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A critical analysis of the *Fragilaria vaucheriae* complex (Bacillariophyta) in Europe

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Abstract: *Fragilaria vaucheriae* is one of the most common *Fragilaria* species in Europe, typically reported from impacted, eutrophic water bodies. Despite its ubiquity, the species presents a broad morphological variability, urging a complete taxonomic revision based on the analysis of the morphology of a substantial number of historic and recent populations. In the present study, type material of *Exilaria vaucheriae*, *Fragilaria rinoi*, and *Echinella fasciculata* β [var.] *truncata* was investigated using LM and SEM observations, together with more than 10 historic and recent populations. The results based on these comparisons show that *Fragilaria vaucheriae* is most likely a rather rare *Fragilaria* species in Europe and that most populations should be identified as *Fragilaria truncata*, a new combination made here based on *Echinella fasciculata* β *truncata*. The observations made in this study also resulted in the description of several new species, often with distinct ecologies and distributions: *Fragilaria catenarinoi* Van de Vijver et D.M.Williams sp. nov., *F. kellyana* Van de Vijver, D.M.Williams et Ector sp. nov., *F. landnama* Van de Vijver et Iris Hansen sp. nov., *F. thingvellirensis* Van de Vijver et G.S.Jónsson sp. nov., *F. vandekerckhoveana* Van de Vijver sp. nov., *F. vaucheriaefalsa* Van de Vijver et D.M.Williams sp. nov. and *F. vaucheriaerobusta* Van de Vijver, C.E.Wetzel et Ector sp. nov. Important features to discriminate the different species include valve outline (linear versus lanceolate), the presence of 'shoulders' beyond the apices, the presence of striae (and the formation of colonies), the stria density and the shape and structure of the central area. Using an analysis of the associated diatom flora, the ecological preferences of each taxon are briefly discussed.

Key words: ecology of diatoms, Europe, *Fragilaria vaucheriae–rinoi* complex, morphology, new species, taxonomy, type analysis

Introduction

The genus *Fragilaria* was originally described by Lyngbye in 1819, although it was only in 1927 that a typus generis was designated by Boyer (1927): *Fragilaria pectinalis* (O.F.Müller) Lyngbye. Williams & Round (1987), later refined and completed by Tuji & Williams (2006a), provided a detailed description for the genus. Almost all species, nowadays transferred to the genus *Fragilaria*, were originally described in the genus *Synedra* Ehrenberg in the nineteenth century. Only a handful of scientists worked on this group then, such as Christian G. Ehrenberg (1795–1876), Friedrich T. Kützing (1807–1893), William Smith (1808–1857), Gottlob Ludwig Rabenhorst (1806–1881), and Albert Grunow (1826–1914). In the eighties of last century, several revisions were made on common *Fragilaria* species, often lumping a lot of taxa under a handful of names (Lange–Bertalot 1980; Krammer & Lange–Bertalot 1991).

Approximately fifteen years ago, a first taxonomic revision of the genus *Fragilaria* started, mainly based

on the reanalysis of original (usually type) material (Tuji 2004, 2007; Tuji & Williams 2006a, b, 2008a, b, c, 2013, 2017; Delgado et al. 2015). This resulted in a better understanding of the historic taxa and the description of several new species, such as *Fragilaria microvaucheriae* C.E.Wetzel et Ector (Wetzel & Ector 2015), *F. misarelensis* S.F.P.Almeida et al. (in Novais et al. 2019), *F. vaucheriaeraetica* Cantonati et Lange–Bertalot (in Cantonati et al. 2019), *F. heatherae* M.Kahlert et M.G.Kelly (in Kahlert et al. 2019), and *F. rinoi* S.F.P.Almeida et C.Delgado (in Delgado et al. 2016). Most of these were split from the catch–all taxon *Fragilaria vaucheriae* (Kützing) J.B.Petersen, one of the most commonly reported *Fragilaria* species worldwide, and in Europe typically reported from eutrophic freshwater ecosystems (Lange–Bertalot et al. 2017). Search engines give back thousands of hits on the name *F. vaucheriae* (including the synonym *F. capucina* var. *vaucheriae* (Kützing) Lange–Bertalot).

Despite these useful revisions, taxonomic uncertainty still prevails regarding the identity of this common *Fragilaria* species. This is mainly because a lot of historic (type) material present in European diatom collections such as the Natural History Museum in London, UK (BM), the Grunow collection in Vienna, Austria (W) and the Van Heurck collection in Meise Botanic Garden, Belgium (BR), was never studied in depth, i.e. applying detailed morphological analyses. A recent new revision currently in progress (see citations below) aims to unravel the correct taxonomic identity of many (often forgotten and neglected) European *Fragilaria* taxa. It is based on the examination of type material and other historic (usually nineteenth century) samples and has steadily increased our knowledge of this group. The following taxa have already been reanalysed: *Fragilaria austriaca* (Grunow) Lange–Bertalot (Van de Vijver et al. 2020a), *F. gloiophila* (Grunow) Van de Vijver et al. (Van de Vijver et al. 2020b, c), *F. perminuta* (Grunow) Lange–Bertalot (Van de Vijver & Ector 2020), *F. deformis* (W.Smith) Van de Vijver et Ector (Van de Vijver et al. 2020d), *F. alpestris* Krasske (Van de Vijver et al. 2020e), *F. septentrionalis* (Østrup) Van de Vijver et al. (Van de Vijver et al. 2020f), *F. ostenfeldii* (Willi Krieger) Van de Vijver et al. (Van de Vijver et al. 2021a), *F. capucina* Desmazières (Van de Vijver et al. 2021b), *F. recapitellata* (Grunow) Lange–Bertalot et Metzeltin (Van de Vijver et al. 2021c), and *F. rumpens* (Kützing) G.W.F.Carlson (Van de Vijver et al. 2022a).

In the present paper, we continue this work and revise the complex of small, short–celled, non–colony–forming, *Fragilaria* taxa often force–fitted into *F. vaucheriae* (basionym: *Exilaria vaucheriae* Kützing). The original material of *E. vaucheriae* (Kützing 1833, 1834) was already restudied several times in the past 10 years (Tuji & Williams 2013; Wetzel & Ector 2015; Delgado et al. 2016; Van de Vijver et al. 2020d) in an attempt to better circumscribe this morphologically and ecologically highly variable taxon. Despite all these morphological observations, the precise interpretation of *F. vaucheriae* remains problematic, partly due to the description of a plethora of taxa. These were historically usually put in the genus *Synedra* but taxonomically linked to *F. vaucheriae* as subspecies, variety, or form, such as *Synedra vaucheriae* var. *truncata* (Greville) Rabenhorst (Rabenhorst 1864), *S. vaucheriae* var. *tenuior* Grunow (Grunow 1862), or *S. vaucheriae* var. *perminuta* Grunow (in Van Heurck 1881). Many of these were later considered to be synonyms to *F. vaucheriae*, despite showing distinct morphological features (see for instance Hustedt 1932 or Patrick & Reimer 1966). This taxonomic broadening of Kützing's original concept of *Fragilaria* (*Exilaria*) *vaucheriae*, makes a meaningful ecological characterization of the species very difficult, likely having a serious impact on water quality monitoring practices.

In an attempt to solve part of this taxonomic problem, unmounted type material of *S. fontinalis* W.Smith (Smith 1857), *S. gloiophila* Grunow (in Van Heurck 1881), *S. vaucheriae* var. *distans* Grunow (in Van Heurck 1881), *S. rumpens* var. *fragilarioides* Grunow (in Van Heurck 1881), and *S. vaucheriae* var. *perminuta* Grunow (in Van Heurck 1881) has already been restudied. Several of these taxa were transferred to the genus *Fragilaria* as independent species, because they were shown to be sufficiently different from all other *Fragilaria* taxa (Van de Vijver & Ector 2020; Van de Vijver et al. 2020a, 2021b). Many other taxa, such as *Echinella fasciculata* var. *truncata* Greville (Greville 1823), however, still need to be re–examined. Moreover, the name '*Synedra vaucheriae*' was used for many *Fragilaria*–populations, often showing only a faint resemblance to its type. To assess the variability of the *F. vaucheriae* species complex in European waters, in the current paper we analyse the pertinent historic material in combination with recently collected European samples including populations from (arranged from north to south) Iceland, Sweden, the United Kingdom, Belgium, Germany, Switzerland, Austria and France. The results are compared with observations of the type material of *F. agnesiae* M.Kahlert & Rimet, *F. heatherae*, *F. misarelensis*, *F. rinoi*, and *F. microvaucheriae* (Wetzel & Ector 2015; Delgado et al. 2016; Kahlert et al. 2019; Novais et al. 2019).

Small, local ecological differences can have an impact on valve morphology and thus by showing, analyzing and discussing a large number of populations, across western Europe with a fair North to South spread and including historical ones, we aim to clarify the taxonomic identity of these taxa. By carefully assessing the associated diatom flora, an attempt is made to refine our understanding of the environmental preferences of the studied taxa. A better knowledge of the morphological and ecological variability of the species in the *F. vaucheriae* complex in European waters will therefore also improve their use in water quality biomonitoring.

Based on these observations, in the current paper we describe and discuss the morphology of all observed

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populations and seven new species are described: *Fragilaria catenarinoi* Van de Vijver et D.M.Williams sp. nov., *F. kellyana* Van de Vijver, D.M.Williams et Ector sp. nov., *F. landnama* Van de Vijver et Iris Hansen sp. nov., *F. thingvellirensis* Van de Vijver et G.S.Jónsson sp. nov., *F. vandekerckhoveana* Van de Vijver sp. nov., *F. vaucheriaefalsa* Van de Vijver et D.M.Williams sp. nov., and *F. vaucheriaerobusta* Van de Vijver, C.E.Wetzel et Ector sp. nov. One new combination and rank change is proposed, *Fragilaria truncata* (Greville) Van de Vijver et D.M.Williams comb. nov. et stat. nov.

Material and Methods

For this study, a mixture of historic (often original as well as type) material and recently collected samples were investigated. The historic material originated from samples from several 19th century diatomists: Kützing (BR, BM), Greville (BM), Grunow (W), Van Heurck (BR), and Walker Arnott (BR, E). Herbarium acronyms throughout are shown according to Index Herbariorum (Thiers 2022). Table 1 lists all investigated samples together with all sample information that could be retrieved (sometimes scant for historical material). In total, 18 samples were included in this study. Given the morphological variability within *Fragilaria* species, it is important to show a broad range along the cell diminution series to express this variability. Moreover, it is also important to show the differences and similarities between populations in order to establish a more or less complete overview of this morphological variability.
Subsamples of all selected 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 minutes at 3700× rpm), the resulting cleaned material was diluted with distilled water to avoid excessive concentrations of diatom valves on the slides. Cleaned diatom material was mounted in Naphrax. The resulting slides were analysed using an Olympus BX53 microscope at 1000× magnification (UPlan FL N 100x oil objective, 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 each population, at least 25, but often many more, valves are illustrated using LM to determine its morphological variability. For each population, an ecological characterization is added based on the accompanying diatom flora, assessed by counting at least 100 diatom valves along random transects. Relative abundances, when given, are expressed as percentage of counted valves.

To complete the morphological analysis, the ultrastructure of each population is assessed using SEM. For that purpose, part of the suspension was filtered through polycarbonate membrane filters with a pore diameter of 1 µm, pieces of which were fixed on aluminum stubs after air–drying. Several stubs were either sputter–coated with a gold–palladium layer reaching a thickness of 20 nm and studied using a ZEISS Ultra SEM microscope at 3 kV (Natural History Museum, London, UK). Or stubs were sputter–coated with a platinum layer reaching a thickness of 20 nm and studied using a JEOL–JSM–7100F field emission scanning electron microscope at 2 kV (Meise Botanic Garden, Belgium). Slides and stubs are stored at the BR–collection. 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*), Tuji & Williams (2006a, genus features for *Fragilaria*) and Williams (2019, spines). The terms 'sternum' for the axial area (Round 1979) and 'ocellulimbus' for the inset apical pore field (Williams 1986) are used. For taxonomic comparisons and/or ecological characterisation, the following papers were consulted: Lange–Bertalot (1980), Krammer & Lange–Bertalot (1991), Tuji & Williams (2006a, 2008c, 2013), Delgado et al. (2015, 2016), Wetzel & Ector (2015), Lange–Bertalot et al. (2017), Cantonati et al. (2019), Kahlert et al. (2019), Novais et al. (2019), Van de Vijver & Ector (2020), and Van de Vijver et al. (2020b, d, f, 2021b, 2022a, b).

For the typification of 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). Although the type is illustrated by all other figures, we chose an appropriate image that can be linked to the designated type by stating "The type is illustrated by Fig. X". In doing so, the identity of the species can be fixed by a valve that is not exclusively showing the type, but may be most characteristic.

Results

In the present paper, a total of 10 taxa, often initially identified as *F. vaucheriae*, were investigated. Our observations demonstrate that the name '*Fragilaria vaucheriae*' has been and is still applied to a broad array of rather small–celled, coarse (=stria density < 15 in 10 µm) valves, but that many of these populations should be distinguished as separate taxa, often occurring in quite different environmental conditions. The results clearly demonstrate that the *Fragilaria vaucheriae* complex is more diverse than currently recognized in the (mainly European) literature, largely due to a too broad interpretation of the original *Exiliaria vaucheriae* population.

We opted to start the analysis and discussion of the species in the *F. vaucheriae* species complex, with three already described taxa: *F. vaucheriae*, *F. rinoi*, and *F. truncata* (Greville) Van de Vijver et D.M.Williams comb. nov. et stat. nov., the latter only a transfer and rank change of *Echinella fasciculata* β [var.] *truncata* Greville, originally described in 1823 (Greville 1823). These are followed by the description and comparison of seven new taxa: *Fragilaria catenarinoi* Van de Vijver et D.M.Williams sp. nov., *F. kellyana* Van de Vijver, D.M.Williams et Ector sp. nov., *F. landnama* Van de Vijver et Iris Hansen sp. nov., *F. thingvellirensis* Van de Vijver et G.S.Jónsson sp. nov., *F. vandekerckhoveana* Van de Vijver sp. nov., *F. vaucheriaefalsa* Van de Vijver et D.M.Williams sp. nov., and *F. vaucheriaerobusta* Van de Vijver, C.E.Wetzel et Ector sp. nov.

Table 2 presents a comparison of the investigated

Table 1. List of all samples used in this paper.

Sample	locality	Investigated taxon	collection date	collector	collection	collection number
Kützing Decas III, 24	Quelle bei Weißenfels	*Exilaria vaucheriae*	???	??? (probably F.T.Kützing)	Meise Botanic Garden (Belgium)	BR–4738
Elias & Delgado, s.n.	Cértima River, Vouga Basin, Mogofores, Coimbra, Portugal	*Fragilaria rinoi*	21.III. 2012	Carmen L. Elias and Cristina Delgado	Meise Botanic Garden (Belgium)	–
Grunow sample 182	Leobendorf, Austria	*Fragilaria rinoi*	28.VIII.1857	A. Grunow	Meise Botanic Garden (Belgium)	W0164831, BR–4739
VMM2019_03	Canal Gent–Oostende, Lievegem, Belgium	*Fragilaria rinoi*	12.IV.2019	VMM	Meise Botanic Garden (Belgium)	BR–4740
Greville, s.n.	Edinburgh	*Echinella fasciculata β truncata*	???	A.Hooker	Natural History Museum London & Meise Botanic Garden (Belgium)	BR–4741
Walker Arnott 417	Haverfordwest, Wales	*Fragilaria truncata*	???	F. Okeden	Meise Botanic Garden (Belgium)	BR–4742
Walker Arnott 146	Loch Leven, Kinross, Scotland, UK	*Fragilaria truncata*	7.X.1854	???	Meise Botanic Garden (Belgium)	BR–4743
Peeters, s.n.	river La Cure, Montsauche–les–Settons, Burgundy, France	*Fragilaria truncata*	???	V. Peeters	Meise Botanic Garden (Belgium)	BR–4744
Kleine Nete 80	River Kleine Nete, Antwerp, Belgium	*Fragilaria truncata*	7.V.1994	B. Van de Vijver	Meise Botanic Garden (Belgium)	BR–4745
Brun	Salvan, Wallis, Switzerland	*Fragilaria truncata*	???	J. Brun	Meise Botanic Garden (Belgium)	VII–12–C5
Kützing 918	Germany	*Fragilaria catenarinoi*	???	????	Meise Botanic Garden (Belgium)	BR–4746
Kelly, s.n.	River Don, Towie, Aberdeenshire, Scotland, UK	*Fragilaria kellyana*	15.V.2018	Sarah Stenhouse	Meise Botanic Garden (Belgium)	BR–4747

Table 1 Cont.

Hansen, s.n.	River Hörgsá, Kirkjubæ-jarklaustur, Suðurland, Iceland	*Fragilaria landnama*	04.VII.2017	Iris Hansen	Meise Botanic Garden (Belgium)	BR–4748
Jónsson, s.n.	Lake Thingvallevatn (Þingvallavatn), Midfell transect, sample depth 0.4 m, Iceland	*Fragilaria thingvellirensis*	12.IX.2018	Gunnar Stein Jónsson	Meise Botanic Garden (Belgium)	BR–4749
Walker Arnott 238	Duddingston Loch, Edinburgh, Scotland	*Fragilaria vandekerckhoveana, F. vaucheriaerobusta*	???	Dr Gregory	Meise Botanic Garden (Belgium)	BR–4750
Walker Arnott 307	Loch Leven, Kinross, Scotland, UK	*Fragilaria vaucheriaefalsa*	???	???	Meise Botanic Garden (Belgium)	BR–4751
Walker Arnott 809S	Crofthead, south of Glasgow, Scotland	*Fragilaria vaucheriaefalsa*	???	???	Meise Botanic Garden (Belgium)	BR–4752

morphological characters for all taxa included in this study.

Fragilaria vaucheriae (Kützing) J.B.Petersen 1938 (Figs 1–58)

Basionym: *Exilaria vaucheriae* Kützing 1833 in Kützing (1833, Algarum Aquae Dulcis Germanicarum, Decas III, No. 24).

Lectotype: slide BM78023 designated in Lange–Bertalot (1980, p. 728), prepared from Kützing (1833), conserved in BM! Numerous sets of these exsiccatae exist, distributed in major collections in Europe and North America.

Isolectotype (here designated): BR–4738 based on sample Kützing (1833), häufig an *Vaucheria clavata* in einer Quelle bei Weißenfels (Germany), original material conserved in BR (=Type material).

Wetzel & Ector (2015, p. 273) used Kützing sample 185 (“*Exilaria vaucheriae* Kg. an *Vaucheria clavata* in Quellen bei Leisling, 18/4 32”) as type material for this species, stating that it was most likely the same material as Decas III, 24 and because Leißling is adjacent to the town of Weißenfels. Lange–Bertalot (1980) however, designated Decas III, sample 24 as type material and therefore this was used in the present paper as original material for *E. vaucheriae*. The isolectotype is illustrated by Fig. 20.

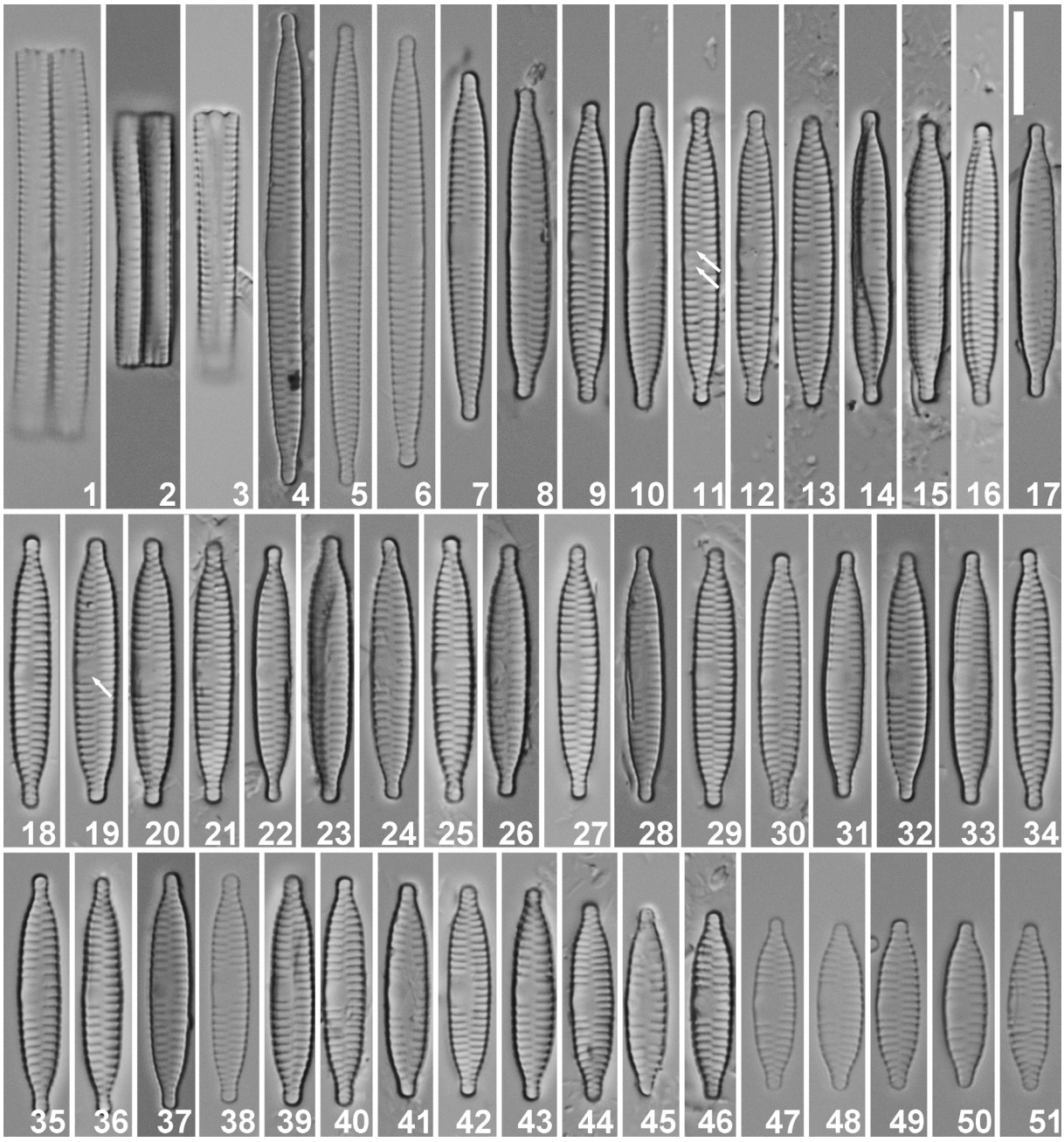
Registration: www.phycobank.org/103097

≡ *Fragilaria capucina* var. *vaucheriae* (Kützing) Lange–Bertalot 1980

LM (Figs 1–51): Frustules in girdle view rectangular, solitary, or two frustules attached to each other (Figs 1–3). Ribbon–like colonies not observed. Valves linear in longer valves to linear–lanceolate in smaller specimens with almost parallel to weakly convex (in smaller specimens) margins. At apices, valves abruptly narrowing, forming moderately developed shoulders. Apices clearly protracted, rostrate to sub–capitate throughout entire valve diminution series. Valve dimensions (n=60): valve length 12–50 µm, width 3.5–4.5 µm. Sternum very narrow but distinct, gradually widening from apices to central area. Central area unilateral with broad hyaline zone at one side of the sternum and only very weakly shortened striae at opposite side. Hyaline zone rarely depressed or inflated. Ghost striae occasionally observed (Figs 11, 19, arrows). Striae parallel in valve middle becoming weakly radiate at apices, alternating, 12–13 in 10 µm. Areolae not discernible in LM.

SEM (Figs 52–58): Girdle composed of several open bands, bearing one row of perforations on the advalvar part (Fig. 55). Mantle striae restricted to the upper part leaving the mantle edge hyaline, covered with large plaques (Figs 53, 55). Short, conical, non–linking marginal spines of variable length, irregularly placed on the valve face/mantle junction, often grouped in short series (Figs 52–54). Occasionally, spines lacking (Fig. 55). Striae uniseriate, composed of very large virgae compared to the small vimines (Fig. 52). Areolae small, rounded, externally covered by individual cribra (Fig. 55). One rimoportula present at one apex, replacing the last stria at the apex (Fig. 52, arrow). Apices devoid of striae. Apical pore field of the ocellulimbus type, large, composed of 7–8 long rows of very small pores, weakly extending onto the valve face (Fig. 55). Internally, rimoportula very large, straight (Figs 56, arrow, 58). Virgae raised (Fig. 57).

Associated diatom flora: The type material is entirely dominated by *F. vaucheriae* (up to 90% of all counted



Figs 1–51. *Fragilaria vaucheriae* (Kützing) J.B.Petersen, LM images taken from the lectotype material (Kützing sample Decas III, 24, BR–4738): (1–3) frustules in girdle view; (4–51) LM views of the population arranged in decreasing length; (11 & 19) show ghost striae (arrows). Scale bar represents 10 µm.

diatoms). Other taxa in the material are *Frustulia vulgaris* (Thwaites) De Toni (5%), *Rhoicosphenia abbreviata* (C.Agardh) Lange–Bertalot (2%), *Diatoma ehrenbergii* Kützing (1%) and *Gomphonella olivacea* (Hornemann) Rabenhorst (1%). All associated taxa are typical for circumneutral to alkaline environments. Most of them prefer eutrophic conditions with saprobity levels up to β–α–mesosaprobic (Lange–Bertalot 2001; Lange–Bertalot et al. 2017). Only the presence of *D. ehrenbergii* is rather unusual as the species is quite sensitive to nutrient enrichment and a higher organic load of its environment (Lange–Bertalot et al. 2017). However, only one valve was observed in the type material.

Taxonomic remarks: *Fragilaria vaucheriae* was originally described as *Exilaria vaucheriae* in 1833 from a *Vaucheria clavata* sample in a spring near the German town of Weißenfels, close to Leipzig (Saxony–Anhalt, central Germany). The original sample (Decas III, No. 24) is part of Kützing's exsiccata set Algarum Aquae Dulcis Germanicarum, with a short description reading "Frustulis hinc solitariis hinc subfasciculatis, inaequalibus, minutissimis, basi cohaerentibus, linearibus, utrinque obtusiusculis, hyalinis, medio lutescentibus. Frustulia parasitica Ag. syst.?". A year later, Kützing (1834, p. 560) refines this description: "Frustulis aut solitariis aut fasciculatis, minutissimis, linearibus, utrinque obtusis,

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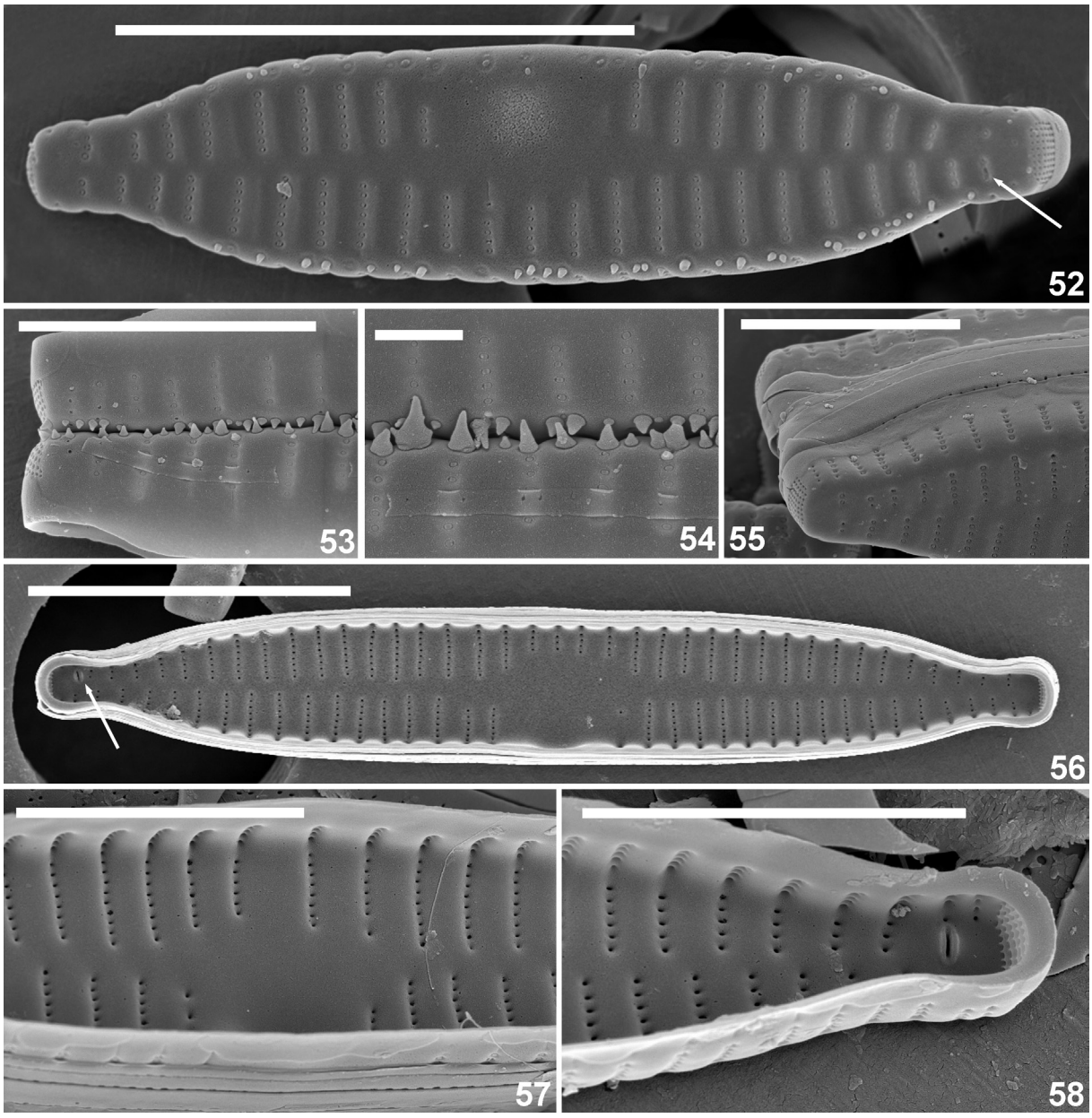
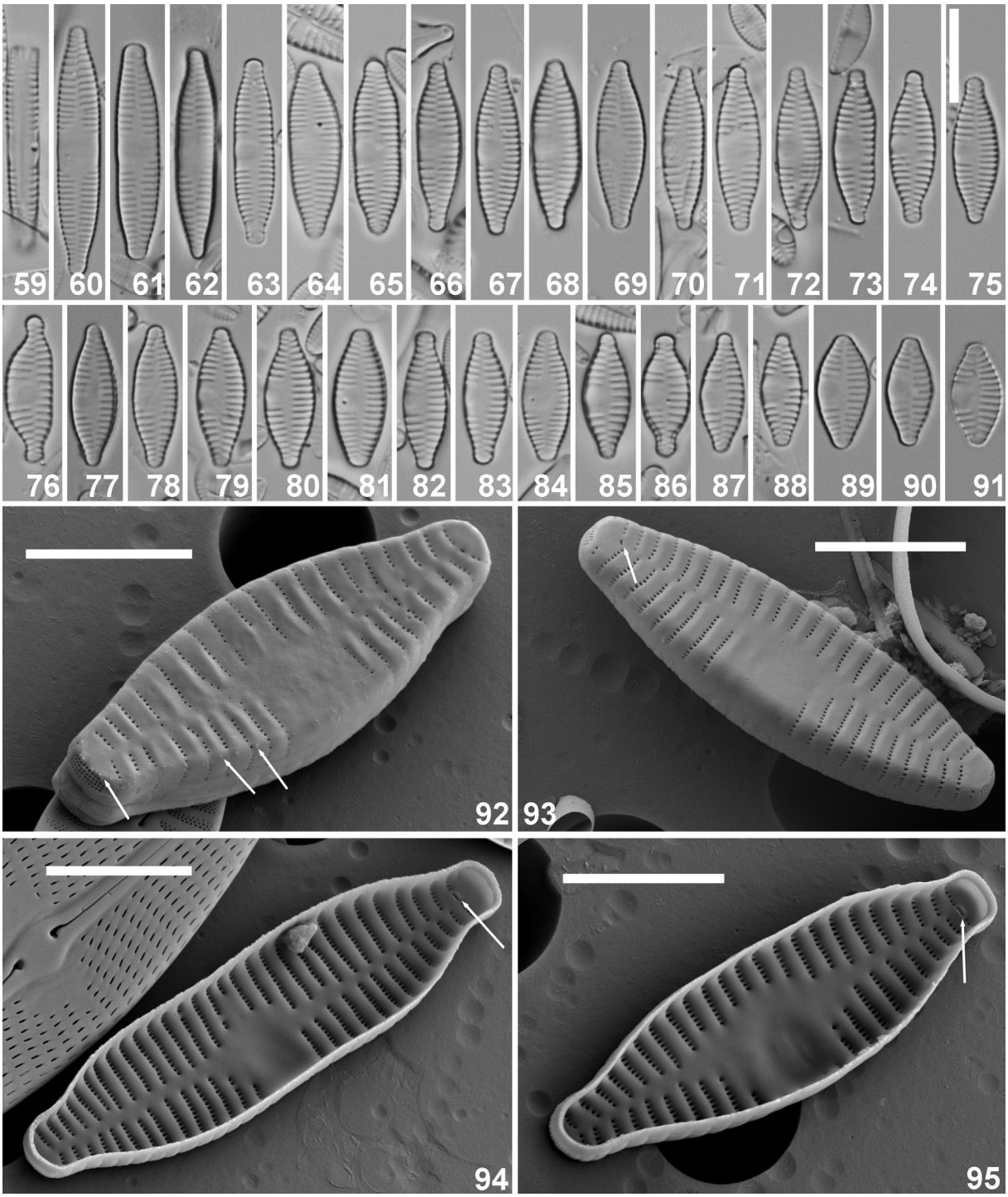


Figs 52–58. *Fragilaria vaucheriae* (Kützing) J.B.Petersen, SEM images taken from the lectotype material (Kützing sample Decas III, 24, BR–4738): (52) SEM external view of an entire valve, note the small marginal spines, the arrow indicates the rimoportula. (53) SEM external detail of the connected apices of two valves; (54) SEM external detail of spines; (55) SEM external detail of valve apex showing apical pore field and girdle structure; (56) SEM internal view of an entire valve, the arrow indicates the rimoportula; (57) SEM internal detail of valve interior showing weakly raised virgae; (58) SEM internal detail of valve apex with rimoportula and the apical pore field. Scale bars 10 µm (52, 56), 5 µm (55, 57, 58), 1 µm (53, 54).

altero latere apicem versus subattenuatis et rotundato–obtusis, viridi–luscentibus et varie maculatis" and adds a small drawing (Kützing 1834, fig. 38). In 1844, Kützing transferred the species to the genus *Synedra* as *S. vaucheriae* (Kützing) Kützing. Van Heurck (1881, plate 40, figs 17–23, 26) illustrated *S. vaucheriae* together with several varieties Grunow described, such as *S. vaucheriae* var. *distans* Grunow (plate 40, fig. 17), var. *gloiophila* Grunow (plate 40, fig. 21), var. *perminuta* Grunow (plate 40, fig. 23), and var. *capitellata* Grunow (plate 40, fig. 26), although for the latter three taxa, Grunow doubted their inclusion in *S. vaucheriae*, adding a '?' after *vaucheriae*. Recently, these varieties have almost all been revised and transferred to the genus *Fragilaria* as separate species (Van de Vijver & Ector 2020; Van de Vijver et al. 2020b, c, 2021c). In the first half of the twentieth century, the taxonomic identity of *Synedra vaucheriae* continuously broadened by systematically adding a large number of heterotypic synonyms to the original *S. vaucheriae*. Hustedt (1932, p. 194) listed more than 20 names including several original Kützing species such as *Frustulia anceps* Kützing, *Synedra minutissima* Kützing, and *Synedra parvula* Kützing. Recent analyses showed that these synonymisations are questionable and



Figs 59–95. *Fragilaria rinoi* S.F.P.Almeida et C.Delgado, LM and SEM images taken from the holotype material (Cértima River, Vouga Basin, Mogofores, Coimbra, Portugal, coll. date 21.III. 2012, leg. Carmen L. Elias and Cristina Delgado): (59) frustule in girdle view; (60–91) LM views of the population arranged in decreasing length; (92) SEM external view of an entire valve, note the small marginal, irregularly placed papillae indicated by arrows; (93) SEM external view of an entire valve, the arrow indicates rimoportula position; (94, 95) SEM internal view of two entire valves, arrows indicate rimoportulae. Scale bars 10 µm.

should be revised. For instance, *Synedra minutissima* was shown to be a *Halamphora* species (Wetzel et al. 2015) and *S. parvula* is most likely a *Nitzschia* (Van de Vijver & Williams, pers. obs.). Additional revision of other taxa resulted in their transfer to *Fragilaria* as *F. deformis* and *F. septentrionalis* (Van de Vijver et al. 2020d, f). These revisions clearly show the importance of a careful reanalysis of all relevant historic types.

Petersen (1938) analysed the type material of *Exilaria* (*Synedra*) *vaucheriae*, transferring it to *Fragilaria* as *F. vaucheriae* (Kützing) J.B.Petersen and stating that *Fragilaria intermedia* (Grunow) Grunow should be considered as conspecific, a species Grunow described in 1862 as *Fragilaria mutabilis* var. *intermedia*, later

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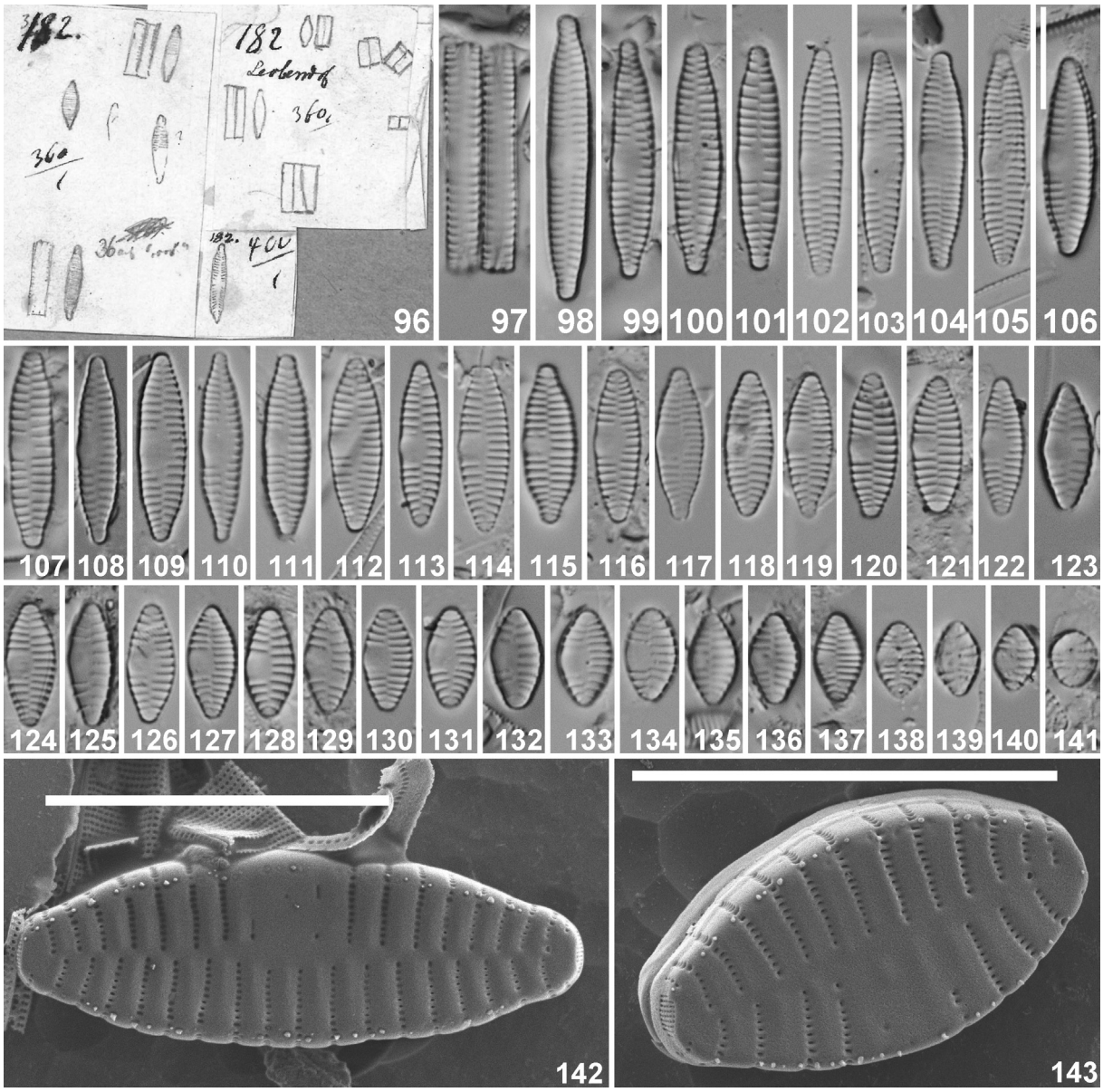
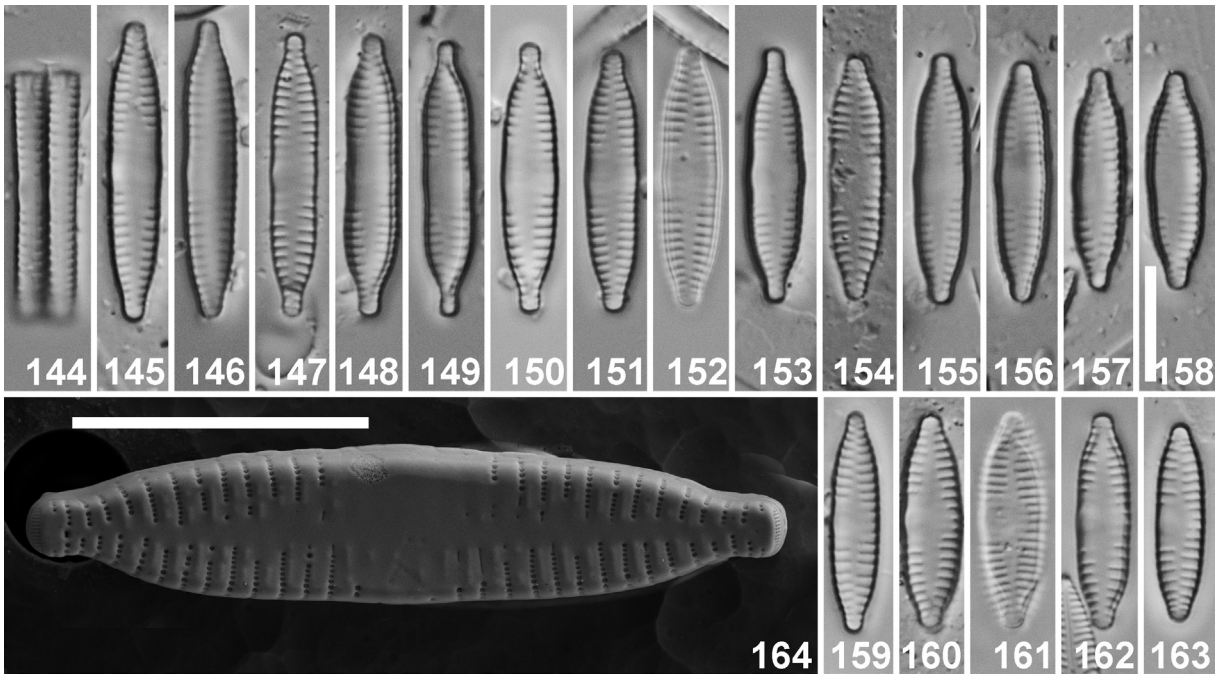


Figs 96–143. *Fragilaria rinoi* S.F.P.Almeida et C.Delgado, LM and SEM images taken from Grunow sample 182 (W0164831, Leobendorf, Austria, BR–4739): (96) original Grunow drawing of some valves observed by Grunow in sample 182, identified as *Synedra truncate*; (97) two connected frustules in girdle view; (98–141) LM views of the population arranged in decreasing length; (142–143) SEM external view of two entire valves. Scale bars 10 μm.

raised to species level in Van Heurck (1881, plate 45, figs 9–10). This possible conspecificity was also discussed and confirmed by Lange–Bertalot (1980, p. 728–729), after having analysed a large number of '*vaucheriae*'–populations worldwide. Although important morphological differences between *F. vaucheriae* and *F. intermedia* (colony formation, presence/absence of linking spines) were observed, both species were and are still considered similar. Tuji & Williams (2013) recently reanalysed this conspecificity and concluded that only part of the illustrated valves in Van Heurck (1881, plate 45, figs 9–11) should be considered similar to *F. vaucheriae*, describing the others as a new species, *F. neointermedia* Tuji et D.M.Williams. Van de Vijver & Kusber (2022) rejected the decision by Tuji & Williams (2013) to consider *F. intermedia* as a synonym of *F. vaucheriae* superseding their lectotypification, as an important feature (formation of colonies by *F. intermedia*) clearly mentioned by Grunow (1862) was not taken into account. Lange–Bertalot (1980) considered *F. vaucheriae* to be a variety of *F. capucina*, adding several other *Synedra* and *Fragilaria* taxa as synonyms to *F. capucina* var. *vaucheriae* (Kützing) Lange–Bertalot, such as *Synedra recapitellata* Grunow, *Synedra amphicephala* Kützing, and *Synedra rumpens* var. *meneghiniana* Grunow. Recent analysis showed that most of them should be removed from synonymy as they represent separate species (Van de Vijver et al. 2021d).



Figs 144–164. *Fragilaria rinoi* S.F.P.Almeida et C.Delgado, LM and SEM images taken from VMM sample 2019_03 (Canal Gent–Oostende, Lievegem, Belgium, BR–4740): (144) two frustules in girdle view, connected to each other; (145–163) LM views of the population arranged in decreasing length. Note the rather broad, distinct sternum and large central area; (164) SEM external view of an entire valve. Scale bars 10 µm.

***Fragilaria rinoi* S.F.P.Almeida et C.Delgado in Delgado et al. (2016) (Figs 59–164)**

Original publication: *Fragilaria rinoi* S.F.P.Almeida et C.Delgado in Delgado et al. (2016, European Journal of Taxonomy 248: p. 5, figs 1, 3–82).

Holotype: Slide BM101794 prepared from Cértima River, Vouga Basin (Mogofores, Coimbra, Portugal, coll. date 21.III. 2012, leg. Carmen L. Elias and Cristina Delgado) kept at BM (London, UK).

Isotype: Slide ZU10/14, kept at BRM (Bremerhaven, Germany).

LM (Figs 59–91): Frustules in girdle view rectangular, solitary or rarely two frustules attached to each other (Fig. 59). Ribbon–like colonies not observed so far. Valves only linear in the longest valves, but most valves lanceolate to elliptic–lanceolate with clearly convex margins gradually narrowing towards the apices. Apices protracted, rostrate, not (sub–)capitate. Valve dimensions (n=50): valve length 9–25 µm, width 4.5–6.0 µm. Sternum narrow at the apices, gradually widening towards the central area. Central area large, unilateral with hyaline zone at one side of the sternum and moderately to strongly shortened striae at opposite side. Valves with broad central area extending from one margin to another, rarely present. Striae parallel to rarely weakly radiate throughout the entire valve, alternating, 14–16 in 10 µm. Areolae not discernible in LM.

SEM (Figs 92–95): Marginal spines absent (Figs 92, 93). At valve face/mantle junction, very small, irregularly placed papillae present (Fig. 92, arrows). Mantle plaques present at the mantle margin (Fig. 93). Striae uniseriate, composed of broad, distinctly raised virgae compared to the small vimines (Fig. 92). Areolae very small, rounded (Figs 92, 93). One small, rimmed rimoportula present at one apex, located on the sternum, replacing one areola of the final stria (Fig. 93, arrow). Apical pore field of the ocellulimbus type, small, composed of only four rows of very small pores, entirely located on the mantle (Fig. 92). Internally, rimoportula large, almost straight, located almost on the sternum, between the last striae at the apex (Figs 94, 95, arrows). Virgae clearly raised (Fig. 95).

Additional populations: Two additional *F. rinoi* populations were examined in the present study. One very large population was found in historic material, Grunow sample 182 (W0164831, BR–4739) that Grunow collected on 28.VIII.1857 from a stream near the town of Leobendorf (potentially also Leobersdorf) (Lower Austria, Austria) (Figs 96–143). The length of the observed valves ranged from 6 to 28 µm, consistent with the type population. According to Grunow's accession books, his original set of notes kept in W, he did not identify the population, and on the drawing (Fig. 96), the name of the locality is clearly indicated. This original Grunow drawing (Fig. 96) shows that he most likely did not observe colonies as he only depicted solitary frustules or paired valves. The second population was collected recently (12.IV.2019) during routine water quality monitoring sampling by the Vlaamse Milieu Maatschappij (Flanders Environmental Agency) from the Canal Gent–Oostende near the Flemish village of Lievegem (Belgium) (BR–4740) (Figs 144–164). This population is slightly aberrant in possessing a very distinct, broader sternum and a larger central area. Nevertheless, we posit this population should be identified as *F. rinoi* given its valve dimensions, general valve outline, the position of the rimoportula opening, and the absence of marginal spines.

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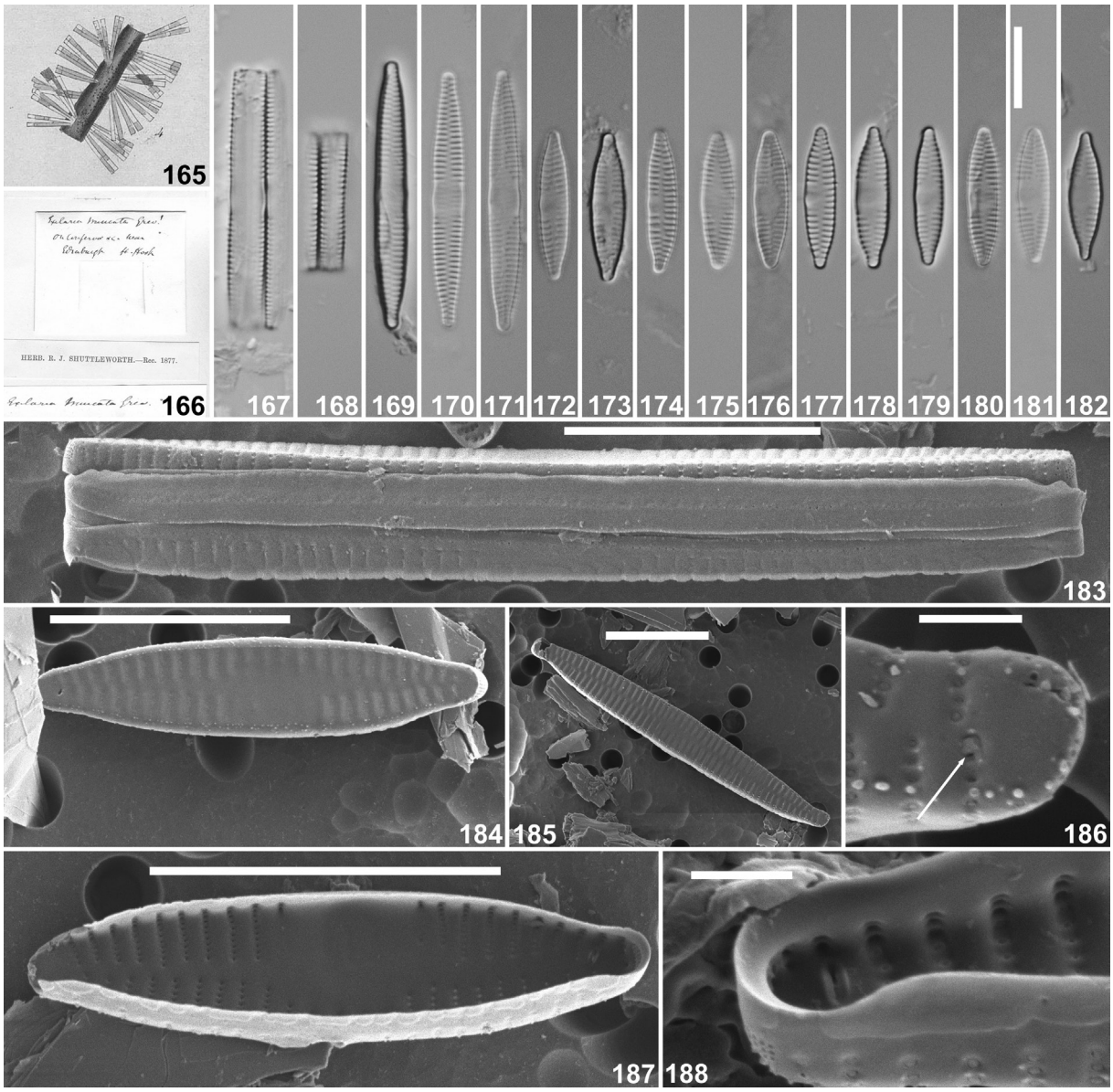
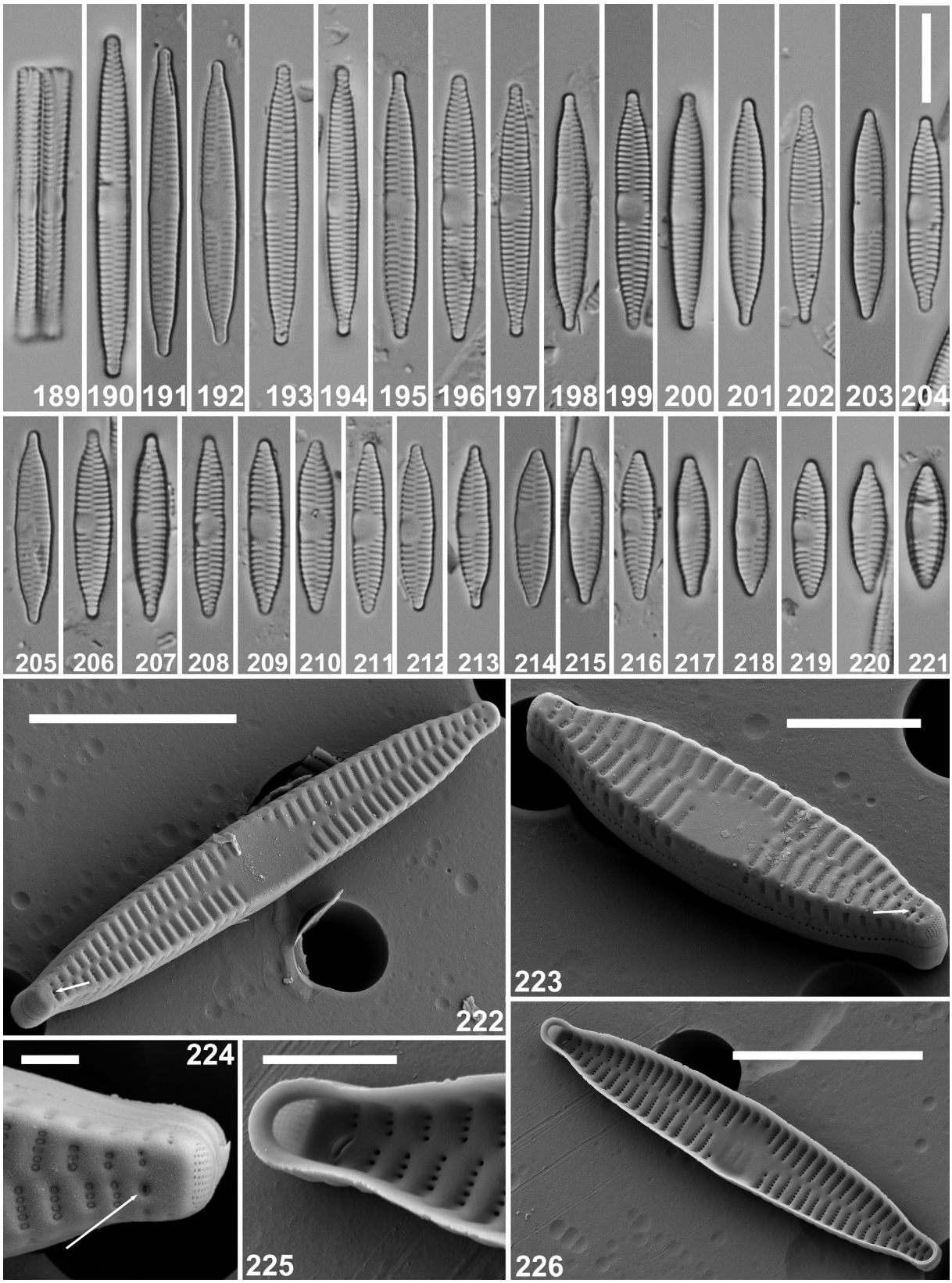


Figs 165–188. *Fragilaria truncata* (Greville) Van de Vijver et D.M.Williams comb. nov. et stat. nov., LM and SEM images taken from the lectotype material based on Greville's original material (BR–4741): (165) scan of the drawing of *Echinella fasciculata* β [var.] *truncata* Greville (Greville 1823); (166) original Greville sample in the Shuttleworth herbarium, conserved in the Natural History Museum, London (UK); (167–168) several frustules or valves in girdle view, connected in twos; (169–182) LM views of the population arranged in decreasing length; (183) SEM external view of an entire frustule in girdle view showing the different open girdle bands; (184–185) SEM external view of two entire valves; (186) SEM external detail of an apex showing irregularly placed small marginal spines, rimoportula marked by an arrow; (187) SEM internal view of an entire valve; (188) SEM internal view of valve apex showing rimoportula. Scale bars 10 µm (165–185, 187), 1 µm (186, 188).

Associated diatom flora: Delgado et al. (2016) discussed the ecological preferences of *F. rinoi*. The species was very rare in all samples where it was observed. The type sample was dominated by *Sellaphora saugerresii* (Desmazières) C.E.Wetzel et D.G.Mann(22%), *Planothidium frequentissimum* (Lange–Bertalot) Lange–Bertalot (17%), *Craticula subminuscula* (Manguin) C.E.Wetzel et Ector (13%), *Gomphonema saprophilum* (Lange–Bertalot et E.Reichardt) N.Abarca et al. (10%), and *Mayamaea permitis* (Hustedt) Bruder et Medlin (8%) with minor frequencies of *Fistulifera saprophila* (Lange–Bertalot et Bonik) Lange–Bertalot, *Encyonema ventricosum* (C.Agardh) Grunow, and *Navicula veneta* Kützing. Delgado et al. (2016) also found *Cyclotella meneghiniana* Kützing, *Nitzschia amphibia* Grunow, and *N. palea* (Kützing) W.Smith in the type material. *Fragilaria rinoi* only occurred as a proportion of 2% of the total counted valves. These taxa are typical for highly impacted, polysaprobic, strongly eutrophic waters (Lange–Bertalot et al. 2017). The two additional populations examined were observed in more or less similar conditions. The Belgian sample was dominated by *Diatoma vulgaris* Bory, *Melosira varians* C.Agardh, *Navicula tripunctata* (O.F.Müller) Bory, *Nitzschia dissipata* (Kützing) Grunow, and *N. filiformis* (W.Smith) Van Heurck together with several *Fragilaria* species,



Figs 189–226. *Fragilaria truncata* (Greville) Van de Vijver et D.M.Williams comb. nov. et stat. nov., LM and SEM images taken from Walker Arnott sample 417 (Haverfordwest, Wales, UK, BR–4742): (189) two connected frustules in girdle view; (190–221) LM views of the population arranged in decreasing length; (222–223) SEM external view of two entire valves, the arrows indicate rimoportulae; (224) SEM external detail of an apex showing rimoportula (arrow) and apical pore field; (225) SEM internal view of valve apex showing rimoportula; (226) SEM internal view of an entire valve. Scale bars 10 µm (189–223, 226), 1 µm (224, 225).

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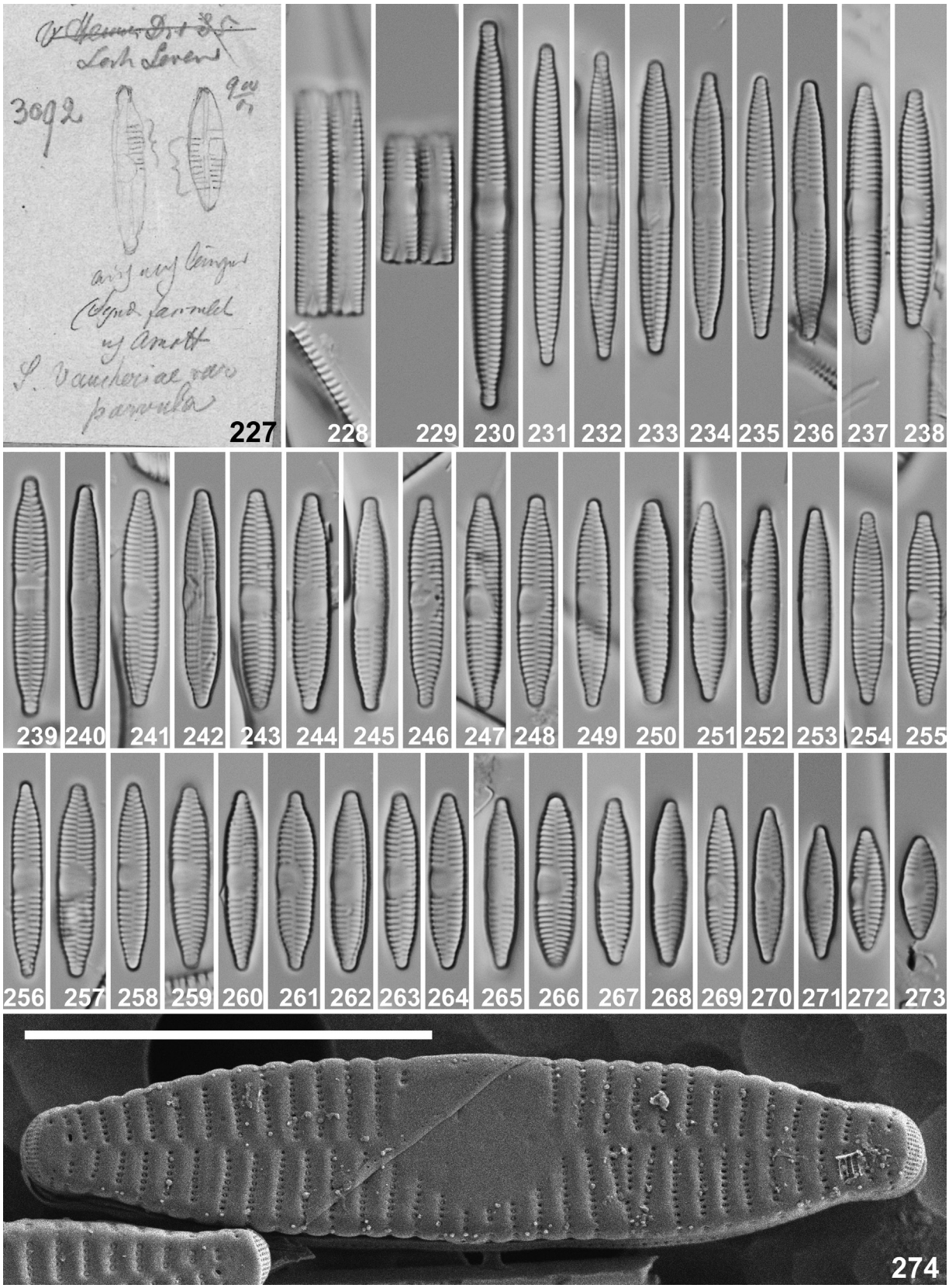
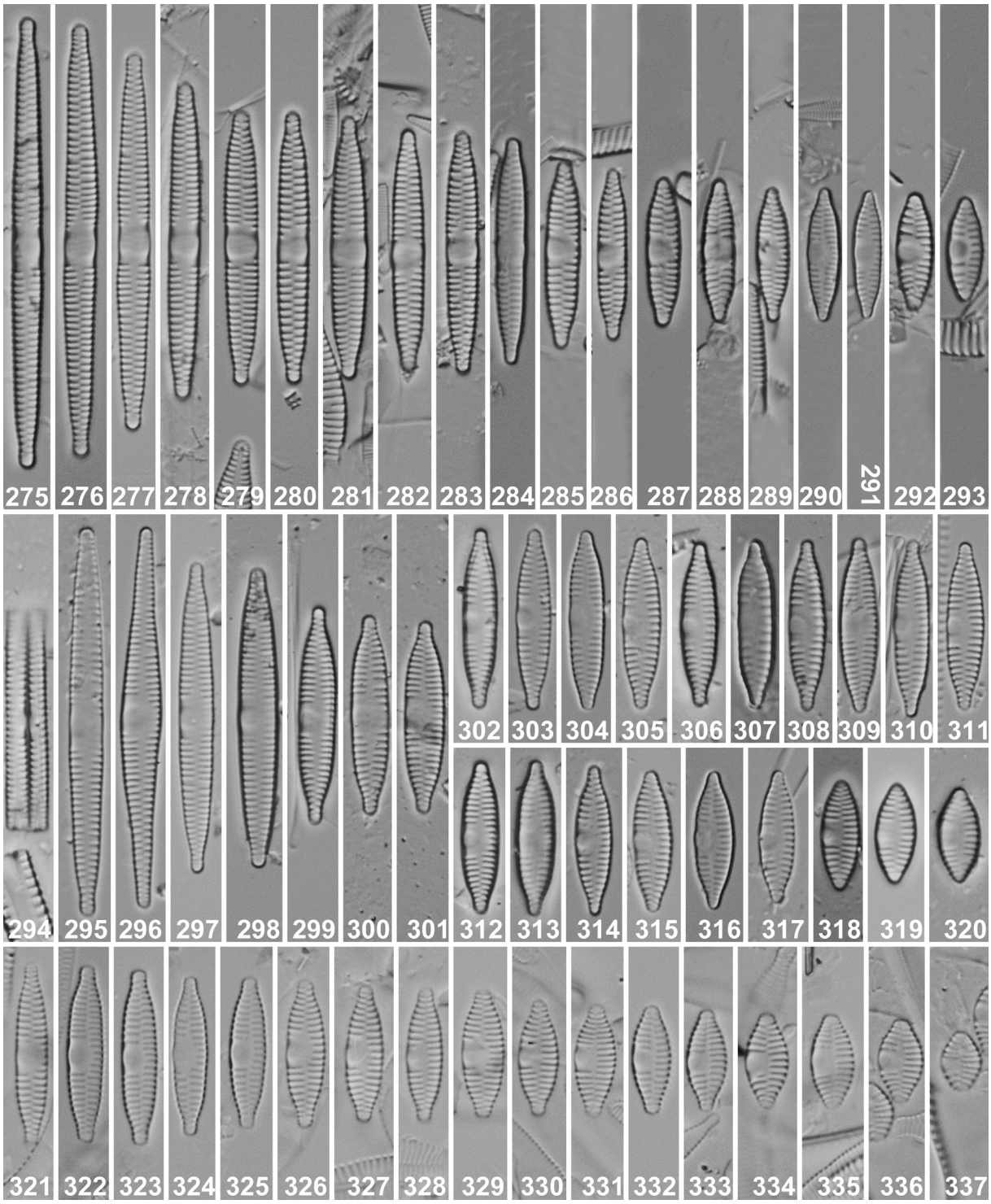


Figs 227–274. *Fragilaria truncata* (Greville) Van de Vijver et D.M.Williams comb. nov. et stat. nov., LM and SEM images taken from Walker Arnott sample 146 (Loch Leven, Kinross, Scotland, UK, BR–4743): (227) scan of the original drawing in the Grunow collection of Grunow sample 3092 (=Walker Arnott sample 146) identified by Grunow as *Synedra vaucheriae* var. *parvula*; (228–229) several frustules in girdle view, connected in twos; (230–273) LM views of the population arranged in decreasing length; (274) SEM external view of an entire valve. Scale bars 10 µm.



Figs 275–337. *Fragilaria truncata* (Greville) Van de Vijver et D.M.Williams comb. nov. et stat. nov., LM images taken from several recently collected populations: (275–293) River La Cure, Montsauche–les–Settons, Burgundy, France (BR–4744); (294–320) River Kleine Nete, Flanders, Belgium (BR–4745); (321–337) Salvan, Wallis, Switzerland (VII–12–C5); (294) represents two frustule in girdle view, connected to each other. Scale bar 10 µm.

such as *F.* cf. *vaucheriae* and *F. radians* sensu Krammer & Lange–Bertalot (1991). Less dominant, but still frequent taxa in the sample include *Ctenophora pulchella* (Ralfs ex Kützing) D.M.Williams et Round, *Gyrosigma acuminatum* (Kützing) Rabenhorst, *Luticola goeppertiana* (Bleisch) D.G.Mann, and several *Navicula* species, such as *N. cryptotenella* Lange–Bertalot and *N. gregaria* Donkin. The Austrian sample, is less species rich and (apart from *F. rinoi*) mainly contains large populations of *Encyonema* cf. *minutum* (Hilse) D.G.Mann, *Surirella minuta* Brébisson, and *Ulnaria* cf. *oxyrhynchus* (Kützing) Aboal. These species compositions also point to more

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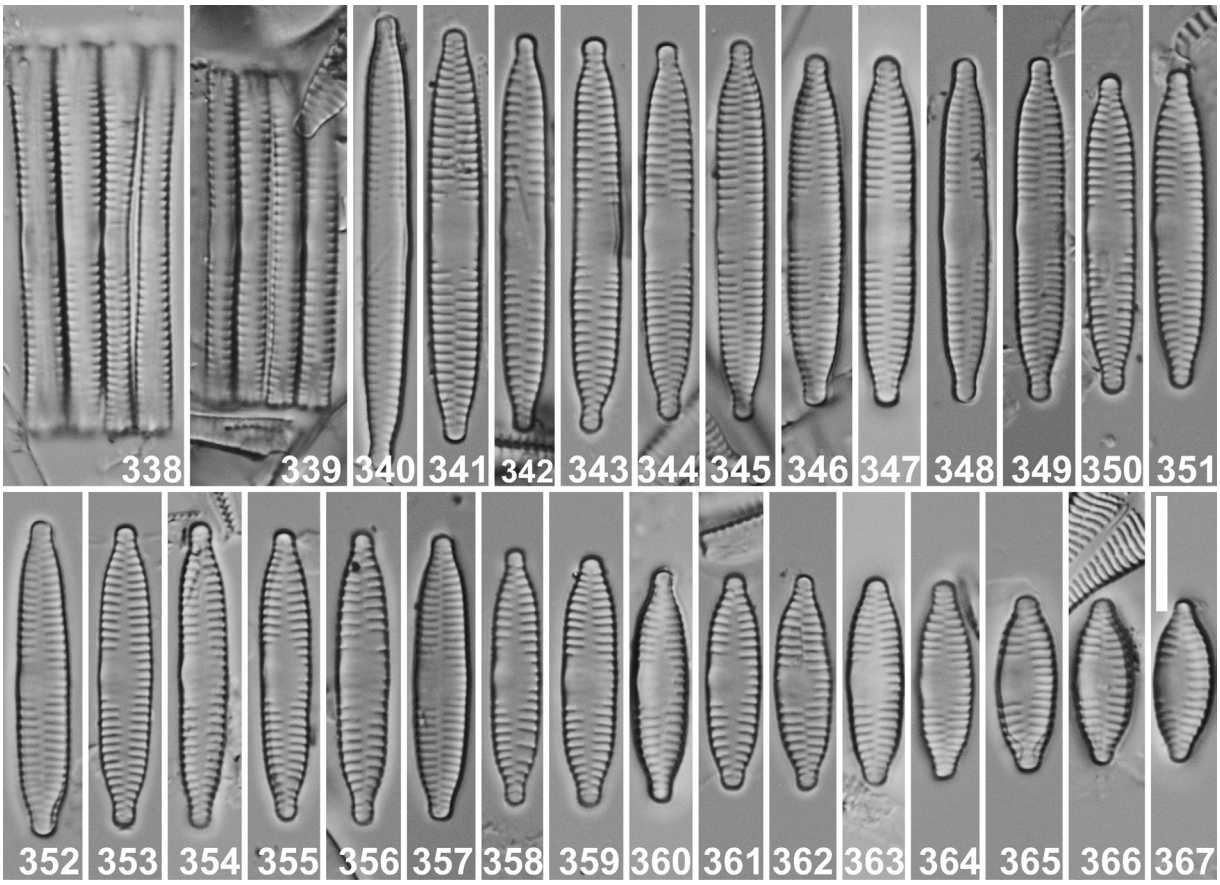


Figs 338–367. *Fragilaria catenarinoi* Van de Vijver et D.M.Williams sp. nov., LM images taken from the holotype material (Kützing sample 918, Germany, BR–4746): (338–339) frustules in girdle view, connected to each other and forming ribbon–like colonies; (340–367) LM views of the population arranged in decreasing length. Scale bars 10 µm.

eutrophic, alkaline conditions of electrolyte–enriched lakes and rivers (Lange–Bertalot et al. 2017). Only the presence of the large population of *E.* cf. *minutum* is somewhat unusual as it prefers anthropogenically less disturbed waters.

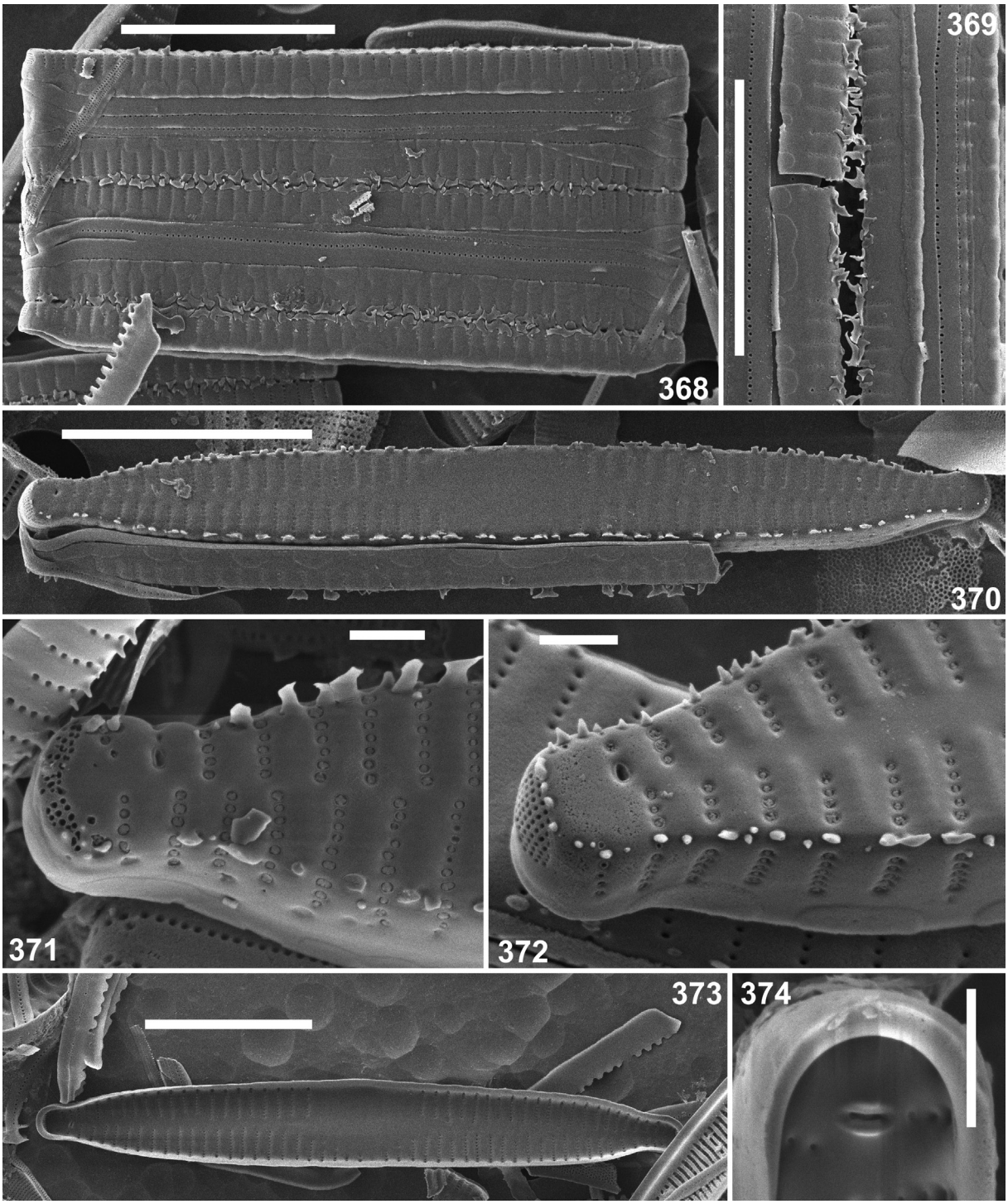
Taxonomic remarks: *Fragilaria rinoi* shows a very high similarity with *Fragilaria deformis* and differs in some minor details (Van de Vijver et al. 2020d). *Fragilaria deformis* has parallel margins in most of its cell diminution series and presents almost always clearly protracted, rostrate apices. The latter are often lacking in the type population of *F. rinoi*. Almost all smaller valves in *F. rinoi* have a lanceolate to even elliptic–lanceolate outline lacking protracted apices, whereas in *F. deformis* even the shortest valves have rostrate apices. Analysis of more populations of both species will be necessary to confirm or reject a possible conspecificity. *Fragilaria rinoi* usually has larger valves reaching 6 µm in valve width whereas in *F. deformis*, the maximum valve width observed is 5 µm.

Fragilaria truncata (Greville) Van de Vijver et D.M.Williams comb. nov. et stat. nov. (Figs 165–337)

Basionym: *Exilaria truncata* Greville (Greville 1827, Scottish Cryptogam. Flora vol. 5: p. 37) – *Echinella fasciculata* β *truncata* Greville (Greville 1823, Scottish Cryptogam. Flora vol. 1: p. 37, pl. 16, fig. 4, nom. inval.).

Lectotype (here designated): BR–4741, slide prepared from Greville, original material. The lectotype is illustrated by Fig. 170.
Registration: http://phycobank.org/103088
≡ *Diatoma truncatum* (Greville) Greville (Greville 1833: p. 407)
≡ *Synedra truncata* (Greville) Ralfs ex Pritchard (Pritchard 1861: p. 789)
≡ *Synedra vaucheriae* var. *truncata* (Greville) Rabenhorst (Rabenhorst 1864: p. 132)
≡ *Synedra vaucheriae* var. *truncata* (Greville) Grunow in Van Heurck (Van Heurck 1881, pl. 40, fig. 20)
≡ *Synedra fasciculata* var. *truncata* (Greville) R.M.Patrick (Patrick & Reimer 1966, p. 142, pl. 5, fig. 16)
≡ *Fragilaria vaucheriae* var. *truncata* (Greville) Stoermer et J.J.Yang nom. inval. (Stoermer & Yang 1969, p. 90)
≡ *Fragilaria vaucheriae* var. *truncata* (Greville) Kharitonov nom. inval. (Kharitonov 2005, p. 1701)
≡ *Fragilaria capucina* var. *truncata* (Greville) Kharitonov nom. inval. (Kharitonov 2010, p. 446)
To be excluded from synonymy
Synedra fasciculata (Kützing) Grunow (Van Heurck 1881, pl. 41, fig. 15), *Synedra tabulata* var. *fasciculata* (C.Agardh) Hustedt (Hustedt 1932, p. 218, figs 710 i–l)

LM (Figs 167–182): Frustules in girdle view rectangular, solitary or two frustules attached to each other (Figs 167, 168). Ribbon–like colonies not observed. Original Greville drawing (Fig. 165) showing valves attached to substratum, solitary or with maximally four cells together. Valves linear in longer valves to linear–lanceolate in smaller specimens with almost parallel margins throughout the entire cell diminution series. Apices weakly protracted, rostrate to sub–capitate. Valve dimensions (n=20): valve length 15–35 µm, width



Figs 368–374. *Fragilaria catenarinoi* Van de Vijver et D.M.Williams sp. nov., SEM images taken from the holotype material (Kützing sample 918, Germany, BR–4746): (368) SEM external view of several frustules in girdle view connected to each other to form a ribbon–like colony; (369) SEM detail of irregularly shaped interlocking linking spines; (370) SEM external view of an entire valve showing rimoportula position and marginal linking spines; (371–372) SEM external detail of apex showing rimoportula, apical pore field, and linking spines; (373) SEM internal view of an entire valve; (374) SEM internal view of valve apex showing rimoportula. Scale bars 10 µm (368–370, 373), 1 µm (371, 372, 374).

3.5–4.0 µm. Sternum narrow but distinct, linear. Central area large, usually unilateral with broad hyaline zone at one side of the sternum and clearly shortened striae at opposite side. Hyaline zone rarely depressed or inflated. In larger valves, central area expanded from one margin to the other, forming a large hyaline zone. Striae almost parallel in valve middle becoming weakly radiate at apices, alternating, 13–15 in 10 µm. Areolae not discernible in LM.

SEM (Figs 183–188): Frustules clearly rectangular in girdle view. Girdle composed of several open bands, bearing one row of perforations on the advalvar part (Fig. 183). Continuous series of very short, blunt, marginal spines present, running

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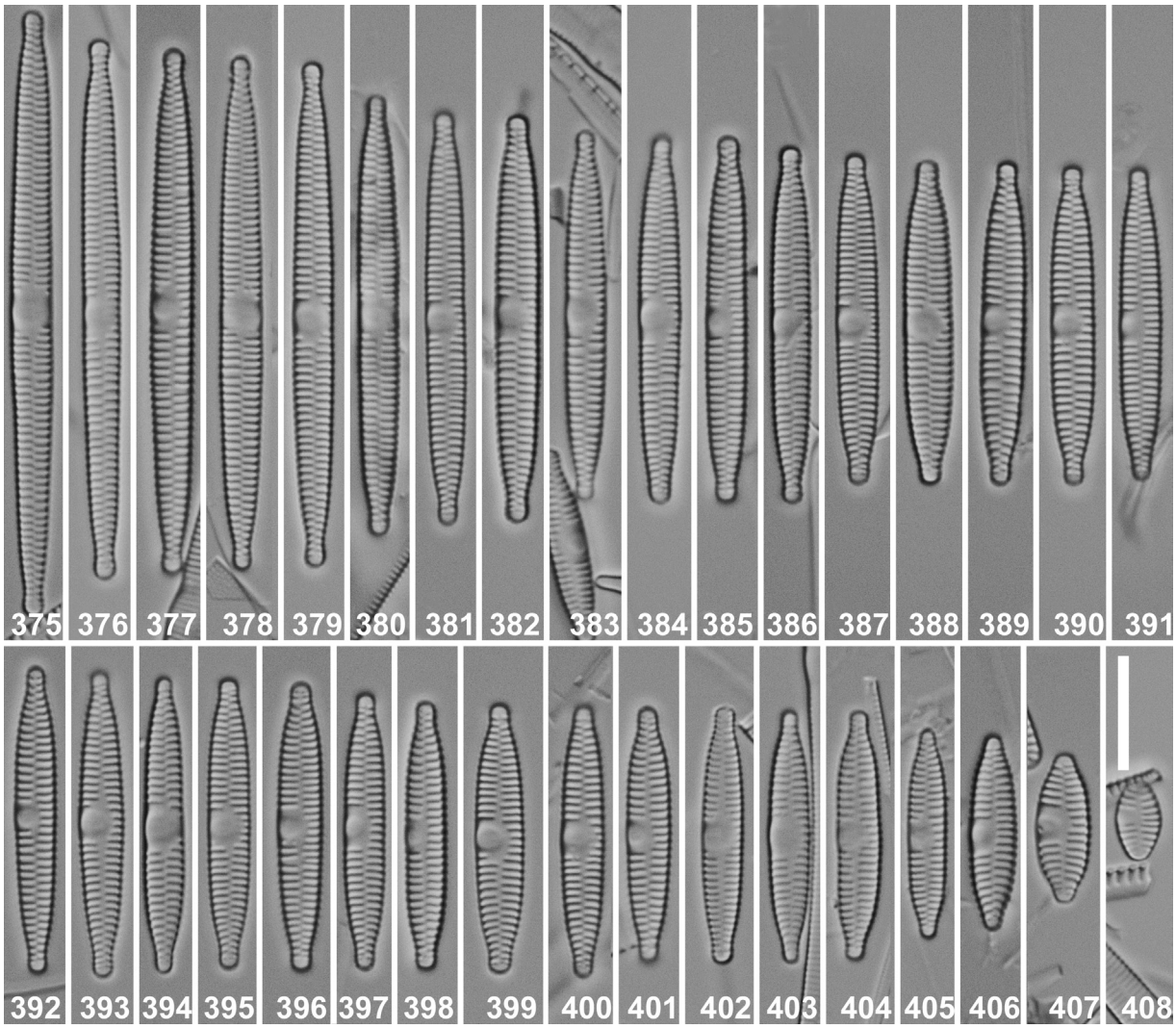
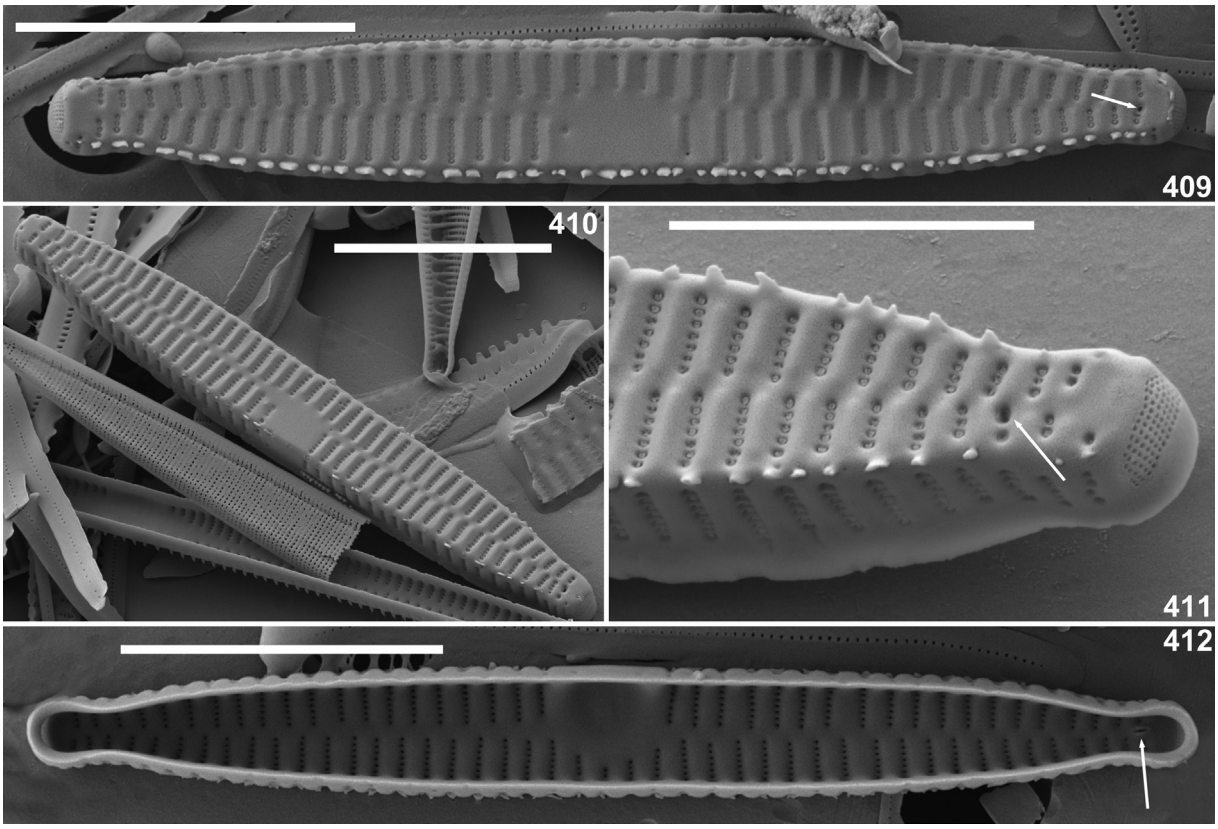


Figs 375–408. *Fragilaria kellyana* Van de Vijver, D.M.Williams et Ector sp. nov., LM images taken from the holotype material (River Don, Towie, Aberdeenshire, Scotland, UK, coll. date 15.V.2018, leg. Sarah Stenhouse, BR–4747): (375–408) LM views of the population arranged in decreasing length. Scale bar 10 μm.

from apex to apex (Figs 184, 186). Striae uniseriate, composed of very large virgae compared to the small vimines (Fig. 184). Areolae, small, rounded, externally covered by individual cribra (Fig. 185). One rimoportula present at one apex, replacing the last stria at the apex (Fig. 186, arrow). Apices devoid of striae. Apical pore field of the ocellulimbus type, large, composed of at least 6 rows of very small pores. Internally, rimoportula very large, straight (Figs 187, 188).

Additional populations: Several samples containing large populations of *Fragilaria truncata* have been examined in order to get a better idea of the morphological variability of this probably widespread species in Europe. These populations include both historic and recently collected material from various localities in the UK (Wales & Scotland), Switzerland, Belgium, and France. Two UK populations were retrieved from the historic samples from the Walker Arnott collection, kept in BR. One population was collected near Haverfordwest (Wales) by F. Okeden (Walker Arnott sample 417, Figs 189–226, BR–4742). Another UK population originated from Loch Leven near Kinross (Scotland, coll. date 7.X.1854) (Walker Arnott sample 146, Figs 227–274, BR–4743) occurring on *Cladophora*. Both populations, originally identified in the handwritten Walker Arnott catalogue (kept in BR, Belgium) as *Synedra vaucheriae*, show a similar variation in valve outline, central area with the longer valves having a larger, often entirely transverse central area, and a stria density of 15–16 striae in 10 μm. The smallest valves in both populations have a lanceolate to almost rhombic–lanceolate valve outline with less protracted, often simply cuneate apices. Larger valves have a more linear outline with parallel to only weakly convex margins. The presence of marginal spines is variable and there are valves with short, blunt spines and those lacking them.

Fragilaria truncata also occurs in mainland Europe, as populations were observed in the River La Cure in Montsauche–les–Settons (Burgundy, France, Figs 275–293, BR–4744), the River Kleine Nete (Flanders,



Figs 409–412. *Fragilaria kellyana* Van de Vijver, D.M.Williams et Ector sp. nov., SEM images taken from the holotype material (River Don, Towie, Aberdeenshire, Scotland, UK, coll. date 15.V.2018, leg. Sarah Stenhouse, BR–4747): (409) SEM external view of an entire valve showing rimoportula position (arrow) and marginal spines; (410) SEM external view of an entire valve with reduced marginal spines; (411) SEM external detail of apex showing rimoportula (arrow), apical pore field, and marginal spines; (412) SEM internal view of an entire valve, the arrow indicates the rimoportula. Scale bars 10 µm.

Belgium, Figs 294–320, BR–4745), and in an historic sample from Salvan (Kanton Wallis, Switzerland) collected by J. Brun (Figs 321–337, VII–12–C5). All populations share the morphological features highlighted above.

Associated diatom flora: The Greville type sample is almost entirely dominated by *F. truncata* and *Navicula gregaria*, the latter clearly indicating higher trophic levels and pollution–tolerant conditions (Lange–Bertalot et al. 2017). The additional samples also contain large populations of *F. truncata*. Walker Arnott sample 417 was collected from a mill overfall at the western Welsh town of Haverfordwest. The entire sample is dominated by *F. truncata* with only a few valves of *Hannaea arcus* (Ehrenberg) R.M.Patrick (identified by Walker Arnott as *Eunotia arcus*) only found after extensive scanning of the entire slide. The second Walker Arnott sample, WA146, from Scotland is slightly more diverse with high frequencies of *Cymbella proxima* Reimer, *Diatoma vulgare*, *Ulnaria* cf. *ulna* (Nitzsch) Compère (together with *F. truncata*) and smaller populations of *Cocconeis pediculus* Ehrenberg and *Encyonema silesiacum* (Bleisch) D.G.Mann. According to Lange–Bertalot et al. (2017) this points to conditions of more meso–eutrophic running water with a substantial presence of aquatic vegetation.

Taxonomic remarks: We propose that *Fragilaria truncata* likely is the name to be applied to most populations formerly and commonly identified as *F. vaucheriae*, at least in Europe. The two species can be differentiated rather easily based on their stria density and non–overlapping range. *Fragilaria vaucheriae* has a stria density of 12–13 striae in 10 µm, resulting in a rather coarse striation pattern, whereas *F. truncata* has a distinctly higher stria density with 15–16 striae in 10 µm, . This higher stria density was confirmed by analysis of a large number of *F. truncata* populations, some reported and illustrated in this paper and others reported in the literature. *Fragilaria vaucheriae* valves have a smaller central area that can reach both margins only in the largest valves. In *F. truncata*, in most valves the central area is much larger and often markedly visible as a depressed hyaline area. In middle–sized valves, a transverse hyaline central area can often be observed, which is never the case in *F. vaucheriae*. *Fragilaria rinoi* can be distinguished from *F. truncata* in having broader valves (up to 6 µm versus 3.5–4.0 µm in *F. truncata*) and a much shorter valve length (maximum 28 µm versus 35 µm in *F. truncata*). The morphological differentiation of pertinent species such as *F. rinoi*, *F. truncata*, and *F. vaucheriae* above and all newly described *Fragilaria* taxa in this paper below will be discussed in the Taxonomic remarks sections at the end of each new species.

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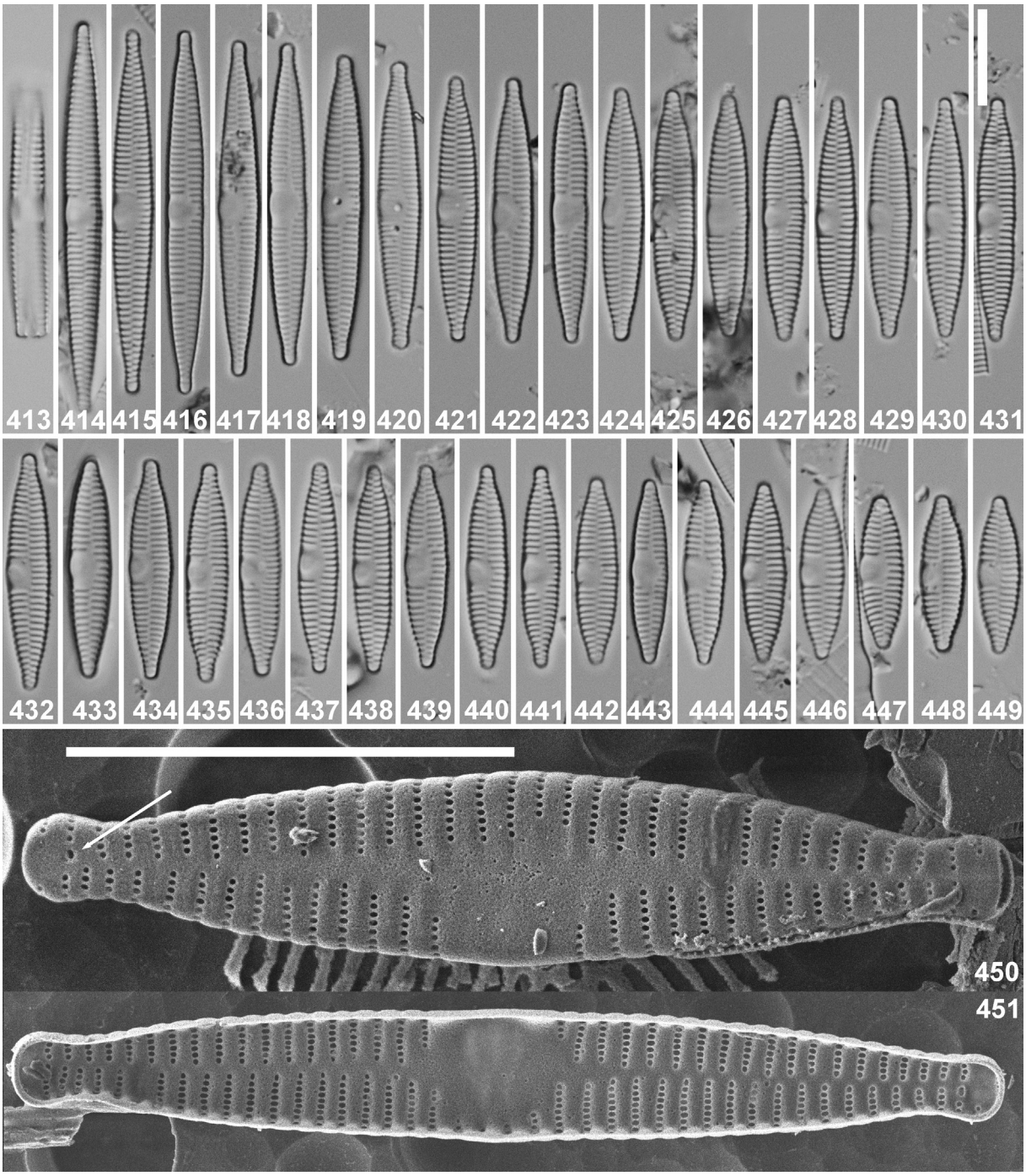
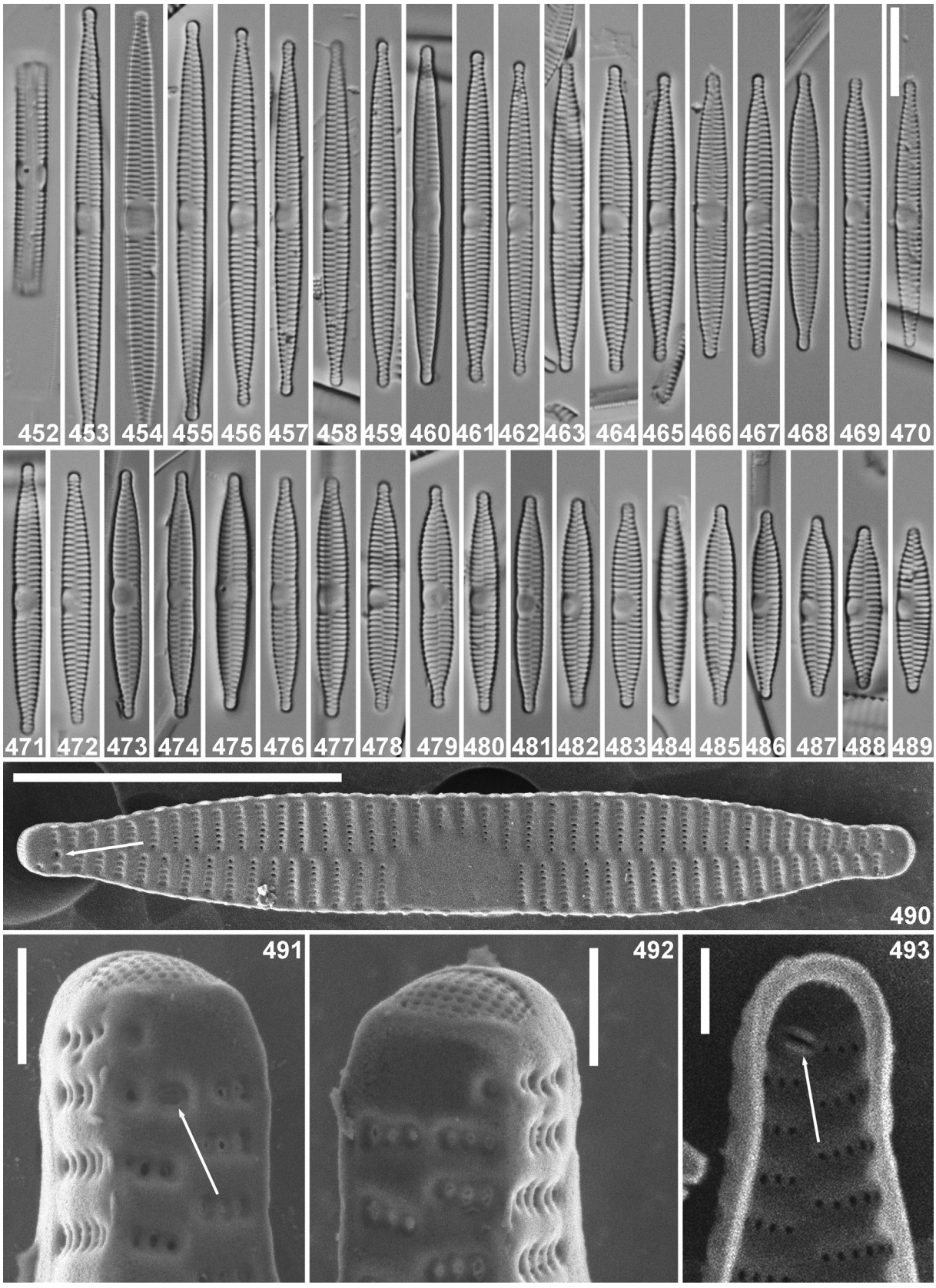


Figs 413–451. *Fragilaria landnama* Van de Vijver et Iris Hansen sp. nov., LM and SEM images taken from the holotype material (River Hörgsá, Kirkjubæjarklaustur, Iceland, coll. date 04.VII.2017, leg. I. Hansen, BR–4748): (413) frustule in girdle view; (414–449) LM views of the population arranged in decreasing length; (450) SEM external view of an entire valve; (451) SEM internal view of an entire valve. Scale bars 10 µm.

Nomenclatural remarks: The epithet *'truncata'* was initially published within the genus *Echinella* Acharius by Greville (1823). Some diatom species have been combined with *Echinella*, however, according to Nordstedt (1906) the nomenclatural type of *Echinella* actually represents a desmid (Farr & Zijlstra 1996). Thus, the genus name falls under the provision of Art. 13.1e (Turland et al. 2018) making it invalidly published as it was published before the later starting point for Desmidiaciae in 1848. When Greville (1827) intended to recombine the designation *Echinella truncata* with *Exilaria* as *Exilaria truncata*, he in fact validated the earlier published designation. However, the generic name *Exilaria* was rejected in favour of *Licmophora* C.Agardh (Wirsema et al. 2018). Thus, *Exilaria truncata* is unavailable for use (Turland et al. 2018, Ar. 56.1), but luckily the combination proposed here is available as basionym according to Art. 56.1 Note 1of the Code (Turland et al. 2018) as it was published legitimately.



Figs 452–493. *Fragilaria thingvellirensis* Van de Vijver et G.S.Jónsson sp. nov., LM and SEM images taken from the holotype material (Lake Thingvallavatn (Þingvallavatn), Midfell transect, sample depth 0.4 m, Iceland, coll. date 12.IX.2018, leg. G.S. Jónsson, BR–4749): (452) frustule in girdle view; (453–489) LM views of the population arranged in decreasing length; (490) SEM external view of an entire valve, the arrow indicates rimoportula; (491) SEM external detail of a valve apex showing rimoportula (arrow); (492) SEM external detail of valve apex without rimoportula with a clear view of the apical pore field; (493) SEM internal detail of a valve apex showing rimoportula (arrow). Scale bars represent 10 µm (452–490), 1 µm (491–493).

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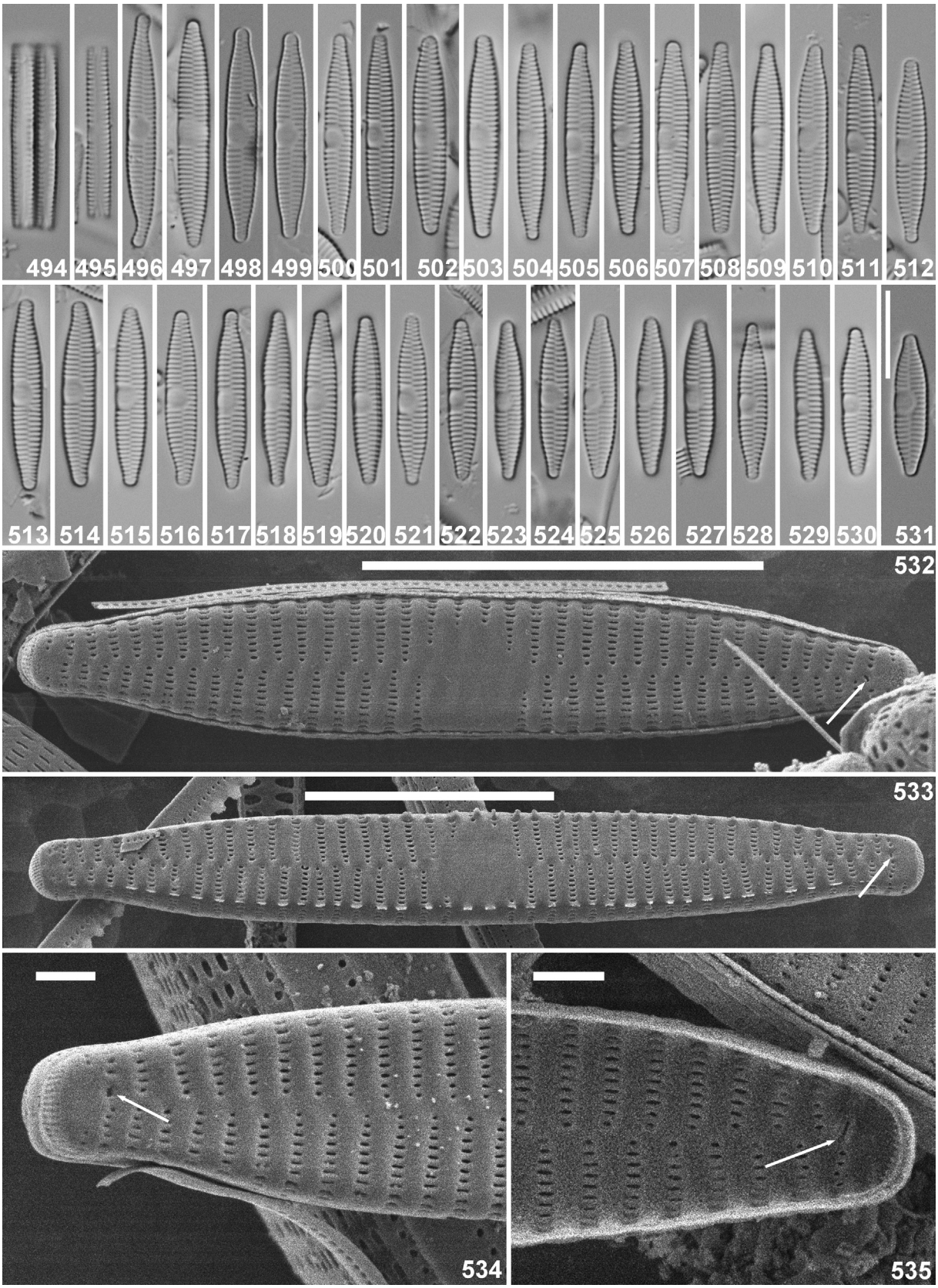
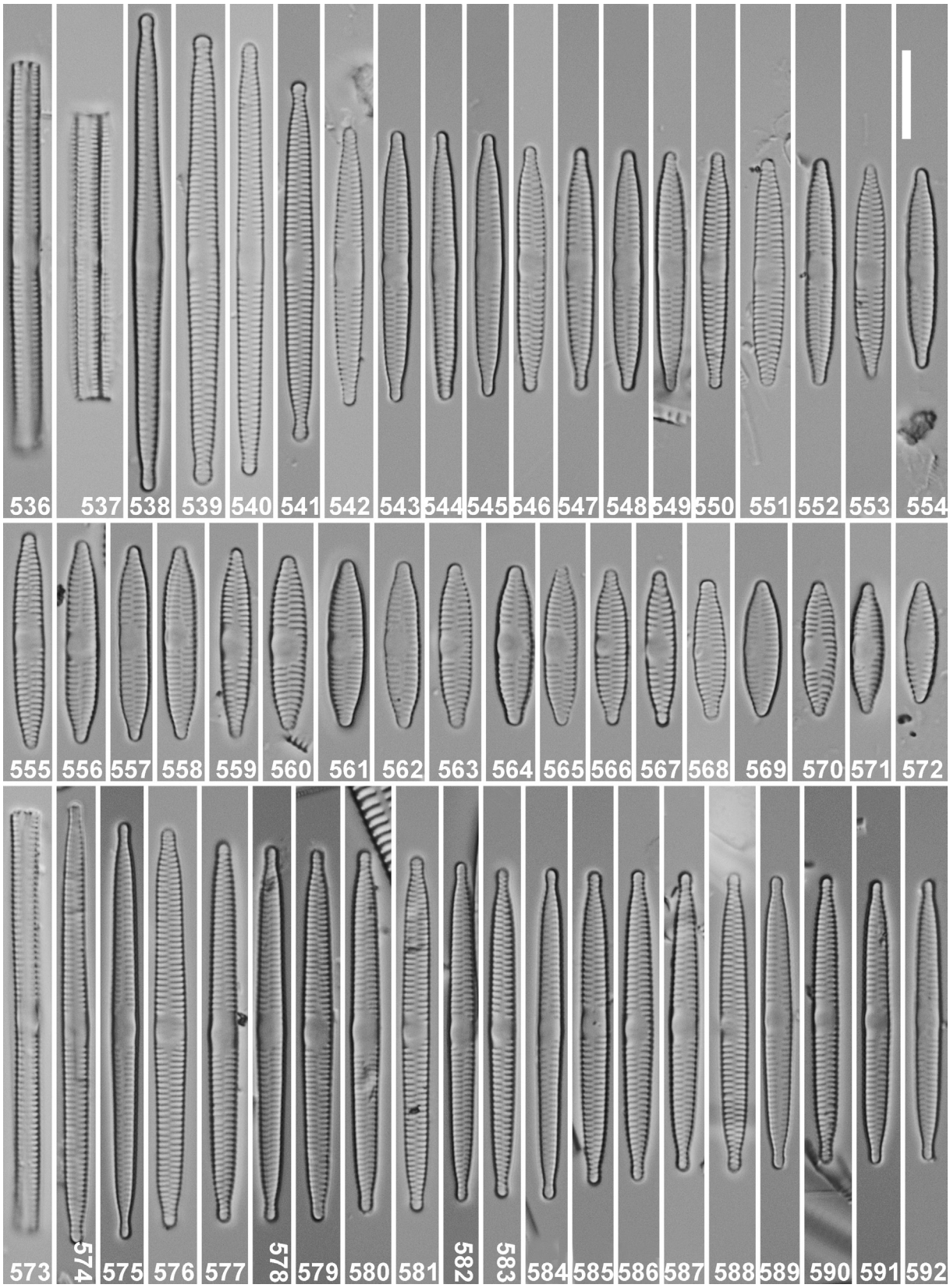


Figs 494–535. *Fragilaria vandekerckhoveana* Van de Vijver sp. nov., LM and SEM images taken from the holotype material (Walker Arnott sample 238, Duddington Loch, Edinburgh, Scotland, UK, BR–4750): (494–495) several frustules in girdle view, connected (494) or solitary (495); (496–531) LM views of the population arranged in decreasing length; (532–533) SEM external view of two entire valves, arrow indicating rimoportula; (534) SEM external detail of a valve apex showing rimoportula (arrow); (535) SEM internal detail of valve apex showing rimoportula (arrow). Scale bars 10 µm (494–533), 1 µm (534–535).



Figs 536–592. *Fragilaria vaucheriaefalsa* Van de Vijver, Kusber et D.M.Williams sp. nov., LM images taken from the holotype material (Walker Arnott sample 307, near Loch Leven, Kinross, Scotland, UK, BR–4751) (Figs 536–572) and one additional population found in an historic sample (Walker Arnott 809S, near Crofthead, Scotland, UK, BR–4752) (Figs 573–592): (536–537, 573) several frustules in girdle view, solitary (536, 573) or connected (537); (538–572, 574–592) LM views of the population arranged in decreasing length. Scale bars 10 μm.

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Newly described *Fragilaria* species

***Fragilaria catenarinoi* Van de Vijver et D.M.Williams sp. nov. (Figs 338–374)**

Registration: http://phycobank.org/103089

LM (Figs 338–367): Frustules in girdle view rectangular, connected to each other in short, ribbon–shaped chains. Valves almost strictly linear in longer specimens, becoming weakly linear–lanceolate in smaller specimens. Apices clearly but shortly protracted, rostrate along the entire cell diminution series. Valve dimensions (n=30): valve length 15–40 µm, width 3.5–5.0 µm. Sternum variable in width ranging from very narrow to moderately broad, gradually widening from the apices towards the central area. Central area large, spanning the entire valve width, in larger valves becoming unilateral, with broad, hyaline zone on one side and weakly to distinctly shortened striae on the opposite side. Ghost striae occasionally observed. Striae parallel to weakly radiate, alternating, 9–14 in 10 µm. Areolae not discernible in LM.

SEM (Figs 368–374): Large, very irregularly shaped spines present, entirely surrounding the valve margin linking neighboring valves (Figs 368–370). Striae uniseriate, composed of broadly, weekly raised virgae (Figs 370, 371). Areolae small, rounded, externally covered by small, individual cribra (Figs 371, 372). One large, oval, rimmed rimoportula present at one apex, located on the last stria, replacing some of the areolae (Figs 371, 372). Apical pore field of the ocellulimbus type, large, composed of up to seven rows of small pores, entirely located on the mantle (Fig. 372), occasionally irregularly shaped (Fig. 371). Internally, rimoportula large, transapically elongated, oblique to straight, positioned on the valve face (Figs 373, 374). Virgae only weakly raised (Fig. 373).

Holotype: BR–4746 (Meise Botanic Garden), slide prepared from Kützing sample 918. The holotype is illustrated by Fig. 345.

Isotype: slide 411 in the collection of the University of Antwerp (Belgium).

Type locality: Germany, Kützing sample 918.

Etymology: The specific epithet refers to the similarity of this species to *F. rinoi* in combination with the feature of building ribbon–like colonies. The Latin word '*catena*' means 'chain'.

Associated diatom flora: The sample is dominated by *Fragilaria catenarinoi*, *Melosira varians*, *Staurosira* cf. *binodis* Ehrenberg occurring with *Meridion circulare* (Greville) C.Agardh, *Nitzschia paleacea* (Grunow) Grunow, *Planothidium frequentissimum*, *P. lanceolatum* (Brébisson) Lange–Bertalot, *Pseudostaurosira* cf. *medlinae* D.M.Williams et E.Morales, and an unidentified species of *Staurosirella*. Most species seem to point to circumneutral to alkaline running water bodies with higher trophic and saprobity levels (Lange–Bertalot et al. 2017).

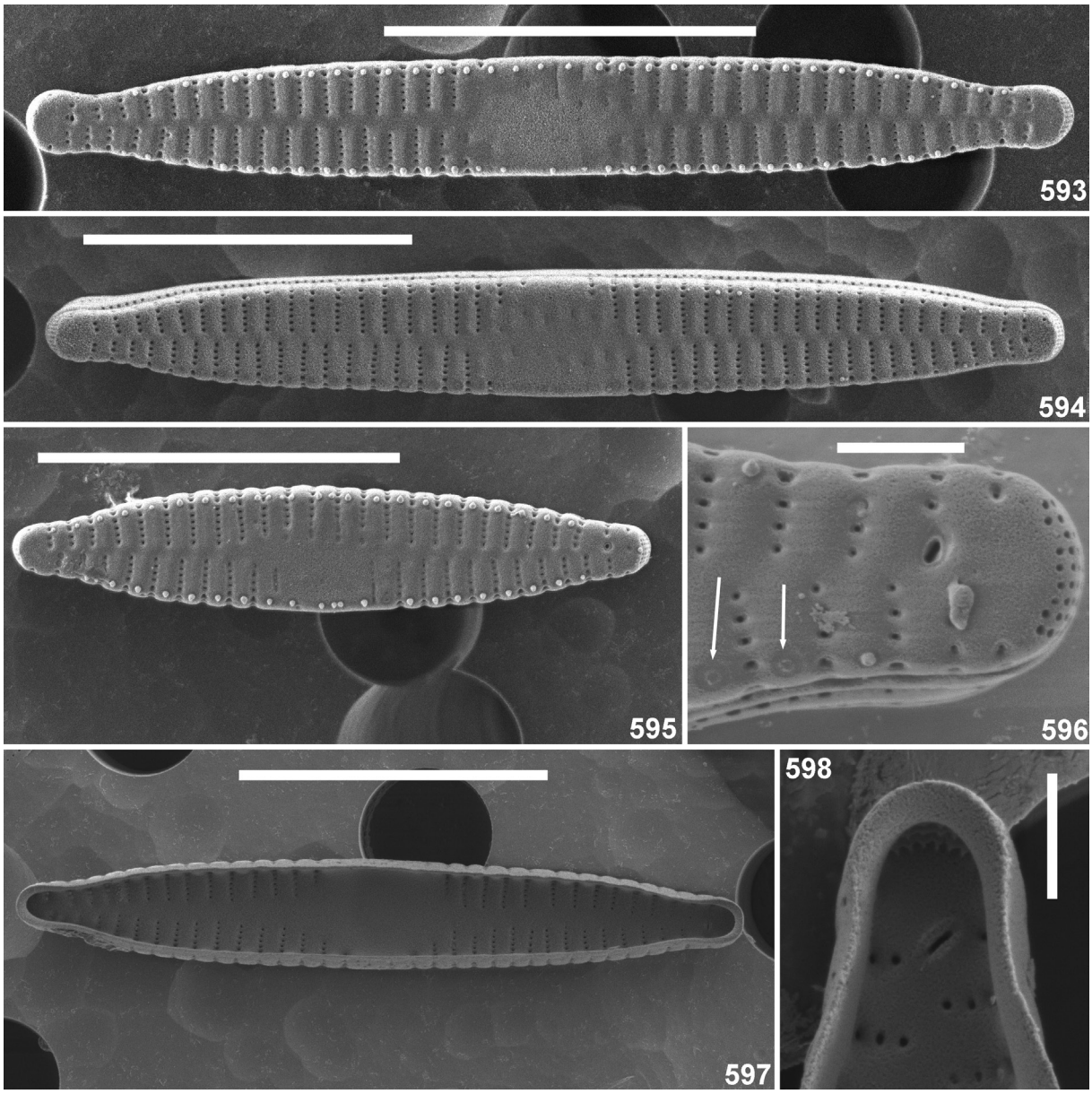
Taxonomic remarks: The smaller valves in *F. catenarinoi* are difficult to distinguish from *F. rinoi*, but when longer valves are considered, the differences become clear. *Fragilaria catenarinoi* forms ribbon–shaped colonies, composed of at least 4 connected frustules whereas all other species discussed in this paper are not known to produce colonies so far. *Fragilaria truncata* was illustrated by Greville to make colonies of up to 4 frustules maximum but the present analysis did so far not show more than two connected cells and this condition should be noted in future populations investigated. Moreover, *F. catenarinoi* has one of the lowest stria densities of all taxa discussed here. A considerable number of valves had a stria density lower than 11 striae in 10 µm. The only other species in this complex with a low stria density is *F. vaucheriae*, although its density is never below 12 in 10 µm. *Fragilaria intermedia* (synonym *F. neointermedia*) has a lower stria density (8–10 versus 9–14 striae in 10 µm) and also forms ribbon–like colonies though they are long. and It has a rimoportula positioned on the valve mantle, which is contrary to *F. catenarinoi* possessing a rimoportula on the valve face (Tuji & Williams 2013; Van de Vijver & Kusber 2022). The valve outline of *F. vaucheriaerobusta* Van de Vijver, C.E.Wetzel et Ector sp. nov. is comparable to *F. catenarinoi*, but it lacks ribbon–shaped colonies. Another colony–forming *Fragilaria* species is *F. fragilarioides* (syn. *F. distans*) but the latter has more regularly formed, almost spathulate linking spines (contrary to the irregularly shaped linking spines in *F. catenarinoi*), has narrower valves (max. 4.5 µm) and an overall more slender outlook (Van de Vijver et al. 2022a).

***Fragilaria kellyana* Van de Vijver, D.M.Williams et Ector sp. nov. (Figs 375–412)**

Registration: http://phycobank.org/103090

LM (Figs 375–408): Frustules in girdle view not observed. Valves linear to weakly linear–lanceolate with parallel margins throughout its entire cell diminution series. Apices clearly protracted, rostrate to weakly subcapitate. Valve dimensions (n=50): valve length 8–55 µm, width (3.5) 4.0–4.5 (5.0) µm. Sternum narrow, gradually widening from the apices towards the central area. Central area large, unilateral, with broad, often depressed hyaline zone on one side and weakly to distinctly shortened striae on the opposite side. Ghost striae not observed. Striae parallel almost throughout the entire valve length, weakly radiate near the apices, alternating, 14–16 in 10 µm. Areolae not discernible in LM.

SEM (Figs 409–412): Large, irregularly shaped, triangular marginal spines present, entirely surrounding the valve margin (Fig. 409). Striae uniseriate, composed of large, raised virgae compared to the small vimines (Figs 409, 410). Areolae small, rounded, externally covered by small, individual cribra (Fig. 411). One small, rimmed rimoportula present at one apex, located on the last or before last stria, replacing some of the areolae (Fig. 411, arrow). Apical pore field of the ocellulimbus



Figs 593–598. *Fragilaria vaucheriaefalsa* Van de Vijver, Kusber et D.M.Williams sp. nov., SEM images taken from the holotype material (Walker Arnott sample 307, near Loch Leven, Kinross, Scotland, UK, BR–4751): (593–595) SEM external view of three entire valves, two with marginal spines (593, 595) and one with few reduced spines (594); (596) SEM external detail of a valve apex showing rimoportula, the arrows indicate vestiges of marginal spines; (597) SEM internal view of an entire valve; (598) SEM internal detail of valve apex showing rimoportula. Scale bars 10 µm (593–595, 597), 1 µm (596, 598).

type, relatively large, composed of up to seven rows of small pores, entirely located on the mantle (Fig. 411). Internally, rimoportula large, apically elongated (Fig. 412). Virgae clearly raised (Fig. 412). Central area depressed (Fig. 412).

Holotype: BR–4747 (Meise Botanic Garden). The holotype is illustrated by Fig. 382.
Isotype: slide 412 in the collection of the University of Antwerp (Belgium).
Type locality: United Kingdom, River Don, Towie (Aberdeenshire, Scotland), coll. date 15.V.2018, leg. Sarah Stenhouse.
Etymology: The species is named after our dear colleague, Dr Martyn Kelly (Bowburn Consultancy, Durham, UK) in honor of his very important contributions to the use of diatoms for water quality monitoring.

Associated diatom flora: The sample contains a large number of species, with the dominant ones never exceeding 10% of the total valve count. Aside of *F. kellyana*, the most important species are long valves identified as *Hannaea arcus*, *Gomphonella olivaceoides* (Hustedt) Tuji, *Ulnaria* cf. *ulna*, several *Fragilaria* taxa such as *F.* cf. *gracilis* Østrup, *F. battarbeeana* Van de Vijver et al., *Achnanthidium gracillimum* (F.Meister) Lange–Bertalot, *A. pyrenaicum* (Hustedt) H.Kobayasi, *Encyonema silesiacum*, and *Odontidium mesodon* (Ehrenberg) Kützing.

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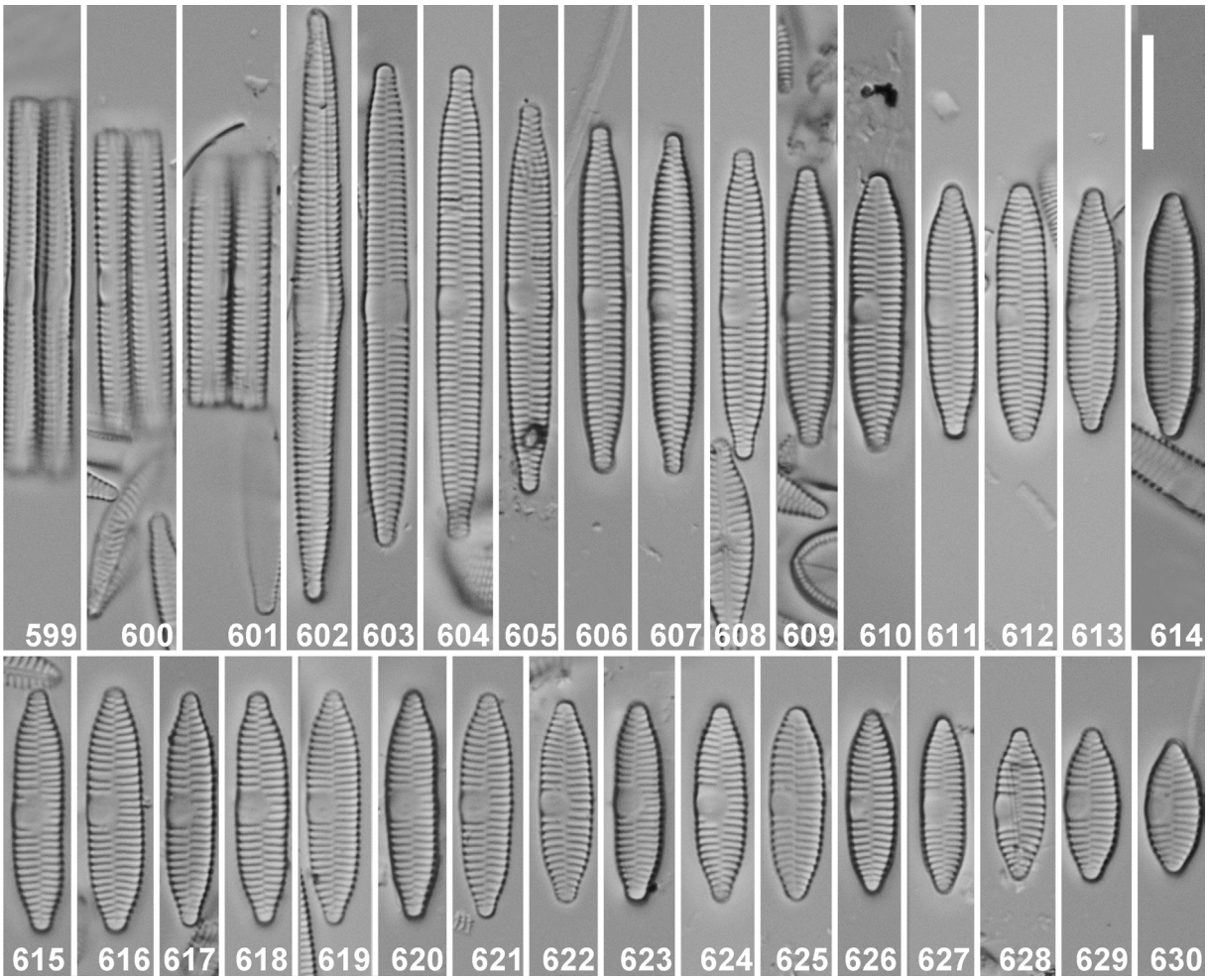


Figs 599–630. *Fragilaria vaucheriaerobusta* Van de Vijver, C.E.Wetzel et Ector sp. nov., LM images taken from the holotype material (Walker Arnott sample 238, Duddington Loch, Edinburgh, Scotland, UK, BR–4750): (599–601) several frustules in girdle view, two connected to each other; (602–630) LM views of the population arranged in decreasing length; (602) most likely represents an initial valve. Scale bar 10 µm.

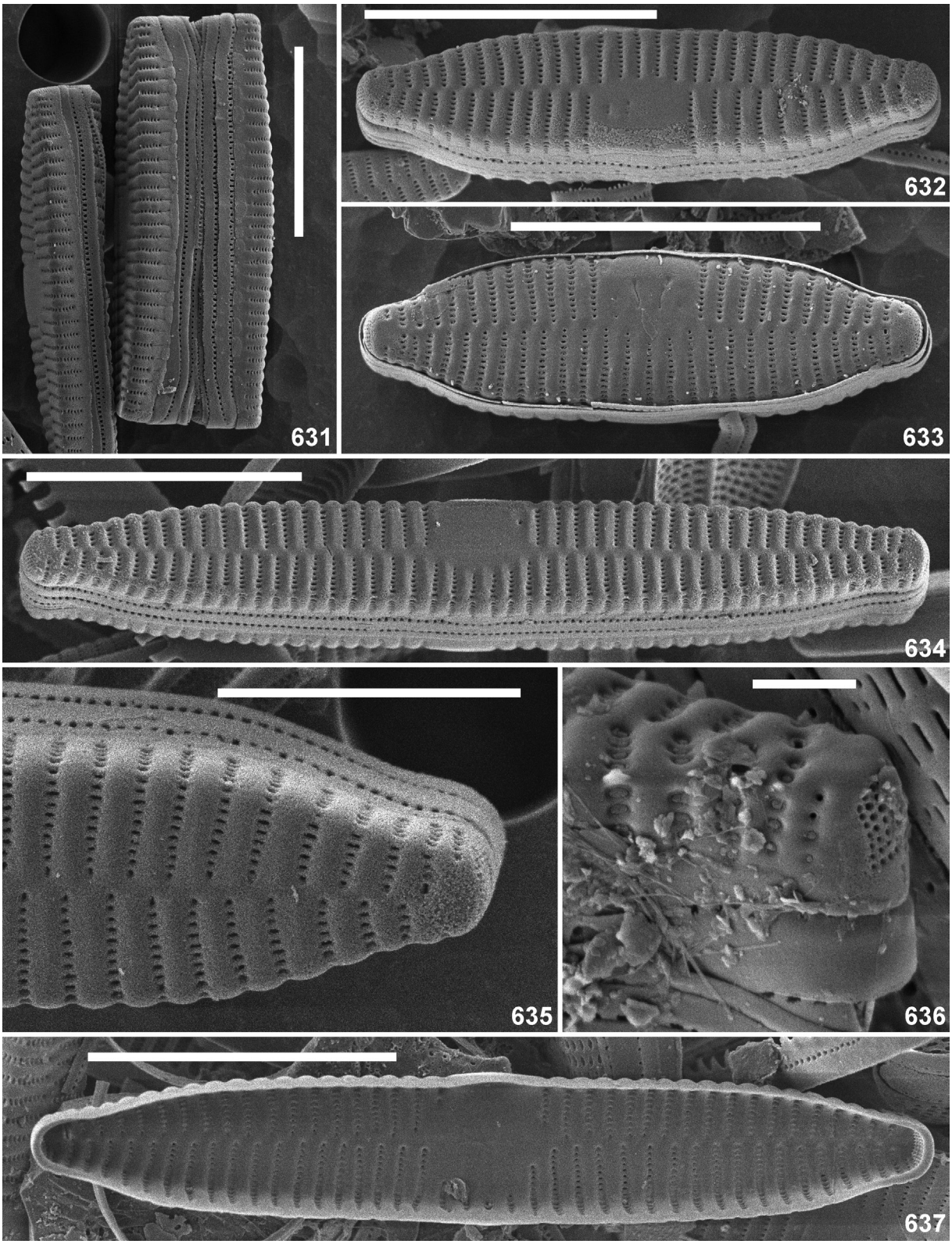
Average water chemistry of the River Don at Towie between November 1999 and December 2016 was as follows: pH: 7.7, conductivity: 124 µS.cm^{-1}, and very high levels of nitrate–N (3.34 mg.l^{-1}). The latter high values may be skewed by one or two extreme values; the average concentration of total nitrogen, by contrast, is 0.57 mg.l^{-1}.

Taxonomic remarks: *Fragilaria kellyana* is one of the more elongated species in the *F. vaucheriae* complex. The species can be separated from other taxa by its almost strictly linear, parallel margins in combination with the relatively large central area, the protracted, almost capitate apices, and the distinct marginal spines. *Fragilaria vaucheriae* possesses small, conical irregularly scattered, marginal spines whereas *F. kellyana* has broader, more regularly placed marginal spines (compare Figs 52 and 409). Moreover, *F. kellyana* has a clearly higher stria density (12–13 versus 14–16 in 10 µm). *Fragilaria rinoi* lacks the marginal spines, has broader valves (up to 6.0 µm), and a more lanceolate valve outline. *Fragilaria kellyana* can also be distinguished from the other more or less linear, new species in the current paper such as *F. thingvellirensis* Van de Vijver et G.S.Jónsson and *F. landnama* Van de Vijver et Iris Hansen, (see below). *Fragilaria batterbeeana* Van de Vijver et al., described in 2021 from the same sample, has a more lanceolate (very rarely linear) valve outline with a much higher stria density (18–19 in 10 µm) (Van de Vijver et al. 2021b). Similarly, *F. ennerdalensis* Van de Vijver et al. has a higher stria density (17–18 in 10 µm) and a linear–lanceolate valve outline lacking parallel margins (Van de Vijver et al. 2021b). The latter two species possess conical, acute marginal spines, contrary to the triangular marginal spines in *F. kellyana*.

***Fragilaria landnama* Van de Vijver et Iris Hansen sp. nov. (Figs 413–451)**

Registration: http://phycobank.org/103091

LM (Figs 413–449): Frustules in girdle view rectangular, solitary. Ribbon–shaped colonies not observed so far. Valves distinctly lanceolate to occasionally linear–lanceolate with convex margins throughout the entire valve diminution series. Apices clearly protracted, rostrate,



Figs 631–637. *Fragilaria vaucheriaerobusta* Van de Vijver, C.E.Wetzel et Ector sp. nov., SEM images taken from the holotype material (Walker Arnott sample 238, Duddington Loch, Edinburgh, Scotland, UK, BR–4750): (631) several frustules in girdle view showing the open girdle bands; (632–634) SEM external view of three entire valves; (635) SEM external detail of a valve apex showing rimoportula; (636) SEM external detail of a valve apex with a clear view of the apical pore field; (637) SEM internal view of an entire valve. Scale bars 10 µm (631–634, 637), 5 µm (635), 1 µm (636).

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only very rarely weakly subcapitate. Valve dimensions (n=30): valve length 16–40 µm, width 4.0–4.5 µm. Sternum narrow, almost not widening from the apices towards the central area. Central area large, unilateral, often buttressed with broad, often depressed hyaline zone on one side and weakly to distinctly shortened striae on the opposite side. Occasionally, central area almost entirely spanning the valve width (e.g. Fig. 423). Ghost striae not observed. Striae parallel to weakly radiate almost throughout the entire valve length, becoming more distinctly radiate at the apices, alternating, 15–17 in 10 µm. Areolae not discernible in LM.

Most diatom valves in the sample were highly eroded making good observations of valve morphology in SEM difficult. Two valves with more or less complete structure could be observed.

SEM (Figs 450–451): Marginal spines absent (even in eroded valves no spine vestiges observed so far) (Fig. 450). Striae uniseriate, composed of large, rounded areolae. Single rimoportula present almost on the sternum between the last striae (Fig. 450, arrow). Internally, central area weakly depressed (Fig. 451).

Holotype: BR–4748 (Meise Botanic Garden). The holotype is illustrated by Fig. 415.

Isotype: slide 413 in the collection of the University of Antwerp (Belgium).

Type locality: Iceland, River Hörgsá, Kirkjubæjarklaustur (South Iceland) (coll. date 04.VII.2017, leg. I. Hansen).

Etymology: The specific epithet *landnama* refers to the medieval Icelandic written work Landnámabók ('book of settlements') that describes the settlement (landnám) of Iceland by the Norse in the 9th and 10th centuries.

Associated diatom flora: The type sample from a lowland stream in southern Iceland situated northeast of Keldunúpur, is dominated by a handful of species: *Fragilaria landnama*, *Gomphonella olivacea*, *Hannaea linearis* (Holmboe) Álvarez–Blanco et S.Blanco, *Meridion circulare*, and *Nitzschia dissipata*. Less frequent species include *Encyonema silesiacum*, *Fragilaria radians* (Kützing) D.M.Williams et Round, and *Planothidium lanceolatum*. According to Lange–Bertalot et al. (2017) this diatom composition is typical for colder, fast–flowing, more alkaline rivers with higher trophic levels.

Taxonomic remarks: The smaller valves of *Fragilaria landnama* show some resemblance to *F. rinoi*, but when the entire population is considered, these species differ considerably. *Fragilaria rinoi* lacks the lanceolate, elongated valves in its cell diminution series, whereas *F. landnama* does not exceed a valve width of 4.5 µm (contrary to *F. rinoi* often reaching 6 µm). The stria density in *F. landnama* is also higher than in *F. rinoi*, with most valves having 16 striae in 10 µm and usually fewer than that in *F. rinoi*, though they can occasionally have 16. *Fragilaria battarbeeana* and *F. ennerdalensis* have conical, acute marginal spines, while there are none in *F. landnama*, and a higher stria density (up to 19 in 10 µm) (Van de Vijver et al. 2021b).

Fragilaria kellyana has parallel margins and a linear valve outline. Lanceolate valves with convex margins, as typical for *F. landnama*, have so far not been observed. In addition, the stria density in *F. landnama* is slightly higher than in *F. kellyana* (15–17 versus 14–16 in 10 µm), although this difference is almost negligible, due to the overlap. Despite only having access to eroded valves for SEM, it appears that *F. landnama* does not possess spines, contrary to *F. kellyana* that has distinct triangular spines. *Fragilaria thingvellirensis*, another new Icelandic species, differs in having a linear, instead of a lanceolate valve outline and a slightly higher stria density.

Another similar species, recorded on Iceland (Van de Vijver, pers. obs.) is *Fragilaria sandellii* Van de Vijver et Jarlman, described in 2012 from Sweden (Van de Vijver et al. 2012, 2021b). *Fragilaria sandellii* has a higher stria density (18–19 versus max. 17 in *F. landnama*) and wider valves (up to 6.0 µm) whereas the valve width in *F. landnama* never exceeds 4.5 µm.

***Fragilaria thingvellirensis* Van de Vijver et G.S.Jónsson sp. nov. (Figs 452–493)**

Registration: http://phycobank.org/103092

LM (Figs 452–489): Frustules in girdle view rectangular, solitary. Ribbon–shaped colonies so far not observed. Valves linear to linear–lanceolate with parallel to weakly convex margins. Apices clearly protracted, rostrate to subcapitate. Valve dimensions (n=40): valve length 18–50 µm, width 3.0–4.0 µm. Sternum narrow, linear not widening near the central area. Central area large, unilateral, often buttressed, with broad, often depressed hyaline zone on one side and weakly to distinctly shortened striae on the opposite side. Occasionally, central area almost entirely spanning valve width (e.g. Figs 454, 460, 468). Ghost striae not observed. Striae parallel almost throughout the entire valve length, becoming weakly radiate at the apices, alternating, 16–17 in 10 µm. Areolae not discernible in LM.

SEM (Figs 490–493): Continuous series of relatively large, narrow, marginal spines present, running from apex to apex (Fig. 490), but absent at the apices (Figs 491, 492). Striae located in depressed grooves, uniseriate, composed of large, raised virgae compared to the small vimines (Fig. 490). Areolae small, rounded (Figs 491, 492). One small, rimmed rimoportula present at one apex, located on the last stria, replacing some of the areolae (Figs 490, 491, arrow). Apical pore field of the ocellulimbus type, very large, composed of up to eight rows of small pores, entirely located on the mantle (Figs 491, 492). Internally, rimoportula large, apically elongated (Fig. 493).

Holotype: BR–4749 (Meise Botanic Garden). The holotype is illustrated by Fig. 461.

Isotype: slide 414 in the collection of the University of Antwerp (Belgium).

Type locality: Iceland, Lake Thingvallavatn (Þingvallavatn),

Table 2. Comparison table of all *Fragilaria* taxa discussed in this paper.

	Fragilaria vaucheriae	***Fragilaria rinoi***	***Fragilaria truncata***	***Fragilaria catenarinoi***	***Fragilaria kellyana***
original reference	Kützing 1833	Delgado et al. 2016	Greville 1827	this study	this study
Figures	1–58	59–164	165–337	338–374	375–412
colonies	no	no	no	**short, ribbon–shaped**	no
length (µm)	12–50	6–28	15–35	15–40	8–55
width (µm)	3.5–4.5	**4.5–6.0**	3.5–4.0	3.5–5.0	(3.5)4.0–4.5(5.0)
valve outline	**linear in longer valves to linear–lanceolate in smaller specimens with almost parallel to (in smaller specimens) weakly convex margins**	linear in the longest valves, but most valves lanceolate to elliptic–lanceolate with clearly convex margins	linear in longer valves to linear–lanceolate in smaller specimens	almost strictly linear in longer specimens, becoming weakly linear–lanceolate in the smaller specimens	linear to weakly linear–lanceolate with parallel margins
apices	clearly protracted, rostrate to sub–capitate	protracted, rostrate, not (sub–) capitate	weakly protracted, rostrate to sub–capitate	clearly but shortly protracted, rostrate	clearly protracted, rostrate to weakly subcapitate
sternum	very narrow but distinct, gradually widening from apices to central area	narrow at the apices, gradually widening towards the central area	narrow but distinct, linear	variable in width ranging from very narrow to moderately broad, gradually widening from the apices towards the central area	narrow, gradually widening from the apices towards the central area
central area	unilateral with broad hyaline zone (rarely depressed or inflated) at one side of the sternum and only very weakly shortened striae at opposite site.	large, unilateral with hyaline zone at one side of the sternum and moderately to strongly shortened striae at opposite site with valves possessing broad central area extending from one margin to another, rarely present	**large, usually unilateral with broad hyaline zone (rarely depressed or inflated) at one side of the sternum and clearly shortened striae at opposite site, in larger valves, central area expanded forming a large, transverse hyaline zone**	large, spanning the entire valve width in larger valves becoming unilateral, with broad, hyaline zone on one side and weakly to distinctly shortened striae on the opposite side	**large, unilateral, with broad, often depressed hyaline zone on one side and weakly to distinctly shortened striae on the opposite side**
ghost striae	occasionally present	absent	absent	occasionally present	absent
striae in 10 µm	**12–13**	14–16	13–14	**9–14**	14–16
rimoportulae per valve	1	1	1	1	1
spines	Short, conical, non–linking marginal spines	**absent, papillae occasionally present**	Continuous series of very short, blunt, marginal spines present	**large, very irregularly shaped, spines present, entirely surrounding the valve margin linking neighboring valves**	Large, irregularly shaped, triangular marginal spines present

Table 2. Comparison table of all *Fragilaria* taxa discussed in this paper (cont.).

	Fragilaria landnama	***Fragilaria thingvellirensis***	***Fragilaria vandekerckhoveana***	***Fragilaria vaucheriaefalsa***	***Fragilaria vaucheriaerobusta***
original reference	this study	this study	this study	this study	this study
Figures	413–451	452–493	494–535	536–598	599–637
colonies	no	no	no	no	no
length (µm)	16–40	18–50	16–28	18–50	12–55
width (µm)	4.0–4.5	3.0–4.0	3.0–4.0	3.0–4.0	**4.0–5.0**
valve outline	distinctly lanceolate to occasionally linear–lanceolate with convex margins	linear to linear lanceolate with parallel to weakly convex margins	linear to weakly linear–lanceolate with almost parallel margins	linear to linear lanceolate with parallel to weakly convex margins	**linear to weakly linear–lanceolate with almost strictly parallel margins, smallest valves with more lanceolate valve outline**
apices	clearly protracted, rostrate, only very rarely weakly subcapitate	clearly protracted, rostrate to subcapitate	weakly protracted, broadly rounded and shortly rostrate to subrostrate	clearly protracted, rostrate to subcapitate	weakly protracted, broadly rounded, rostrate to subrostrate.
sternum	narrow, almost not widening from the apices towards the central area	narrow, linear not widening near the central area	very narrow, linear, not widening towards the central area	narrow, linear not widening near the central area	narrow, almost not widening near the central area
central area	**large, unilateral, often buttressed with broad, depressed hyaline zone on one side and weakly to distinctly shortened striae on the opposite side, occasionally, central area almost entirely spanning the valve width**	large, unilateral, often buttressed, with broad, often depressed hyaline zone on one side and weakly to distinctly shortened striae on the opposite side, occasionally, central area almost entirely spanning the valve width	area large, unilateral, with broad, often depressed hyaline zone on one side and weakly to distinctly shortened striae on the opposite side	large, unilateral, often buttressed, with broad, often depressed hyaline zone on one side and weakly to distinctly shortened striae on the opposite side, occasionally, central area almost entirely spanning the valve width	large, strictly unilateral, with broad, often depressed hyaline zone on one side and weakly to distinctly shortened striae on the opposite side
ghost striae	absent	absent	ocassionally present	absent	ocassionally present
striae in 10 µm	15–17	**16–17**	**18–19**	16–17	15–16
rimoportulae per valve	1	1	1	1	1
spines	absent	continuous series of relatively large, narrow, marginal spines present	usually absent, rarely valves with large, triangular marginal spines present, running almost from apex to apex, but absent at the apices	**continuous series of relatively large, narrow, marginal spines present**	small in the type population, irregularly shaped, well–developed in conspecific populations

Midfell transect, sample depth 0.4 m (64°10.077' N, 21°03.983' W, coll. date 12.IX.2018, leg. G.S. Jónsson).
Etymology: The specific epithet *thingvellirensis* refers to Thingvellir (Þingvellir), the name of the old parliament site (Alþingi) and now the name of the national park where Lake Thingvallavatn (Þingvallavatn) is located. This is the largest natural lake in Iceland and where the type sample was collected.

Associated diatom flora: The type sample was collected at a depth of 0.4 m of Lake Thingvallavatn. In his ecological analysis of the lake, Jónsson (1987) observed that after the disappearance of the winter ice in early spring, the ice–freed stones and boulders were rapidly colonized by *Ulothrix* species down to 40 cm depth. Below, and between the *Ulothrix* filaments, diatoms were first noticed as tufts of stalked species, growing to form a continuous bottom cover in late May. Dominant species in the sample include several species of *Ulnaria* identified as *Synedra joursacensis* Héribaud (most likely belonging to the genus *Ulnaria*; Van de Vijver, pers. obs.), *Cymbella neocistula* var. *islandica* Krammer, *Epithemia turgida* (Ehrenberg) Kützing, *Gomphonema* cf. *rhombicum* M.Schmidt, and *Nitzschia* cf. *perminuta* (Grunow) Peragallo.

Taxonomic remarks: *Fragilaria thingvellirensis* is one of the more elongated members of the *F. vaucheriae* complex showing linear valves throughout its entire cell diminution cycle. The new species can be separated from *F. kellyana*, another linear species, in having a higher stria density (16–17 versus 14–16 in 10 µm), a slightly lower valve width (3–4 versus 4–4.5 µm), and longer protracted apices. The other new Icelandic species, *F. landnama*, differs in possessing a strictly lanceolate (contrary to a linear to linear–lanceolate) valve outline and a slightly higher valve width (4–4.5 µm). *Fragilaria battarbeeana* and *F. ennerdalensis* have a higher stria density (up to 19 in 10 µm), larger marginal spines, and a more lanceolate valve outline (Van de Vijver et al. 2021b).

Fragilaria vandekerckhoveana Van de Vijver sp. nov. (Figs 494–535)

Registration: http://phycobank.org/103093
LM (Figs 494–531): Frustules in girdle view rectangular, solitary or two valves connected to each other (Figs 494, 495). Up to now, ribbon–shaped colonies not observed. Valves linear to weakly linear–lanceolate with almost parallel margins throughout the entire cell diminution series. Apices weakly protracted, broadly rounded and shortly rostrate. Valve dimensions (n=30): valve length 16–28 µm, width 3.0–4.0 µm. Sternum very narrow, linear, not widening towards the central area. Central area large, unilateral, with broad, often depressed hyaline zone on one side and weakly to distinctly shortened striae on the opposite side. Ghost striae occasionally observed (Fig. 497). Striae parallel almost throughout the entire valve length, very weakly radiate near the apices, alternating, 18–19 in 10 µm. Areolae not discernible in LM.
SEM (Figs 532–535): Most valves lacking marginal spines (Figs 532, 534). Occasionally, valves present (< 1% of total population) with large, irregularly triangular–shaped, marginal spines running almost from apex to apex, but absent at the apices (Fig. 533). Striae uniseriate, composed of large, raised virgae compared to the small vimines (Fig. 532). Areolae small, apically elongated (Figs 532–534). One, more or less isolated, small rimoportula present at one apex, located on the sternum (Figs 532–534, arrows). Apical pore field of the ocellulimbus type, fairly large, composed of several long, parallel rows of small pores (Fig. 534). Internally, rimoportula obliquely positioned (Fig. 535).

Holotype: BR–4750 (Meise Botanic Garden). The holotype is illustrated by Fig. 506.
Isotype: slide 415 in the collection of the University of Antwerp (Belgium).
Type locality: United Kingdom, Duddingston Loch, Edinburgh, Scotland, Walker Arnott 238 (leg. Dr. Gregory)
Etymology: The species is named after my dear colleague Mr. Omer Van de Kerckhove, botanical illustrator and mycologist at Meise Botanic Garden (Belgium) in honor of his lifelong and important contributions to nature conservation in Belgium.

Associated diatom flora: The type slide is mainly composed of (at present unidentified) *Fragilaria* taxa (*F.* cf. *radians*, *F. vandekerckhoveana*, *F. vaucheriaerobusta*) as well as *Cocconeis euglypta* Ehrenberg, *C. pediculus*, *Gomphonella olivacea*, different species of *Navicula* (*N. gregaria*, *N. metareichardtiana* Lange–Bertalot et Kusber, *N. tripunctata*), and *Rhoicosphenia abbreviata*. This species composition indicates that the sample was most likely collected from submerged filamentous macroalgae such as *Cladophora*, because diatom species such as *R. abbreviata* and both *Cocconeis* species are typical for this habitat. It also points to rather alkaline, eutrophic conditions with a high electrolyte content (Lange–Bertalot et al. 2017). Most taxa seen occur up to the β–α–mesosaprobic level.

Taxonomic remarks: *Fragilaria vandekerckhoveana* is one of the smaller species in this complex and the only species discussed in the present paper that has broadly rounded, only weakly protracted, rostrate to subrostrate apices. The species also possesses the highest stria density (up to 19 striae in 10 µm) compared to all other species described here. It resembles slightly smaller specimens of *F. malouana* Van de Vijver et Jarlman, but the latter can be separated based on its lanceolate valve outline, regular, conical marginal spines, and usually much longer valve length (up to 70 µm). *Fragilaria vaucheriae* and *F. truncata* can be distinguished from it by their much coarser striation pattern, never exceeding 15 striae in 10 µm. *Fragilaria*

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misarelensis S.F.P.Almeida et al., described in 2019 from Portugal, has slightly wider valves (3.5–5.0 µm) and a typically rhombic–lanceolate valve outline (Novais et al. 2019). Another recently described species, *F. vaucheriaeraetica* Cantonati et Lange–Bertalot, can be distinguished by the lower stria density (16–18 in 10 µm), the round (and not apically elongated) areolae and its lanceolate valve outline, mostly typical for the smaller specimens (Cantonati et al. 2019). *Fragilaria pectinalis* (O.F.Müller) Lyngbye sensu Van de Vijver et al. (2020d) (not sensu Wetzel & Ector 2015) shows some resemblance, but can be differentiated by a lower stria density (14–15, very rarely up to 18 striae in 10 µm) and a larger valve width (up to 5.0 µm).

***Fragilaria vaucheriaefalsa* Van de Vijver, Kusber et D.M.Williams sp. nov. (Figs 536–598)**

Registration: www.phycobank.com/103094

LM (Figs 536–572): Frustules in girdle view rectangular, solitary, occasionally two (or potentially more) connected. Long, ribbon–shaped colonies not observed so far. Valves linear to weakly linear–lanceolate with parallel margins in longer valves, becoming more lanceolate in shorter specimens. Apices weakly protracted, broadly rounded, subrostrate to rostrate. Longer specimens with more subcapitate apices. Valve dimensions (n=30): valve length 16–55 µm, width 3.0–4.0 µm. Sternum narrow, weakly widening near the central area. Central area large, forming a transverse hyaline zone in longer specimens. In smaller valves central area unilateral, with broad, often depressed hyaline zone on one side and weakly to distinctly shortened striae on the opposite side. Ghost striae occasionally observed (Fig. 551). Striae parallel to weakly radiate almost throughout the entire valve length, more radiate near the apices, alternating, 14–16 in 10 µm. Areolae not discernible in LM.

SEM (Figs 593–598): Continuous series of small but distinct, conical marginal spines running from apex to apex (Figs 593–595) but absent on the apices. Removed spines visible by distinct, round, basal marking between the striae (Fig. 596, arrows). Striae uniseriate, composed of large, markedly raised virgae compared to the small vimines (Figs 593–595). Areolae small, more or less rounded (Fig. 596). One small, rimmed rimoportula present at one apex, located on the last stria, replacing some of the areolae (Fig. 596). Apical pore field of the ocellulimbus type, large, composed of a large number of rows of small pores, weakly continuing on the valve face (Fig. 596). Internally, rimoportula large, elongated, straight (Fig. 597) or obliquely positioned. Virgae weakly raised (Fig. 598).

Additional populations: During the survey, another Scottish population was observed in an historic Walker Arnott sample, WA809S, collected near Crofthead, south of Glasgow, Scotland (Figs 573–592, BR–4752). This population differs slightly from the type population in the absence of smaller specimens. Only longer valves with a large, almost completely transverse central area could be observed.

Holotype: BR–4751 (Meise Botanic Garden). The holotype is illustrated by Fig. 543.

Isotype: slide 416 in the collection of the University of Antwerp (Belgium).

Type locality: United Kingdom, Scotland, Kinross, near Loch Leven, Walker Arnott sample 307.

Etymology: The specific epithet refers to the similarity to *F. vaucheriae*.

Associated diatom flora: Aside form *F. vaucheriaefalsa*, the type sample is dominated by several small–celled araphid species such as *Pseudostaurosira pseudoconstruens* (Marciniak) D.M.Williams et Round, *P. robusta* (Fusey) D.M.Williams et Round, and *Staurosira construens* Ehrenberg, as well as *Amphora ovalis* (Kützing) Kützing, *Encyonema silesiacum*, *E. minutum*, *F. vaucheriaefalsa*, *Navicula metareichardtiana*, and *Nitzschia fonticola* Grunow. Another sample Walker Arnott sample 809S, contains large populations of *Ulnaria ulna*, *Achnanthidium affine* (Grunow) Czarnecki, *Cymbella cymbiformis* C.Agardh, *C. hustedtii* Krasske, and *Gomphonema acuminatum* Ehrenberg in addition to *F. vaucheriaefalsa*. According to Lange–Bertalot et al. (2017) this is a rather mixed composition of more oligo– to mesotraphent and rather eutraphent species. The composition also points to more alkaline (even calcium–bicarbonate), mesosaprobic conditions.

Taxonomic remarks: Looking at their shape, the longer valves of *Fragilaria vaucheriaefalsa* seem to differ from the smaller specimens. However, when considering the entire cell diminution series, a continuum can be observed between the longer and the shorter valves. In addition, both groups show similar features such as stria density, the presence of small, conical spines, a similar valve surface with rather well raised virgae and a similar valve width.

Fragilaria vaucheriaefalsa can be distinguished from the other species in the *F. vaucheriae* complex by the presence of the conical spines, since none of the discussed species possess similar spines. *Fragilaria battarbeeana*, recently described from the United Kingdom (Van de Vijver et al. 2021b), shows identical spines (and spine vestiges, see Van de Vijver et al. 2021b, figs 218 & 219), but has a much higher stria density (18–19 striae in 10 µm) and a typically lanceolate valve outline. Species in the *F. capucina* complex, such as *F. capucina* or *F. nevadensis* Linares–Cuesta et Sánchez–Castillo, form long, ribbon–shaped colonies, contrary to *F. vaucheriaefalsa* where colonies so far have not been observed. *Fragilaria vandekerckhoveana* presents some similarities but has a different spine structure (absent to broad flattened versus small, conical; see Figs 532 versus 595), and more apically elongated areolae, contrary to *F. vaucheriaefalsa* that has rounded areolae.

***Fragilaria vaucheriaerobusta* Van de Vijver, C.E.Wetzel et Ector sp. nov. (Figs 599–685)**

Registration: http://phycobank.org/103095

LM (Figs 599–630): Frustules in girdle view rectangular, solitary or two valves. Ribbon–like colonies not observed. Valves linear to weakly linear–lanceolate with almost strictly parallel margins throughout its entire cell diminution series. Smallest valves with more lanceolate valve outline. Apices weakly protracted, broadly rounded, rostrate to subrostrate. Valve dimensions (n=40): valve length 12–55 µm, width 4.0–5.0 µm. Sternum narrow, almost not widening near the central area. Central area large, strictly unilateral, with broad, often depressed hyaline zone on one side and weakly to distinctly shortened striae on the opposite side. Ghost striae occasionally observed (Fig. 608). Striae weakly radiate in the valve middle to more strongly radiate near the apices, especially visible in smaller specimens. Striae alternating, 15–16 in 10 µm. Areolae not discernible in LM.

SEM (Figs 631–637): Large mantle plaques present (Fig. 631). Occasionally, very small spines irregularly scattered along the valve face/mantle junction (Fig. 633), most valves lacking spines (Figs. 632, 634). Striae uniseriate, composed of large, raised virgae compared to the small vimines (Fig. 635). Areolae small, apically elongated, located in shallow grooves (Figs 634, 635). Areolae diminishing in size, becoming almost rounded at the sternum (Fig. 633). One small, rimmed rimoportula present at one apex, located on the last stria, replacing some of the areolae (Fig. 636). Apical pore field relatively large, composed of up to seven rows of small pores, entirely located on the mantle (Fig. 636). Internally, rimoportula large, apically elongated (Fig. 637). Virgae weakly raised (Fig. 637).

Holotype: BR–4750 (Meise Botanic Garden). The holotype is illustrated by Fig. 606.

Isotype: slide 415 in the collection of the University of Antwerp (Belgium).

Type locality: United Kingdom, Duddingston Loch, Edinburgh, Scotland, Walker Arnott 238 (leg. Dr Gregory).

Etymology: The specific epithet refers to the similarity to *F. vaucheriae* but also to the broader, more robust character of the valves ('*robusta*')

Associated diatom flora: In addition to *Fragilaria vaucheriaerobusta* and *F. vandekerckhoveana* the type slide is mainly composed of (at present unidentified) *Fragilaria* taxa (e.g., *F.* cf. *radians*), *Cocconeis euglypta*, *C. pediculus*, *Gomphonella olivacea*, different *Navicula* species (*N. gregaria*, *N. metareichardtiana*, *N. tripunctata*), and *Rhoicosphenia abbreviata*. The presence of *R. abbreviata*, *C. euglypta*, and *C. pediculus* point to a habitat where the sample was most likely collected from submerged filamentous macroalgae including *Cladophora*. The species composition also points to rather alkaline, eutrophic conditions with a high electrolyte content (Lange–Bertalot et al. 2017). Most taxa observed are tolerant up to the β–α–mesosaprobic level.

Taxonomic remarks: *Fragilaria vaucheriaerobusta* shows considerable resemblance to both *F. rinoi* and *F. catenarinoi*. These three species seem to form a separate group within the *F. vaucheriae* complex, characterized by shortly protracted, broadly rounded, subrostrate to rostrate apices and very broad valves (width on average between 4 and 5 µm). *Fragilaria catenarinoi* differs in having short ribbon–shaped colonies, at present not observed in *F. vaucheriaerobusta*. Moreover, *F. catenarinoi* has a lower stria density, often lower than 11 striae in 10 µm. *Fragilaria rinoi* typically has convex, almost never straight, parallel margins, whereas in *F. vaucheriaerobusta*, most valves, except the smallest individuals, have a linear valve outline with parallel margins (Delgado et al. 2016). The longer valves in the Flemish population identified as *F. rinoi* (Figs 144–163) may form an intermediate population between *F. rinoi* and *F. vaucheriaerobusta*. The maximum valve width in *F. vaucheriaerobusta* does not exceed 5 µm, whereas in *F. rinoi*, the valve width can go up to 6 µm. On the other hand, the maximum valve length in *F. vaucheriaerobusta* is almost double the length of *F. rinoi*. The striae in both species share a similar density but in *F. vaucheriaerobusta*, striae tend to be more radiate than in *F. rinoi* where striae are clearly parallel, even in the smaller specimens.

Discussion

The is provisionally the last large paper revising the former group of species centred around *Fragilaria capucina* (Van de Vijver et al. 2020 and its varieties *rumpens* (Van de Vijver et al. 2022a), *gracilis* (Van de Vijver et al. 2022b) and *vaucheriae* (this paper). Each revision was based analysis of numerous type materials and other historic samples, and resulted in the description of several new species and the resurrection of formerly described but forgotten species. Important changes were implemented. For instance, the name *Fragilaria radians* should be used for populations formerly identified as *F. gracilis*, making a new name for the species formerly identified as *F. radians*, necessary (Van de Vijver & Williams, in press). The revisions also show that the former catch–all taxa such as *F. capucina*, *F. rumpens* and *F. vaucheriae* are, in fact, very rare species, usually confused with more widespread, often forgotten species such as *F. nevadensis* (for *F. capucina*), *F. campyla* (Hilse) Van de Vijver, Kusber et D.M.Williams (for *F. rumpens*) and *F. truncata* (for *F. vaucheriae*).

Each complex was characterized by a typical morphology, usually shared by all taxa discussed in the group. However, it is not possible at present to indicate a single feature to characterize each group, and the identification

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of the different species (and groups) should be based on a combination of morphological features. All taxa in the *Fragilaria vaucheriae* group share a more or less low stria density not exceeding 16 striae in 10 µm, clearly different from the *F. rumpens*– and *F. radians* (former *F. gracilis*) group where the average stria density is almost 20 µm. The presence of colonies seems to be present in each group and can therefore not be used as a discriminating feature to separate the different groups. All revisions, however, showed that the typical ribbon–like colonies in *Fragilaria* can only be formed using linking spines and all colony–forming species possess well–developed spines, usually spathulate in shape, to join the frustules together.

The revisions also indicated that a certain regionalism within the genus *Fragilaria* may exist, although, as this is based on the descriptions of new taxa, it is possible that these new species will later be found in other localities on the European continent. For instance, at the moment, a distinct, and most likely even endemic, *Fragilaria* flora seems to be present on the British Isles. Several species such as *F. kellyana*, *F. vandekerckhoveana* and *F. vaucheriaefalsa* (in the *F. vaucheriae*–group) and *F. battarbeeana* and *F. ennerdalensis* (in the *F. capucina*–group), have so far not been recorded from the rest of the European continent. On the other hand, species such as *F. rinoi* seem to be more widespread that their original distribution showed. More research, based on the application of the revised *Fragilaria* flora will be necessary to establish a better biogeographical analysis of the genus *Fragilaria* in Europe. At the moment, the newly described (and resurrected) species do not appear yet in published species lists and diatom counts.

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