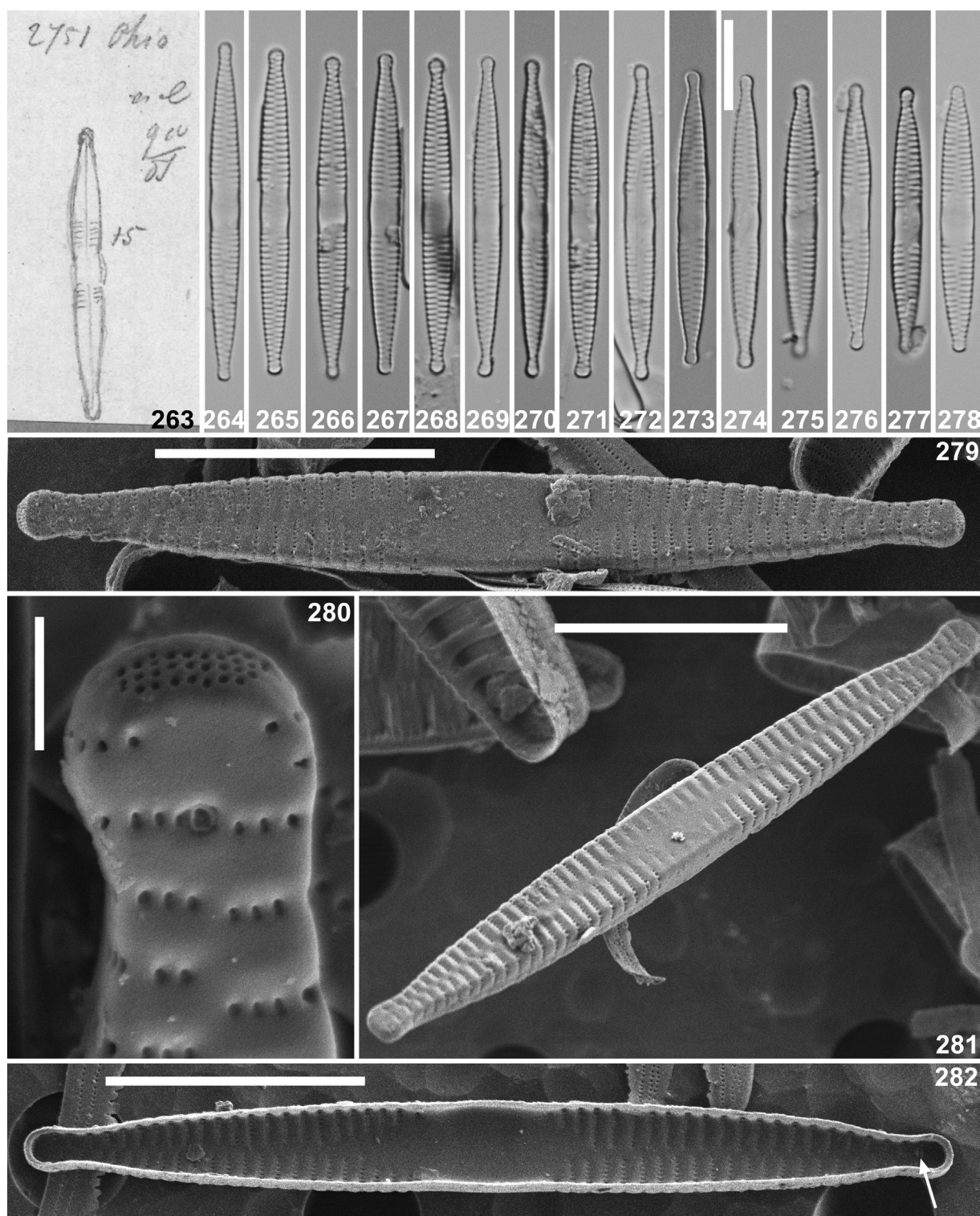
Analysed material: Grunow sample 2907, Klebschiefer von Dubravica (Besztercebánya, Slovakia, formerly Neusohl, Hungary), leg. J. KLEMENS s.n.

Etymology: The species is named after Prof. Dr Sarah E. Metcalfe (University of Nottingham, UK) in honor of her important contributions to diatom paleoecology. Prof. Metcalfe (1988) discussed the taxonomic identity of this taxon.

Associated diatom flora: GRUNOW (1882) discussed the diatom composition of this sample, dating from the Upper Miocene and reported the presence of a very diverse diatom flora. The investigated sample is dominated by several (unidentified) *Ulnaria* and *Fragilaria* taxa occurring together with a broad array of other genera such as *Eunotia*, *Epithemia*, *Navicula*, *Placoneis*, and *Staurosira*. Several of these taxa have been the subject of further taxonomic studies (e.g. OGNJANOVA–RUMENOVA & BUCZKÓ 2010; BUCZKÓ 2012; MORALES et al. 2014).

Fragilaria fragilarioides (Grunow) Cholnoky 1963

In the present paper, we recognise several taxa that were formerly combined within the *Synedra rumpens* group (Table S2 cont.). *Fragilaria fragilarioides*, originally described under the name *Synedra rumpens* var. *fragilarioides*, was transferred to the genus *Fragilaria* by CHOLNOKY (1963), who stated that the valves possessed two rimoportulae and formed long colonies, the latter, at that time, not a feature of *Synedra* but *Fragilaria*. Although the identification of his valves as *F. fragilarioides* seems incorrect based on analyses of the type material here, his new combination is valid and should therefore be used. The valves in the type material of *F. fragilarioides* have only one rimoportula rather than two, less coarse striae, lower valve dimensions and a less swollen central area as compared to CHOLNOKY (1963). Grunow had described another taxon forming similar ribbon-like colonies: *Synedra vaucheriae* var. *distans*, now *F. distans*. Analysis of the type material here showed that the latter is conspecific with *F. fragilarioides*, despite the lack of SEM observations. Both taxa were originally illustrated on the same page in VAN HEURCK's Atlas (1881, pl. XL) but since the combination at species level for *F. fragilarioides* was made in 1963, whereas the new combination *F. distans* was published later in 1995 (BUKHTIYAROVA 1995), the former has priority (see ICN art. 11 (TURLAND et al. 2018)). KRAMMER & LANGE–BERTALOT (1991, p. 124, pl. 109, fig. 16 & pl. 113, figs 16–21) illustrated and briefly discussed both taxa and combined them as '*distans/fragilarioides*–Sippen'. However, the valves they showed most likely represent *Fragilaria radians* (Kützing) D.M. Williams et Round. LANGE–BERTALOT et al. (2017) recently discussed these specimens adding that these 'Sippen' are synonyms of *F. radians*. TUJI & WILLIAMS (2013) could not retrieve the type material for *Synedra vaucheriae* var. *distans* as



Figs 263–282. *Fragilaria bahlsiana* Van de Vijver, C.E. Wetzel et Ector sp. nov. Drawing, LM and SEM images taken from the lectotype material (BR-4675, Walker Arnott sample S 907, Gambier, Ohio, USA): (263) original drawing for Grunow sample 2751 (=Walker Arnott S 907) in the Grunow drawing collection archived at W; (264–278) LM views of population arranged in decreasing length; (279) SEM external view of an entire valve showing absence of marginal spines; (280) SEM detail of valve apex showing rimoportula and apical pore field; (281) SEM external view of an entire valve showing absence of marginal spines and ghost striae in central area; (282) SEM internal view of an entire valve. The arrow indicates the rimoportula. Scale bar represent 10 μm (264–279, 281, 282) and 1 μm (280).

the original slide 440 is missing from the Grunow collection in W, but based on the drawing in VAN HEURCK (1881), they concluded that the species is conspecific with *F. vaucheriae*. The latter, however, does not produce

colonies excluding conspecificity. Regarding *F. distans*, REICHARDT (2018) stated that *F. rumpens* var. *fragilarioides* had more similarity with *F. rumpens*, whereas *F. distans* likely belonged to the *F. vaucheriae* group (REICHARDT

2018, pp. 90–91). The results of our study contradict this statement, since these taxa are conspecific. *Fragilaria fragilarioides* can be distinguished from similar taxa such as *F. vaucheriae* (no colonies, unilateral hyaline central area), *F. radians* (no colonies, coarser striae), *F. pectinalis* (no colonies, finer striae), and *F. gloiophila* (Grunow) Van de Vijver et al. (no colonies, narrower valves, unilateral hyaline central area), justifying its recognition as an independent species (VAN DE VIJVER et al. 2020c). *Fragilaria pararumpens* showed some similarity with *F. fragilarioides*. The species was shown to be conspecific with *Synedra rumpens* var. *meneghiniana* (VAN DE VIJVER et al. 2021a) and is characterized by typically building very long colonies with apices not connected to each other (see LANGE–BERTALOT et al. 2017, pl. 9, figs 9–14). This colony type was not observed in *F. fragilarioides*. Moreover, *F. pararumpens* has a distinct swollen central area, contrary to *F. fragilarioides* where a large, hyaline, but not swollen central area is observed. Finally, *F. socia* (J.H. Wallace) Lange–Bertalot, a North American species described in 1955 from the Savannah River, Georgia, USA (WALLACE 1960), has broader valves (3.5–4.0 µm), a higher stria density (17 vs. 10–11 in 10 µm), does not produce ribbon-like colonies and has a more swollen central area (LALIBERTE & VACCARINO 2015).

***Fragilaria fragilarioides* (Grunow) Cholnoky 1963 (Figs 218–246)**

Basionym: *Synedra rumpens* var. *fragilarioides* Grunow in Van Heurck 1881, VAN HEURCK (1881), Synopsis des Diatomées de Belgique Atlas pl. XL, fig. 12 (original drawing: our Fig. 218).

≡ *Fragilaria rumpens* var. *fragilarioides* (Grunow) A.Cleve (CLEVE–EULER 1953).

≡ *Fragilaria capucina* var. *fragilarioides* (Grunow) T.A.V.Ludwig et T.L.Flores 1997.

Description

LM (Figs 218–241): Frustules in girdle view rectangular, tightly joined together forming long, ribbon-like colonies (Figs 219, 220). Valves linear with parallel margins, distinctly protracted, capitate to subcapitate apices, throughout entire cell diminution series. Valve dimensions (n=40): length 30–45 µm, width 3.5–4.0 µm. Sternum narrow, linear, not widening near central area. Central area forming a large, slightly swollen, hyaline rectangular zone. Ghost striae occasionally visible in central area. Striae alternating, almost parallel to weakly radiate throughout entire valve, slightly radiate near the apices, 10–11 in 10 µm. Areolae not discernible in LM. **SEM (Figs 242–246):** Frustules linked to each other via well developed, spatulate to bifurcate linking spines, forming a continuous series at valve face margin (Fig. 242). Spines located on vimen (Figs 243, 244), near apices spines becoming more acute, shark tooth-shaped (Fig. 245). Large mantle plaques present at mantle edge (Fig. 243). Valve face flat with very weakly raised virgae (Fig. 244). Striae uniseriate composed of apically elongated areolae (Fig. 245). Apical pore field of the ocellulimbus type, large, composed of 6 rows of moderately large, rounded to square poreds (Fig. 246).

External rimoportula opening transapically elongated, rimmed, centrally located between the last striae at one apex (Fig. 245). Internal view not observed since most frustules remained intact. Girdle composed of epi- and hypo-cingulum, each of four open bands (Figs 243, 244, 246). All bands ligulate, first three tapering abruptly, opening at valve pole with arms almost parallel (Figs 243, 244, 246). Fourth band considerably narrower than the preceding three, ligulate, tapering sharply (Figs 243, 244, 246). Each band with one row of pores (Figs 243, 244, 246), visible externally.

Lectotype (designated here): BR–4673 (Meise Botanic Garden, Belgium), slide prepared from Grunow sample 30484, conserved in BR.

Isolectotype (designated here): W0164805 (W, Natural History Museum, Vienna, Austria).

Analysed material: Grunow sample 30484 (Lengmooser Weiher, Longomoso, South Tirol, Italy, coll. date 1860, collected from *Oedogonium capillare*), material kept in BR and W.

Associated diatom flora: The sample is entirely dominated by *F. fragilarioides* with up to 90% of all counted valves. Other taxa in the sample include *Gomphonema parvulum*, *G. italicum* Kützing, *Nitzschia amphibia* Grunow, *N. paleacea* (Grunow) Grunow, and *Rhoicosphenia abbreviata* (C.Agardh) Lange–Bertalot. According to LANGE–BERTALOT et al. (2017), this species composition is typical for meso- to eutrophic, β-α-mesosaprobic conditions with higher electrolyte contents.

***Fragilaria distans* (Grunow) Bukhtiyarova 1995 (Figs 247–262)**

Basionym: *Synedra vaucheriae* var. *distans* Grunow in Van Heurck 1881, VAN HEURCK (1881), Synopsis des Diatomées de Belgique Atlas pl. XL, fig. 17.

LM (Figs 247–262): Frustules in girdle view rectangular, linked, forming ribbon-like colonies (Figs 247, 249). Valves linear with parallel margins, apices clearly protracted, capitate to subcapitate throughout entire cell diminution series. Valves occasionally asymmetrical (maybe due to teratogeny, Figs 255, 259). Valve dimensions (n=15): length 30–45 µm, width 3.5–4.0 µm. Sternum narrow to moderately broad, linear, weakly widening near the central area. Central area forming large, occasionally slightly swollen, hyaline rectangular zone. Ghost striae rarely visible in central area. Striae alternating, parallel throughout entire valve, slightly radiate near apices, 10–11 in 10 µm. Areolae indiscernible in LM.

Due to the rarity of specimens, it was not possible to make SEM observations.

Lectotype (here designated): BR–4674 (Meise Botanic Garden, Belgium), slide prepared from Grunow sample 440, conserved in BR.

Isolectotype (here designated): W0164803 (W, Natural History Museum, Vienna, Austria).

Analysed material: Grunow sample 440 (Bozen (=Bolzano), South Tyrol, Italy, coll. date 25.IX.1859).

Associated diatom flora: Grunow sample 440 is dominated by *Ulnaria ulna*. Other taxa in the sample are *Achnanthisium eutrophilum* (Lange–Bertalot) Lange–Bertalot, *A. cf. microcephalum*, *Amphora pediculus* (Kützing) Grunow, *Cymbella aspera*, *Encyonema leibleinii* (C. Agardh) W.J. Silva, R. Jahn, T.A.V. Ludwig, et M. Menezes, *Epithemia argus* (Ehrenberg) Kützing, *Gomphonema parvulum*, *Navicula tripunctata* (O.F. Müller) Bory, and *Nitzschia media* Hantzsch. *Fragilaria distans* is only very rarely present. According to LANGE–BERTALOT et al. (2017), this community is found in eutrophic, oligo- to β -mesosaprobic lakes and rivers with medium electrolyte content.

***Fragilaria bahlsiana* Van de Vijver, C.E. Wetzel et Ector sp. nov.**

Fragilaria bahlsiana, described as a new species in this paper occurs in North America and has so far not been observed in European waters. It differs from *F. fragilarioides* by not forming ribbon-like colonies, the lack of spines on the valve face margin and a higher stria density (15–16 vs. 10–11 in 10 μm). *Fragilaria bahlsiana* can be distinguished from *F. socia* by its less swollen central area and its more elongated valve outline.

***Fragilaria bahlsiana* Van de Vijver, C.E. Wetzel et Ector sp. nov. (Figs 263–282)**

Registration: <http://phycobank.org/102752>

LM (Figs 263–278): Frustules in girdle view rectangular, solitary. Ribbon-like colonies not observed. Valves linear-lanceolate with weakly convex margins and distinctly protracted, capitate to subcapitate apices throughout entire cell diminution series. Valve dimensions (n=25): length 30–40 μm , width 3.0–4.0 μm . Sternum narrow, linear, gradually widening towards central area. Central area forming distinct, large, swollen, rectangular hyaline zone. Ghost striae occasionally visible in central area (Fig. 265). Striae alternating, almost parallel to weakly radiate throughout entire valve, slightly more radiate near apices, 15–16 in 10 μm . Areolae not discernible in LM. **SEM (Figs 279–282):** Spines, or vestiges of spines, not observed. Valve face flat with only very weakly raised virgae (Figs 279, 281). Ghost striae in central area visible as shallow grooves (Fig. 281). Striae uniseriate, composed of small, rounded to transapically elongated areolae (Figs 280, 281). Apical pore field of the ocellulimbus type, moderately large, composed of only 3 rows of relatively large, rounded poroids (Fig. 280). External rimoportula opening rounded, rimmed, replacing one areola in last stria, close to sternum at one apex (Fig. 280). Internally, rimoportula straight, aligned with virga (Fig. 282).

Holotype: BR–4675 (BR, Meise Botanic Garden, Belgium), slide made from Walker Arnott sample S 907. **Isotypes:** PLP–392 (University of Antwerp, Belgium), W0164809 & W0164810 (Natural History Museum, Vienna, Austria)

Etymology: The species is named in honor of Dr. Loren L. Bahls (Montana Diatom Collection, Helena, USA) in appreciation of his contributions to the knowledge of

the Montana diatom flora.

Type locality: Walker Arnott sample S 907 (Gambier, Ohio, USA, leg. H.L. SMITH s.n.).

Associated diatom flora: This north American sample, provided by H.L. Smith contains a very large population of ‘*Meridion lineare*’ D.M. Williams, forming long, ribbon-like colonies. Other important taxa in the sample include *M. circulare* and *Fragilaria bahlsiana*.

***Fragilaria perdelicatissima* Lange–Bertalot et Van de Vijver in LANGE–BERTALOT & ULRICH (2014)**

Fragilaria perdelicatissima Lange–Bertalot et Van de Vijver was only described in 2014, but the species was known for a long time as *F. delicatissima* (W. Smith) Lange–Bertalot, a combination made by LANGE–BERTALOT (1980). TUJI & HOUKI (2004) and LANGE–BERTALOT & ULRICH (2014, p. 21) explained the taxonomic history of this taxon. In the original type material from Lough Neagh, Ireland, two different taxa were found, one apparently described by WILLIAM SMITH in 1853 as *Synedra delicatissima* W. Smith and a second unnamed taxon. PATRICK & REIMER (1966, pl. 5, fig. 2) lectotypified that taxon, but their drawing clearly differs from the later interpretation in KRAMMER & LANGE–BERTALOT (1991, pl. 115, fig. 13), erroneously indicating their figure as representing the lectotype. TUJI & HOUKI (2004) illustrated the correct lectotype and suggested that the valve indicated by KRAMMER & LANGE–BERTALOT (1991) was a different *Fragilaria*. This was finally corrected with the description of *F. perdelicatissima* in LANGE–BERTALOT & ULRICH (2014). *Synedra delicatissima* was transferred to the genus *Ulnaria* as *U. delicatissima* (W. Smith) Aboal et P.C. Silva (ABOAL & SILVA 2004).

***Fragilaria perdelicatissima* (W. Smith) Lange–Bertalot et Van de Vijver in LANGE–BERTALOT & ULRICH (2014) (Figs 283–335)**

Original description: *Fragilaria perdelicatissima* Lange–Bertalot et Van de Vijver in LANGE–BERTALOT & ULRICH (2014), p. 19, pl. 8, figs 1–7 \equiv *Fragilaria delicatissima* (W. Smith) Lange–Bertalot 1980 nom. illeg. **To exclude from synonymy:** *Synedra delicatissima* W. Smith 1853.

LM (Figs 283–305, 310–335): Frustules in girdle view rectangular, solitary or two cells linked (Fig. 310). Ribbon-like colonies not observed. Valves elongated, linear-lanceolate with parallel margins, gradually tapering towards distinctly protracted, capitate apices throughout entire cell diminution series. Valve dimensions for type population (n=50): length 30–100 μm , width 2.0–2.5 μm . Valve length in additional Swedish population 25–70 μm . Sternum distinct, broad, linear to lanceolate, gradually widening towards central area. Central area usually forming apically elongated, rectangular hyaline zone. Ghost striae occasionally visible in central area (Fig. 297). Striae alternating, short, almost parallel to weakly radiate throughout entire valve, 15–16 in 10 μm . Areolae not discernible in LM.

SEM (Figs 306–309): Spines absent (Fig. 306). Valve face flat, virgae weakly raised (Fig. 306). Striae uniseriate, short, almost marginal, composed of a small number

of apically elongated areolae (Figs 306, 308). Ghost striae weakly visible in central area, mainly because of slightly raised virgae (Fig. 308). Apical pore field of the ocellulimbus type, large, composed of at least 5 rows of small poroids (Fig. 307). External rimoportula opening small, rounded, located between last stria and apex (Fig. 307). Internally, rimoportula opening oblique, quite large (Fig. 309).

Holotype: slide VI-46-B8, leg. W. SMITH, sample *Campylodiscus hibernicus*, Lough Neagh (Antrim, North Ireland, UK), Meise Botanic Garden (BR, Belgium).

Analysed material: slide VI-46-B8, William Smith, *Campylodiscus hibernicus* sample, Lough Neagh (Antrim, North Ireland, UK, coll. date 1850, leg. Dr G. DICKIE s.n.), BR-4676, Apmeljåkkå River, Sweden, 2002 (leg. AMELIE JARLMAN s.n., 2002)

Associated diatom flora: The type material was dominated by several *Achnantheidium* taxa such as *Achnantheidium affine* (Grunow) Czarnecki and *A. cf. microcephalum*, *Cymbella lange-bertalotii* Krammer, *Denticula tenuis* Kützing, *Diatoma ehrenbergii* Kützing, *Fragilaria perdelicatissima*, and *Tryblionella brunoi* (Lange-Bertalot) Cantonati et Lange-Bertalot. The other investigated sample was collected in a small, Swedish river called Apmeljåkkå. The most dominant species in that sample include *A. minutissimum* (Kützing) Czarnecki, *Fragilaria perdelicatissima*, *F. tenera* (W. Smith) Lange-Bertalot, *Hannaea linearis* (Holmboe) Álvarez-Blanco et S. Blanco, and *Tabellaria cf. flocculosa*. Other important (raphid) species are *Brachysira neoexilis*, various *Cymbella* species, and *Achnantheidium lineare* W. Smith. The site where the sample was collected was characterized by an alkaline pH (8.0), a low conductivity value of 88 $\mu\text{S}\cdot\text{cm}^{-1}$, low nitrogen (NH_4^+-N 5 $\mu\text{g}\cdot\text{l}^{-1}$, $\text{NO}_2^-+\text{NO}_3^- -\text{N}$ 25 $\mu\text{g}\cdot\text{l}^{-1}$) and phosphate ($\text{PO}_4^{3-}-\text{P}$ 1 $\mu\text{g}\cdot\text{l}^{-1}$) levels (A. JARLMAN, Lund, pers. comm.). The observed diatom composition in both samples is typical for circumneutral to weakly alkaline, oligosaprobic, oligo- to mesotrophic conditions (LANGE-BERTALOT et al. 2017).

***Fragilaria spinaspeciosa* Lange-Bertalot et Cantonati in CANTONATI et al. (2019)**

Fragilaria spinaspeciosa, recently described from Italy (CANTONATI et al. 2019), is superficially similar to *F. rumpens* and is included here to aid comparison with the *Synedra rumpens* complex. Both *F. rumpens* and *F. spinaspeciosa* form ribbon-like colonies and have similar valve outlines, but differ in the shape of their central area. In *F. spinaspeciosa* the central area is almost absent whereas in *F. rumpens* a large, weakly swollen, hyaline central area is clearly present, as can be seen in all illustrated valves below. Additionally, *F. spinaspeciosa* has a slightly lower valve width (2.5–3.0 vs. 3.0–3.5 μm), and a lower stria density (15–17 vs. 19–20 in 10 μm) (Table S2).

***Fragilaria spinaspeciosa* Lange-Bertalot et Cantonati in CANTONATI et al. (2019) (Figs 336–358)**

Original description: *Fragilaria spinaspeciosa* Lange-Bertalot et Cantonati in CANTONATI et al. (2019), Phytotaxa 404, p. 262, figs 1–13, 69–75.

LM (Figs 336–357): Frustules rectangular, linked together to form short ribbon-like colonies (Fig. 336). Valves strictly linear with parallel margins, only narrowing near protracted, capitate apices. Valve dimensions (n=25): length 25–45 (57) μm , width 2.5–3.0 μm . Sternum narrow, linear, not widening near central area. Central area almost absent, very rarely formed by slight widening of sternum. Hyaline central area not observed. Striae parallel throughout the entire valve length, 15–17 in 10 μm . Areolae indiscernible in LM.

SEM (Fig. 358): Large, conical marginal spines present between the valve face and mantle striae. Three large spines visible at the valve apex. Apical pore field of the ocellulimbus type, composed of several rows of large poroids.

Holotype: cLIM004 DIAT 1985 (TR, MUSE – Museo delle Scienze, Trento, Italy).

Analysed material: Sample cLIM004 DIAT 1985, helo-crenic spring close to Lago Scuro (Northern Apennines, Municipality of Corniglio, Province of Parma, Italy, coll. date 31.VII.2011, leg. M. Cantonati s.n.).

Associated diatom flora: The type material was dominated by several *Eunotia* taxa such as *E. minor* (Kützing) Grunow in VAN HEURCK, *E. islandica* Østrup, *E. nymanniana* Grunow in VAN HEURCK and *E. tetraodon* Ehrenberg, *Encyonema neogracile* Krammer, *Frustulia saxonica* Rabenhorst, *Gomphonema acidoclinatum* Lange-Bertalot et E. Reichardt in WERUM & LANGE-BERTALOT, *Navicula angusta* Grunow, *Pinnularia sinistra* Krammer, and *Tabellaria flocculosa* (CANTONATI et al. 2019). More details on the environmental parameters of the analysed sample are given in CANTONATI et al. (2019). According to LANGE-BERTALOT et al. (2017), the observed diatom composition is found in electrolyte-poor, weakly acid to circumneutral, oligotrophic, oligosaprobic standing water bodies.

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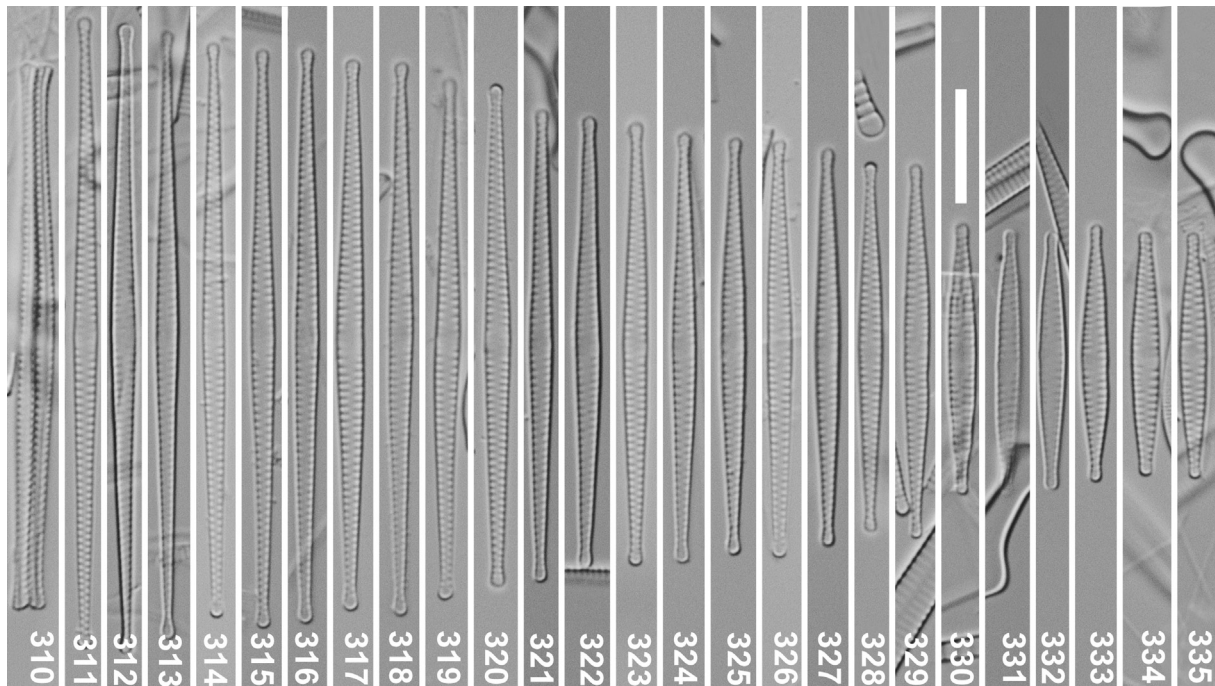
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Figs 283–309. *Fragilaria perdelicatissima* (W.Smith) Lange–Bertalot et Van de Vijver, LM and SEM images taken from the type material (slide VI–46–B8, W. Smith, Lough Neagh, Antrim, North Ireland, UK): (283–305) LM views of population arranged in decreasing length; (306) SEM external view of an entire valve showing absence of marginal spines; (307) SEM detail of valve apex showing rimoportula and apical pore field; (308) SEM external view of central and broad sternum, note ghost striae in central area; (309) SEM internal detail of valve apex with rimoportula. Scale bar represent 10 μm (283–306) and 1 μm (307–309).

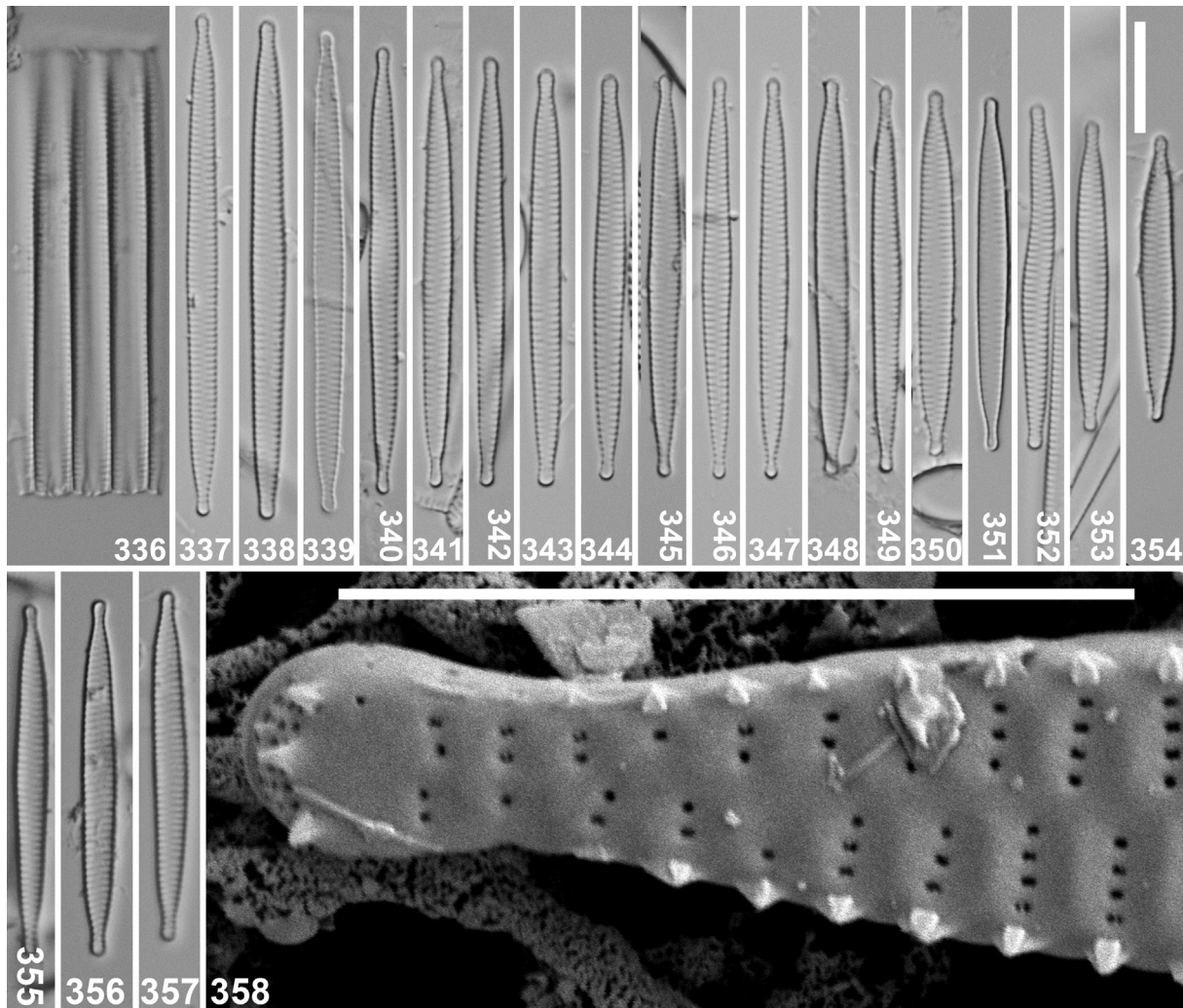
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Figs 310–335. *Fragilaria perdelicatissima* (W.Smith) Lange–Bertalot et Van de Vijver. LM images taken from Swedish river samples of Apmeljåkkå (BR–4676) with views of population arranged in decreasing length: (310) shows two frustules attached to each other. Scale bar represents 10 μm .

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Figs 336–358. *Fragilaria spinaspeciosa* Lange–Bertalot et Cantonati, LM and SEM images taken from the holotype material (Sample cLIM004 DIAT 1985, Helocrenic spring close to Lago Scuro, Northern Apennines, Municipality of Corniglio, Province of Parma, Italy): (336–357) LM views of population arranged in decreasing length; (336) represents frustules in girdle view linked to form a ribbon-like colony; (358) SEM external detail of the apex with apical pore field. Note the large marginal spines. Scale bar represents 10 μm (336–357) and 5 μm (358).

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