

***Fragilaria radians* (Kützing) D.M. Williams et Round, the correct name for *F. gracilis* (Fragilariaceae, Bacillariophyta): a critical analysis of this species complex in Europe**

Bart VAN DE VIJVER^{1,2*}, David M. WILLIAMS³, Wolf–Henning KUSBER⁴, Marco CANTONATI⁵, Paul B. HAMILTON⁶, Carlos E. WETZEL⁷ & Luc ECTOR^{7,†}

¹Meise Botanic Garden Meise, Research Department, Nieuwelaan 38, 1860 Meise, Belgium

²University of Antwerp, Department of Biology – ECOSPHERE, Universiteitsplein 1, B–2610 Wilrijk, Belgium;

*Corresponding author e-mail: bart.vandevijver@plantentuinmeise.be

³Department of Life Sciences, the Natural History Museum, Cromwell Road, London, SW7 5BD, UK

⁴Botanischer Garten und Botanisches Museum Berlin, Freie Universität Berlin, Königin–Luise– Straße 6–8, 14195, Berlin, Germany

⁵Department of Biological, Geological and Environmental Sciences, Alma Mater Studiorum, BIOME Lab, University of Bologna, 40126 Bologna, Italy

⁶Canadian Museum of Nature, Research Division, PO Box 3443, Station D, Ottawa, ON, Canada K1P 6P4

⁷Luxembourg Institute of Science and Technology (LIST), Environmental Research & Innovation (ERIN) Department, Observatory for Climate, Environment and Biodiversity (OCEB), 41 rue du Brill, L–4422 Belvaux, Luxembourg

Abstract: *Fragilaria gracilis* is one of the most reported *Fragilaria* species in Europe, observed in a broad range of water bodies, ranging from (ultra)oligotrophic rivers to even eutrophic lakes. A revision of this important taxon based on the analysis of the morphology of a large number of historic and recent populations was highly needed. In the present study, type material of *Fragilaria gracilis* and several related taxa such as *Synedra radians*, *Fragilaria pseudolaevissima*, *S. utermoehlii*, *F. aquaplus*, *F. boreomongolica* and *F. tridentina* together with more than 10 modern populations were investigated using LM and SEM observations. The results based on these comparisons show that *Fragilaria* (*Synedra*) *radians* is the name for the taxon formerly known as *F. gracilis*. Moreover, detailed analysis demonstrated that *F. pseudolaevissima* and *Synedra utermoehlii* are conspecific with *F. radians* and should be considered as heterotypic synonyms. The observations made in this study also resulted in the description of several new species, often with distinct ecologies and distribution areas: *Fragilaria huerlimannii* Van de Vijver sp. nov., *F. acerosa* Van de Vijver, C.E. Wetzel, Jarlman et Ector sp. nov., *F. neglecta* Van de Vijver, C.E. Wetzel, Jarlman et Ector sp. nov., *F. heudreana* Van de Vijver, C.E. Wetzel et Ector sp. nov., *F. eutrapphenta* Van de Vijver, Kusber et D.M. Williams sp. nov., and *F. mertensiana* Van de Vijver, C.E. Wetzel et Ector sp. nov. Using an analysis of the associated diatom flora, the ecological preferences of each taxon are briefly discussed.

Key words: Europe, *Fragilaria gracilis* complex, *Fragilaria radians*, morphology, new species, taxonomy, type analysis

INTRODUCTION

The genus *Fragilaria* was originally described by LYNGBYE (1819) but it was much later that *Fragilaria pectinalis* (O.F. Müller) Lyngbye was designated as *typus generis* (BOYER 1927: 183). WILLIAMS & ROUND (1987) and later TUJI & WILLIAMS (2006b) provided a detailed description of the genus. Initially LYNGBYE (1819) stressed only the formation of colonies linking cells together rather than having them attached to a substrate, as a necessary feature for all species. Today it is generally accepted that colony

formation is omitted from the description as the majority of *Fragilaria* species do not produce colonies of this kind (TUJI & WILLIAMS 2006b). Nevertheless, the lack of colony–formation was, for a long time, probably the reason most species of *Fragilaria* were originally placed in the genus *Synedra* Ehrenberg. Although currently the name *Synedra* is restricted to a handful of marine taxa (WILLIAMS & KARTHICK 2021), in the past, the concept of the name *Synedra* was much broader, including a large number of taxa, considered not to produce ribbon–like colonies. KÜTZING (1844) put the genera *Fragilaria* and

Synedra into two different families (Fragilariaceae and Surirelleae) but did not mention the colony formation as possible principal feature separating both genera. *Fragilaria rumpens* (Kützing) G.W.F. Carlson, was originally described in the genus *Synedra*, despite the fact that the species produces long, ribbon-like colonies (KÜTZING 1844). Interestingly, KÜTZING (1844, plate 16) illustrated his new species on the plate with *Fragilaria* species, all showing ribbon-like colonies. It was, however, GRUNOW (1862) who suggested to put both in the same family (Diatomeae) separating them by their colony formation. This idea was followed by VAN HEURCK (1881) and later also by HUSTEDT (1932) who separated both genera *Fragilaria* and *Synedra* by their ability to form filamentous colonies.

Most new *Synedra* taxa have been described in the nineteenth century, with many transferred decades later to the genus *Fragilaria* (LANGE-BERTALOT 1980; WILLIAMS & ROUND 1987; KRAMMER & LANGE-BERTALOT 2000). In the past 15 years, revision of the genus *Fragilaria* has focused on the reanalysis of historic (usually type) material (TUJI 2004, 2007; TUJI & WILLIAMS 2006a, b, 2008a, b, c, 2013, 2017; DELGADO et al. 2015, 2016; WETZEL & ECTOR 2015; CANTONATI et al. 2019; KAHLERT et al. 2019; NOVAIS et al. 2019). These revisions resulted in a better understanding of the identity of the previously published taxa and allowed the description of several new species such as *Fragilaria microvaucheriae* C.E. Wetzel et Ector (WETZEL & ECTOR 2015), *F. misarelensis* Almeida et al. (in NOVAIS et al. 2019), *F. tridentina* Cantonati et Lange-Bertalot (in CANTONATI et al. 2019) and *F. heatherae* Kahlert et M.G. Kelly (in KAHLERT et al. 2019).

Two years ago, a second revision of the genus *Fragilaria* began, aiming to unravel the taxonomic identity of several forgotten or neglected European *Fragilaria* taxa. The revisions are based on the examination of type material and other historic (usually nineteenth century) samples, present in several 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)]. Several taxa such as *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 (in VAN DE VIJVER et al. 2020d), *F. alpestris* Krasske (VAN DE VIJVER et al. 2020e), *F. septentrionalis* (Østrup) Van de Vijver et al. (2020f), *F. ostensfeldii* (Willi Krieger) Van de Vijver, Alexson et Reavie (VAN DE VIJVER et al. 2021a), *F. capucina* Desmazières (VAN DE VIJVER et al. 2021b) and *F. recapitellata* (Grunow) Lange-Bertalot et Metzeltin (VAN DE VIJVER et al. 2021c) have already been reanalysed.

Most of the reported taxa are characterized by a stria density of less than 16 in 10 µm, giving the striation

pattern in these species a rather coarse appearance. There is, however, a whole plethora of small-celled (length usually < 50 µm) *Fragilaria* taxa with a stria density of around 20 in 10 µm, making the striae often not easily discernible in LM. These taxa can be subdivided into two complexes based on the average width of the valves: *Fragilaria rumpens* (valve width > 3 µm) and *F. gracilis* Østrup (valve width < 2–3 µm). Both groups are often reported from European rivers and play an important role in water quality biomonitoring programs (LANGE-BERTALOT et al. 2017) preferring oligo-mesotrophic (*F. rumpens*) and oligotrophic (*F. gracilis*) conditions. The type material of *F. gracilis* and *F. rumpens* was examined by TUJI (2007) and TUJI & WILLIAMS (2006a), respectively. In the latter publication, the authors stated that *F. rumpens*, typically forming long, ribbon-like colonies, also occurring as single cells in the periphyton. They questioned whether these single cells belonged to *F. rumpens*. Recently, VAN DE VIJVER et al. (2022) reanalysed therefore the type of *F. rumpens* together with the original material of a large number of similar taxa, separating at least 6 (2 of them newly described) individual taxa. However, a large number of finely striated *Fragilaria* populations showing a valve width < 3 µm have yet to be studied. Although commonly identified as *F. gracilis*, they were observed in a broad range of trophic conditions, making their conspecificity less likely.

The present paper aims to revise these finely striated taxa by analysing a large number of *Fragilaria* populations in European rivers identified as *F. gracilis* or, occasionally, *F. rumpens* comparing them with the type populations of *F. gracilis*, *F. pseudolaevissima* Van Landingham (= *F. laevissima* Østrup), *F. aquaplus* Lange-Bertalot et Ulrich, *F. tridentina*, *Synedra utermoehlii* Hustedt (now *F. utermoehlii* (Hustedt) Lange-Bertalot) and *F. boreomongolica* Kulikovskiy et al. Although some of these types have recently been illustrated in detail (TUJI 2007; KULIKOVSKIY et al. 2010; LANGE-BERTALOT & ULRICH 2014; CANTONATI et al. 2019), we have studied them in the same way to allow consistent comparative interpretations. Recently, KAHLERT et al. (2019) used molecular data in their analysis of several European *Fragilaria* populations. Their results show that *Fragilaria gracilis* was separated from the other *Fragilaria* species as a subcluster, and that within *F. gracilis*, two groups could be identified, separated by differences in valve outline and stria density. Nevertheless, they considered both groups to represent *F. gracilis* and included, for instance, *Fragilaria aquaplus* Lange-Bertalot et S. Ulrich in *F. gracilis*, although the original type material of both taxa was not re-analysed.

Fragilaria gracilis was described in 1910 by ØSTRUP, whereas most other, usually common, *Fragilaria* taxa, such as *F. capucina*, *F. vaucheriae*, *F. rumpens* or *F. mesolepta* were described in the nineteenth century, often more than 70 years prior to *F. gracilis*. A literature analysis of the most important taxonomic contributions in the nineteenth century (e.g. KÜTZING 1844; SMITH

1853; VAN HEURCK 1881) apparently did not show any relevant taxa similar to *F. gracilis*. Further analysis, including more recent, twentieth century taxonomic contributions (HUSTEDT 1932; MAYER 1937; PATRICK & REIMER 1966; LANGE–BERTALOT 1980; KRAMMER & LANGE–BERTALOT 1991) also referred only to the taxon described by ØSTRUP in 1910. However, drawings in KÜTZING (1844, plate 14), showed several finely striated taxa with a similar valve outline as *F. gracilis*. One of these was described as *Synedra radians* Kützing. Our current concept of this taxon, transferred in 1987 by WILLIAMS & ROUND to the genus *Fragilaria* as *F. radians* (Kützing) D.M. Williams et Round, shows a species with capitate apices and a very coarse (< 12 striae in 10 µm) stria density, based on the taxonomic analysis discussed in KRAMMER & LANGE–BERTALOT (1991, p. 122). As the latter interpretation apparently conflicts with the original description and illustration in KÜTZING (1844), the type slide (BM18192) for *Synedra radians* from Tennstädt (Germany) is reanalysed and compared with the observations of the current study.

Following the morphological analysis and comparison with the currently available literature on this topic, several European populations could not be identified and are described as new: *F. acerosa* Van de Vijver, C.E. Wetzel, Jarlman et Ector sp. nov., *Fragilaria eutrapphenta* Van de Vijver, Kusber et D.M. Williams sp. nov., *F. heudreana* Van de Vijver, C.E. Wetzel et Ector sp. nov., *F. huerlimannii* Van de Vijver, sp. nov., *F. mertensiana* Van de Vijver, C.E. Wetzel et Ector sp. nov. and *F. neglecta* Van de Vijver, C.E. Wetzel, Jarlman et Ector sp. nov. By carefully assessing the associated diatom flora, an attempt is made to refine the environmental preferences of the taxa studied. A better knowledge of the morphological and ecological variability of these species in European waters will therefore also improve their use as powerful indicators in water quality biomonitoring.

MATERIAL AND METHODS

For this study, both type material and recently collected samples were investigated. Table 1 lists all investigated samples together with all sample information that could be retrieved. In total 18 samples were included in this study.

Sub-samples of the selected material were prepared for light and scanning electron microscopy observations following the method described in VAN DER WERFF (1955). Small parts of the sub-samples were cleaned by adding 37% H₂O₂ and heating to 80 °C for about 1 h. The reaction was completed by addition of saturated KMnO₄. Following digestion and centrifugation (three times 10 minutes at 3700× rpm), the resulting cleaned material was diluted with distilled water to avoid excessive concentrations of diatom valves on the slides and mounted in Naphrax. The diatom slides were analysed using an Olympus BX53 microscope at ×1000 magnification (N.A. 1.30), equipped with Differential Interference Contrast (Nomarski) optics and the Olympus UC30 Imaging System. For each taxon, the number of specimens, measured at random on the type slide, is indicated (n=X).

For scanning electron microscopy (SEM), parts of the oxidized suspensions were filtered through a 5-µm Isopore™ polycarbonate membrane filter (Merck Millipore). The stubs were sputter-coated with a platinum layer of 10 nm and studied using the ultra-high-resolution analytical field emission (FE) scanning electron microscopes Hitachi SU-70 (Hitachi High-Technologies, Europe, GmbH) operated at 5 kV and 10 mm working distance (LIST, Luxemburg), JEOL-JSM-7100F field emission scanning electron microscope operated at 2 kV and 4 mm working distance (Meise Botanic Garden, Belgium) and ZEISS Ultra scanning electron microscope at 3 kV (Natural History Museum London, UK). Slides and stubs analysed in this study are stored at the BR-collection (Meise Botanic Garden, Belgium). Plates were prepared using Photoshop CS5.

Terminology used in the description of the various structures of the siliceous cell wall is based on ROSS et al. (1979, areola structure), COX & ROSS (1981, stria structure), WILLIAMS & ROUND (1987, *Fragilaria* genus features) and TUJI & WILLIAMS (2006b, *Fragilaria* genus features). The terms ‘sternum’ for the axial area (ROUND 1979) and ‘ocellulimbus’ for the inset apical pore field (WILLIAMS 1986) are used. For taxonomic comparisons, the following papers were used: ØSTRUP (1910), LANGE–BERTALOT (1980), KRAMMER & LANGE–BERTALOT (1991), TUJI (2004, 2007), TUJI & WILLIAMS (2006a), KULIKOVSKIY et al. (2010), LANGE–BERTALOT & ULRICH (2014), LANGE–BERTALOT et al. (2017), CANTONATI et al. (2019), KAHLERT et al. (2019), VAN DE VIJVER et al. (2020a, d, 2021b, in press).

For the typification of the new species, we chose to use the entire slide as the holotype following article 8.2 of the International Code for Botanical Nomenclature (TURLAND et al. 2018).

RESULTS

In the present paper, the original material of fourteen taxa commonly identified as *F. gracilis* (taxa with valve width < 3 µm) or *F. rumpens* (valve width > 3 µm) was investigated. Results of the present study demonstrate that the populations commonly identified as *Fragilaria gracilis* in Europe often belong to different, usually unknown, species. Since, based on the observations in the current paper, a lot of these taxa are split in separate, newly described, species, it has important consequences for the taxonomy and the ecology of the *F. gracilis*-complex occurring in Europe.

A total of ten species is discussed (Table 2). Species are combined in 7 artificial groups facilitating the discussion of the taxonomic history, similarities and morphological features of the different species.

Fragilaria radians (Kützing) D.M. Williams et Round 1987

In 1844, Kützing described a new *Synedra* species, *S. radians*, using a *Cladophora fracta* sample collected near Tennstädt (now Bad Tennstedt, Thuringia, Germany): *S. debilis*, *angustissima*, *linearis*, *radiatim et densissime aggregata*, *altero latere truncata*, *altero attenuata obtusiuscula* [Small *Synedra*, very narrow, linear,

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

Sample	locality	investigated species	collection date	collector	collection	collection number
Kützing sample 188	Tennstädt, Germany	<i>Synedra radians</i>	???	A. de Brébisson s.n.	Natural History Museum, London (UK)	BM18192
BERW-03510	Eau noire, Viroinval, Belgium	<i>Fragilaria radians</i>	25.V.2020	Service Public de Wallonie	Meise Botanic Garden (Belgium)	BR-4694
Østrup sample 1342	Botanic Garden Copenhagen, Denmark	<i>Fragilaria gracilis</i>	???	E.Østrup ?	Natural History Museum of Denmark	C-A-99085
Østrup sample 8681	Kandestederne, Jutland, Denmark	<i>Fragilaria pseudolaevissima</i> , <i>F. heudreaana</i>	???	E.Østrup ?	Natural History Museum of Denmark	BR-4695
Hustedt sample E4360	Dobersdorfer See, Schleswig-Holstein, Germany	<i>Synedra utermoechlii</i>	12.V.1921	F. Hustedt	Hustedt collection, AWI, Bremerhaven, Germany	BRM K1/10
Meister 624	Lago della Croceta, Switzerland	<i>Fragilaria aquaplus</i>	11.VIII.1905	A. Meister	Meister Collection, Zurich, Switzerland	Meister 624
Hürlimann 5236	Lagh da la Cruceta, Switzerland	<i>Fragilaria aquaplus</i>	04.VIII.2015	J. Hürlimann	Meise Botanic Garden (Belgium)	BR-4696
Hürlimann 6671	Fiume Ticino, canton Ticino, Switzerland	<i>Fragilaria huerlimannii</i>	08.VII.2020	J. Hürlimann	Meise Botanic Garden (Belgium)	BR-4697
Haraldsjöän	Haraldsjöän, Riddarhyttan Kommun, Västmanlands län, Sweden	<i>Fragilaria acerosa</i>	30.IX.2004	A. Jarlman s.n.	Jarlman (Sweden) & Meise Botanic Garden (Belgium)	BR-4698
Hammarbäcken	Hammarbäcken, Ups Vägen, Hätjedalen, Sweden	<i>Fragilaria acerosa</i>	10.IX.2005	A. Jarlman s.n.	Jarlman (Sweden) & Meise Botanic Garden (Belgium)	BR-4699
Stridbäcken	Stridbäcken, Under Botniabanan, Nordmaling, Sweden	<i>Fragilaria acerosa</i>	24.IX.2004	A. Jarlman s.n.	Jarlman (Sweden) & Meise Botanic Garden (Belgium)	BR-4700
Norrhultsbäcken	Norrhultsbäcken, Åseda, Sweden	<i>Fragilaria acerosa</i>	04.X.2004	A. Jarlman s.n.	Jarlman (Sweden) & Meise Botanic Garden (Belgium)	BR-4701
Bjurbäcken	Bjurbäcken, Burträsk, Sweden	<i>Fragilaria acerosa</i>	23.IX.2004	A. Jarlman s.n.	Jarlman (Sweden) & Meise Botanic Garden (Belgium)	BR-4702
Mälksarbäcken	Mälksarbäcken, Vilhelmina Kommun, Västersbotten Län, Sweden	<i>Fragilaria neglecta</i>	12.IX.2005	A. Jarlman s.n.	Jarlman (Sweden) & Meise Botanic Garden (Belgium)	BR-4703
RIKA DE BIE 17	River Grote Nete, Balen, Belgium	<i>Fragilaria eutrappenta</i>	3.V.1995	B. Van de Vijver	Meise Botanic Garden (Belgium)	BR-4704
APM17-98	River Molse Neet, Geel, Belgium	<i>Fragilaria mertensiana</i>	10.V.2017	VMM	Meise Botanic Garden (Belgium)	BR-4705
Russia Peat Bog 101	<i>Sphagnum</i> Bog Nur, Hentei Highlands, Mongolia	<i>Fragilaria boreomongolica</i>	05.IX.2005	N. Dorofeyuk	Institute of Marine Sciences, University of Szczecin, Poland	SZCZ-12529
cLIM004 DIAT 2513	Lake Ritoro Outlet, Adamello-Brenta Natural Park, Trentino, southeastern Alps	<i>Fragilaria tridentina</i>	24.IX.2012	M. Cantonati s.n.	MUSE, Trento, Italy & Meise Botanic Garden (Belgium)	TR cLIM004 DIAT 1985

radiantly and densely aggregated, one side truncate, the other tapering and more obtuse] (KÜTZING 1844, p. 65). The illustrated specimens (see our Fig. 1) showed bundle-shaped colonies and thin, linear, acutely rounded non-protracted valves. In 1853, SMITH used the same name, *S. radians* W.Smith, for a different species, already described, according to him, under a few different names (i.e. *Synedra splendens* Kützing, *Exilaria ulna* Hassall, *Diatoma truncatum* Greville), illustrating specimens that nowadays would belong in the genus *Ulnaria*. *Synedra radians* sensu SMITH (1853) and the morphological concept SMITH (1853) linked to it, quickly became widely accepted and in later taxonomic contributions, Smith's concept was connected to Kützing's original name of *S. radians*. HUSTEDT (1930, p. 155, 1932, p. 202) considered the species to be a variety of *Synedra acus* Kützing as *S. acus* var. *radians* (Kützing) Hustedt. PATRICK & REIMER (1966, p. 137) kept *S. radians* as a separate taxon. Their illustrated valve (plate 5, fig. 4, from Van Heurck 312, Brussels, Belgium), showed a taxon clearly related to *Ulnaria* with a length of up to 140 µm, clearly in contrast with the original concept KÜTZING published in 1844. WILLIAMS & ROUND (1987) transferred the species to the genus *Fragilaria*, clearly contradicting this generally accepted view that *S. radians* should be connected to *S. acus*. KRAMMER & LANGE-BERTALOT (1991, p. 122), although neglecting this transfer, also presented this interpretation of *S. radians* Kützing being part of the more broadly interpreted concept of the genus *Fragilaria*, based on the analysis of Kützing sample 188 from Tennstädt. According to this analysis, several taxa are present in the slide BM18192, designated previously as lectotype by reference. They observed at least *Ctenophora pulchella* (Ralfs) D.M. Williams & Round, *Fragilaria famelica* (Kützing) Lange-Bertalot and several taxa from what they called the *F. capucina*-Sippenspektrum including *F. rumpens* and *F. gracilis*. They also found and illustrated several valves that they identified as *S. radians* 'Konform mit dem Protolog' [according to the protologue]. The two illustrated valves (KRAMMER & LANGE-BERTALOT 1991, plate 109, figs 17 & 18) show a rather large, coarsely striated (10 striae in 10 µm), capitate species, thus defining the nowadays still accepted, morphological concept of *F. radians* (see LANGE-BERTALOT et al. 2017). The re-examination of the lectotype slide, performed for this revision of the *F. gracilis*-complex, contradicts this actually accepted concept of *F. radians* for several reasons. 1. The illustrated valves in KRAMMER & LANGE-BERTALOT (1991) conflict with the original description and illustration in KÜTZING (1844), as the latter described the species as very thin, linear lacking capitate apices. 2. In the lectotype slide, several valves could be found connected to each other forming most likely short, ribbon-like colonies. This clearly contradicts the bundle-shaped aggregates of specimens KÜTZING (1844) depicted. 3. The original catalogue of the KÜTZING collection kept in BR, lists both *Synedra radians* and *Exilaria truncata* Greville, for sample 188,

the latter also hand-written on the package conserved in BM. Analysis of the type material of *Exilaria truncata* (VAN DE VUVER et al., unpubl. res.) showed specimens with a coarse striation pattern, although they lack the very distinct capitate apices. In the lectotype slide of *S. radians*, there is only one taxon that shows some similarity with the type of *Exilaria truncata* and these valves have been, most likely mistakenly, identified by KRAMMER & LANGE-BERTALOT (1991) as *S. radians*. 4. The lectotype sample contains a fairly large population of a thin-celled, finely striated taxon lacking distinctly protracted apices, largely resembling the drawing in KÜTZING (1844, plate 14, fig. 7).

Based on these observations, we believe that the currently accepted concept for *Fragilaria* (*Synedra*) *radians* needs to be modified. Moreover, the revised concept of *F. radians* shows that these valves are identical to those for the species described by ØSTRUP (1910) as *Fragilaria gracilis* and should the latter name be considered a younger synonym of *F. radians*.

Additionally, the morphological analysis of several historic samples in the present paper, also showed that *Synedra utermoehlii* Hustedt (HUSTEDT 1932, see SIMONSEN 1987, p. 132, pl. 217, figs 1, 2) should be considered a heterotypic synonym of *Fragilaria radians*.

***Fragilaria radians* (Kützing) D.M. Williams et Round 1987 (Figs 1–32)**

Basionym: *Synedra radians* Kützing (1844): *Die Kieselschaligen Bacillarien oder Diatomeen*, p. 64, plate 14, fig. VII, 1–4 (here reproduced as Fig. 1)

= *Fragilaria gracilis* Østrup 1910

= *Fragilaria laevissima* Østrup 1910, nom. illeg., non *Fragilaria laevissima* Cleve 1898

= *Synedra utermoehlii* Hustedt 1932

= *Fragilaria capucina* var. *gracilis* (Østrup) Hustedt 1950

= *Synedra tenera* var. *utermoehlii* (Hustedt) Cleve-Euler 1953

= *Fragilaria pseudolaevissima* VanLandingham 1971

= *Fragilaria utermoehlii* (Hustedt) Lange-Bertalot 1993

To be excluded from synonymy:

Synedra radians sensu SMITH (1853)

Synedra acus var. *radians* (Kützing) Hustedt 1930 sensu HUSTEDT (1930)

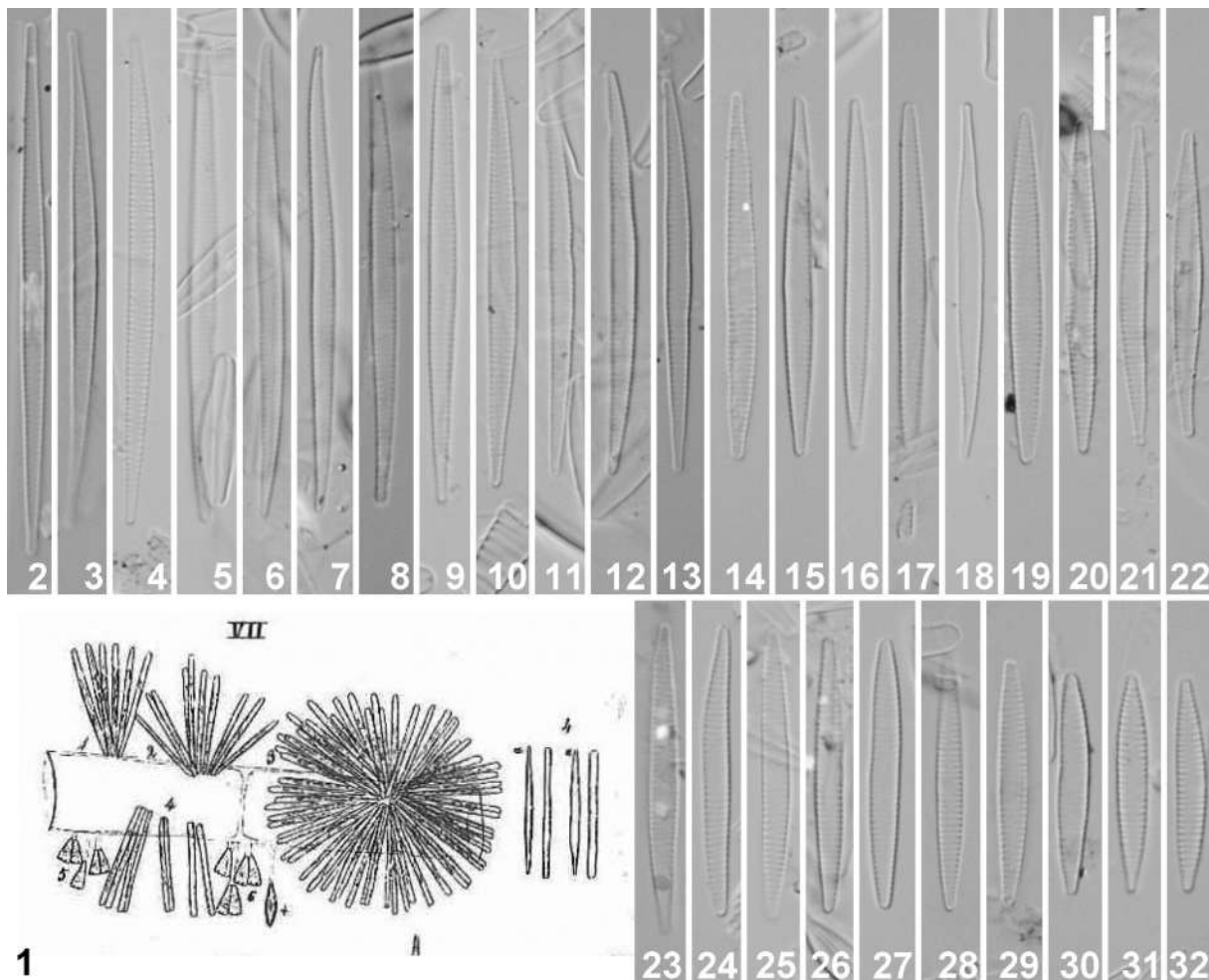
LM (Figs 2–32): Frustules in girdle view rectangular, narrow, solitary. Rarely two cells observed connected to each other. Ribbon-like colonies of more than 3 cells together not observed so far. Valves linear to narrowly lanceolate. Smaller valves usually less lanceolate (Figs 28–32). Margins weakly but gradually tapering from central area to apices. Apices usually not protracted, acutely rounded. Valve dimensions (n=20): length 15–45 µm, width 2.0–3.0 µm. Sternum very narrow but discernible in LM, linear, widening near the central area. Central area moderately large, forming a clear rectangular hyaline area. Marginal striae in the central area unilaterally present in smaller specimens (e.g. Fig. 32). Striae alternating or opposite (mostly near the apices), parallel throughout entire valve, 19–21 in 10 µm. Areolae not discernible in LM.

Lectotype (designated in WILLIAMS & ROUND 1987, p. 269): BM18192, prepared from KÜTZING sample 188. KRAMMER & LANGE–BERTALOT (1991, p. 448), illustrated a “lectotypisierte Sippe” (lectotypified taxon) and argued that these selected specimens represent the species described by KÜTZING (1844). In fact, this treatment does not conform to TURLAND et al. (2018: Art. 9.14) because when a type contains more than one taxon “the name must remain attached to the part that corresponds most nearly with the original description or diagnosis”. Thus, we here present the taxon from the lectotype slide that fits perfectly Kützing’s protologue.

Associated diatom flora: The lectotype slide is dominated by (in decreasing abundance) *Achnanthisidium microcephalum* Kützing, *Denticula tenuis* Kützing, *Fragilaria radians*, *Gomphonema lateripunctatum* E.Reichardt et Lange–Bertalot, *Nitzschia denticula* Grunow, *Ctenophora pulchella*, *Cymbella vulgata* Krammer and *Diatoma moniliformis* Kützing. Additionally, the following species were observed but in lower abundances: *Gomphonella olivacea* (Hornemann) Rabenhorst, *Gomphonema*

pumilum var. *rigidum* E.Reichardt et Lange–Bertalot, *G. parvulum* (Kützing) Kützing, *Encyonopsis subminuta* Krammer, *Fragilaria fragilarioides* (Grunow) Cholnoky and *Cocconeis euglypta* Ehrenberg. Although KÜTZING (1844) only provided a sample locality (Tennstädt), he added that the sample was collected from *Cladophora fracta* (O.F.Müller ex Vahl) Kützing, a species known to prefer higher nutrient and electrolyte levels (MICHALAK & MESSYASZ 2021). The dominant taxa in the sample, however, point to a more mesotrophic (not eutrophic) calcium–bicarbonate enriched, alkaline to highly alkaline condition with a medium to high electrolyte content, the latter indicated by the presence of *Diatoma moniliformis*, *Ctenophora pulchella* and *Gomphonella olivacea* (LANGE–BERTALOT et al. 2017).

Although the unmounted material of the lectotype of *F. radians* (KÜTZING sample 188, subsamples conserved in BR and BM) was carefully prepared following the same methods applied for the other samples, no *S. radians* valves were found. Inspection of the pieces of the original mica on which the sample was preserved,



Figs 1–32. *Fragilaria radians* (Kützing) D.M. Williams et Round. Line drawing and LM images taken from the lectotype material (KÜTZING sample 188, B.M.18192): (1) original drawing from KÜTZING (1844, pl. 14, fig. IX 1–4); (2–32) LM views of the population arranged in decreasing length. Scale bar 10 μ m.

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

	<i>Fragilaria radians</i>	<i>Fragilaria gracilis</i>	<i>Fragilaria pseudo-laevisima</i>	<i>Fragilaria utermosthii</i>	<i>Fragilaria aquaplus</i>	<i>Fragilaria huertlii</i>	<i>Fragilaria acerosa</i>
original reference	Kützing 1844	Østrup 1910	Østrup 1910	Hustedt 1932	Lange-Bertalot & Ulrich 2014	this paper	this paper
Figures	1–87	88–112	113–139	140–165	166–215	216–243	244–410
colonies	no	no	no	no	no	no	no
length (µm)	15–45	17–60	25–42	10–37	20–50	20–50	13–70
width (µm)	2.0–3.0	2.0–3.0	2.0–2.5	2.0–3.0	1.5–2.5	1.5–2.0	1.5–2.5
valve outline	linear to narrowly lanceolate, smaller valves less lanceolate with weakly but gradually tapering margins	linear to narrowly lanceolate with weakly but gradually tapering margins from central area to apices	linear to narrowly lanceolate with almost parallel to gradually narrowing margins	linear to linear-lanceolate with weakly convex margins	needle-shaped, narrowly lanceolate with weakly but gradually tapering margins	needle-shaped, narrowly lanceolate with gradually tapering margins	Longer valves elongated, needle-shaped, linear to very narrowly lanceolate, shorter valves more lanceolate, with gradually narrowing margins
apices	usually not protracted, acutely rounded	almost not protracted, occasionally very slightly rostrate, usually acutely rounded	very weakly protracted, acutely rounded to slightly rostrate	non-protracted, acutely rounded	not protracted, slightly rostrate to acutely rounded	protracted, rostrate to weakly capitate	weakly protracted, very acutely rounded
sternum	very narrow but discernible in LM, linear, widening near the central area	very narrow but discernible in LM, linear, slightly widening near the central area	narrow but distinct in LM, linear, gradually widening towards the central area	very narrow, linear, not to very weakly widening near the central area	absent at the apices, only very slightly formed at the central area	narrow but clearly discernible	narrow but distinct, gradually widening from apices to the central area
central area	moderately large, forming a clear rectangular hyaline area	moderately large, forming a clear rectangular hyaline area	rather small, forming a small, unclear hyaline area	asymmetrical, often forming a rectangular to unilateral hyaline area	rather large, rectangular, occasionally weakly expanded	large, forming a clear hyaline zone, weakly, occasionally distinctly swollen	very small due to irregular shortening of a few central striae
ghost striae	not visible	barely visible	only weakly visible	present	present	absent	absent
striae in 10 µm	19–21	(19–) 21–24	19–20	20–22	22–24	20–21	18–22
rimoportulae per valve	1	1	1	1	1	1	1
spines	no	no	no	no	no	no	no

Table 2. Cont.

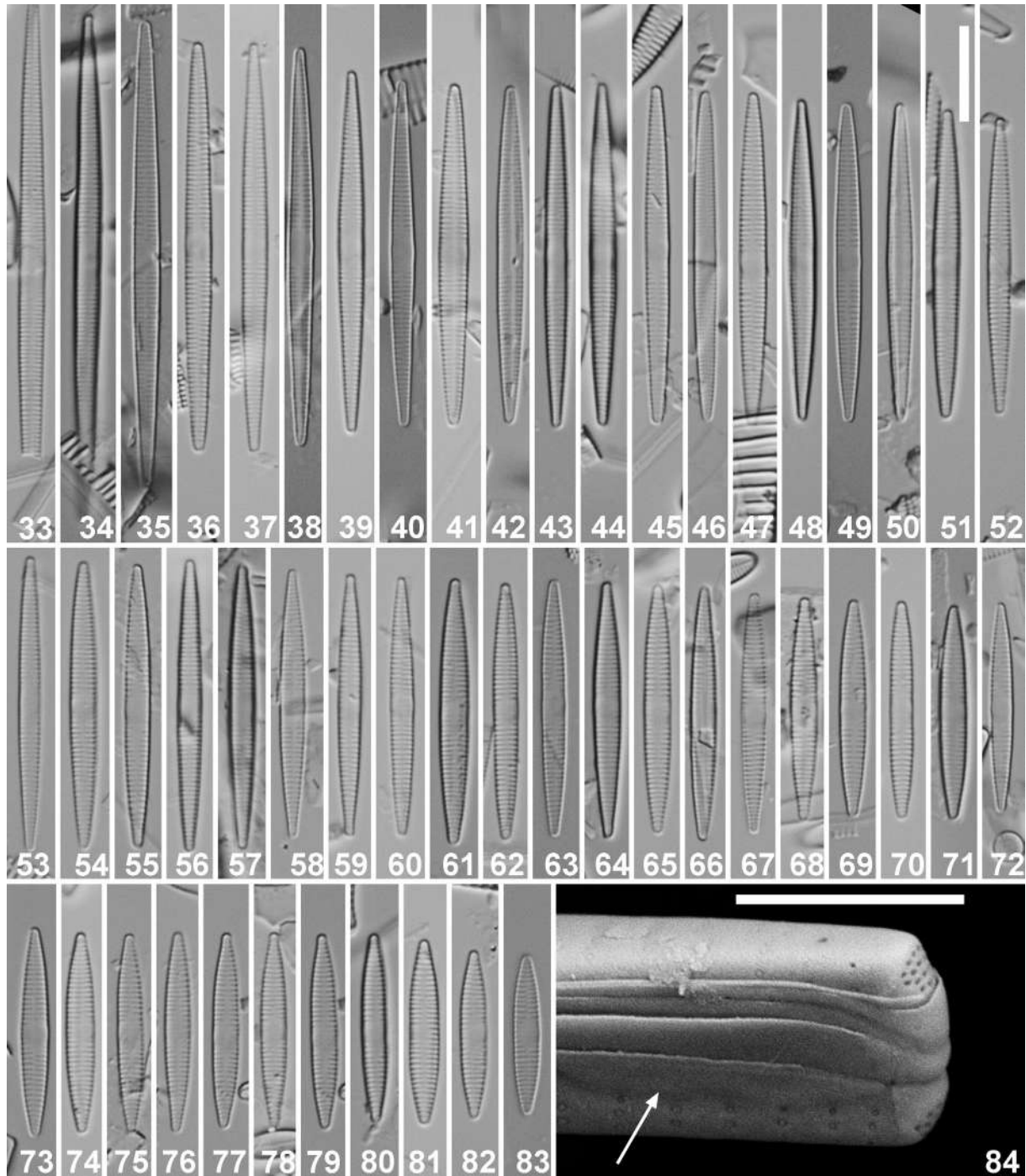
	<i>Fragilaria neglecta</i>	<i>Fragilaria heudreana</i>	<i>Fragilaria eutrappenta</i>	<i>Fragilaria mertensiana</i>	<i>Fragilaria boreomongolica</i>	<i>Fragilaria tridentina</i>
original reference	this paper	this paper	this paper	this paper	Kulikovskiy et al. 2010	Cantonati et al. 2019
Figures	411–437	438–476	477–520	521–546	547–561	562–587
colonies	no	no	no	no	no	no
length (µm)	30–70	12–50	20–75	15–40	15–30	14–25
width (µm)	1.5–2.0	3.0–5.0	3.0–4.0	2.5–3.0	2.5–3.0	2.5–3.5
valve outline	linear with strictly parallel margins	linear to narrowly lanceolate with almost parallel margins	linear with parallel, almost straight to very weakly convex margins	Valves (narrowly) lanceolate with clearly convex, never parallel margins	mostly linear with parallel margins	almost linear to narrowly lanceolate with parallel margins
apices	not protracted, broadly rounded	protracted, rostrate	slightly protracted, weakly rostrate	distinctly protracted, subcapitate to rostrate	slightly protracted, rostrate	weakly protracted, distinctly cuneate, not rostrate
sternum	narrow but distinct, linear throughout the entire valve length	narrow to occasionally moderately broad, distinct, gradually widening from apices to central area	moderately narrow, distinct, gradually widening from apices to central area	broad, distinct, clearly widening at the central area	distinct, gradually widening from apices to central area	narrow, discernible in LM, almost not widening from apices to central area
central area	absent to very small due to unilateral shortening of a few central striae	unilateral, forming a large, irregularly shaped hyaline area	large, irregularly shaped hyaline area, occasionally bordered by several shortened striae	large, rectangular hyaline area, occasionally irregularly bordered by several shortened striae	area variable, occasionally absent, usually forming a large, unilateral hyaline area	small, unilateral hyaline area, bordered on one side by several, irregularly shortened striae
ghost striae	absent	very prominently present	absent	absent	absent	absent
striae in 10 µm	20–21	18–21	19–20	17–20	18–21	19–22
rimoportulae per valve	1	1	1	1	1	1
spines	no	yes	no	no	no	no

showed no diatom valves on the mica. Therefore, sample BERW–03510 from the Eau noire (Viroinval, Wallonia, Belgium) is designated as epitype linked to the lectotype in accordance with ICN Art. 9.8 (TURLAND et al. 2018). The population in this sample (Figs 33–87) shows almost exactly the same combination of morphological and morphometric features (despite a slightly lower stria density) as the type of *F. radians* and can therefore be considered conspecific with it.

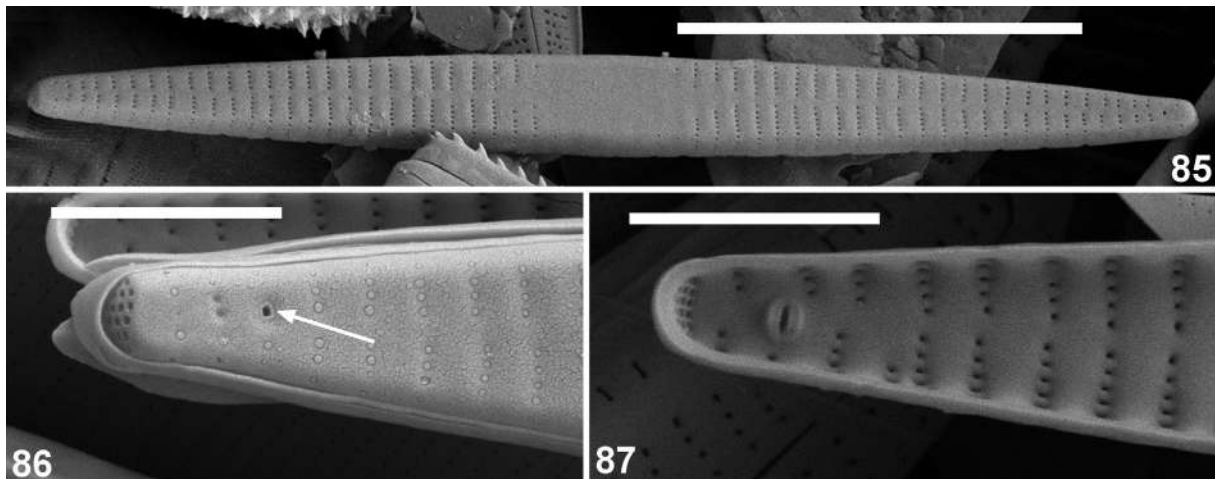
***Fragilaria radians* (Kützing) D.M. Williams et Round 1987 – epitype population BERW–03510 (Figs 33–87)**

Registration: <http://phycobank.org/102953>

LM (Figs 33–83): Valves linear to narrowly lanceolate with gradually tapering margins towards the only weakly protracted, acutely rounded to slightly rostrate to cuneate apices. Valve dimensions (n=40): length 17–60 µm, width 2.5–3.0 µm. Sternum narrow but distinct in LM,



Figs 33–84. *Fragilaria radians* (Kützing) D.M. Williams et Round. LM and SEM images taken from the epitype material (BERW–03510, BR–4694): (33–83) LM views of the population arranged in decreasing length; (84) SEM external detail of the apex of an entire frustule showing the apical pore field and some mantle plaques (arrow). Scale bar 10 µm (33–83) and 2 µm (84).



Figs 85–87. *Fragilaria radians* (Kützing) D.M. Williams et Round. SEM images taken from the epitype material (BERW–03510, BR–4694): (85) SEM external view of entire valve. Note the absence of spines and the large, hyaline central area; (86) SEM external detail of a valve apex showing the apical pore field and the rimoportula (arrow); (87) SEM internal detail of a valve apex showing the rimoportula. Scale bar 10 μm (85) and 2 μm (86, 87).

linear, slightly widening near the central area. Central area moderately large forming a rectangular, occasionally unilateral, hyaline area. Marginal striae in the central area present in smaller specimens. Striae usually alternating, becoming opposite near the apices, parallel throughout entire valve, 19–21 in 10 μm . Areolae not discernible in LM.

SEM (Figs 84–87): Large plaques present on the mantle (Fig. 84). Sternum very narrow near the apices, becoming gradually wider towards the central area (Fig. 85). Spines, or vestiges of spines, not observed (Fig. 85). Ghost striae only very weakly visible in the central area (Fig. 85). Valve face flat, virgae not raised (Fig. 85). Striae uniseriate, composed of very small, rounded areolae, externally occluded by individual vela (Figs 85, 86). Apical pore fields identical on both apices, covering the entire apex mantle, of the ocellulimbus type, composed of 3–4 rows of very large, rounded poroids (Figs 84, 86). External rimoportula opening small, rounded, rimmed, replacing one areola in one of the last striae (Fig. 86, arrow). Internally, rimoportula straight, transapically oriented (Fig. 87).

Epitype (here designated for the above lectotype of *Fragilaria radians* (Kützing) D.M. Williams et Round): BR–4694, Sample BERW–03510, Eau noire, Viroinval, Belgium (coll. date 25.V.2020, leg. Service Public de Wallonie).

Associated diatom flora: The epitype slide is dominated by several *Achnanthisdium* taxa such as *A. microcephalum*, *A. rivulare* Potapova et Ponader, *A. pyrenaicum* (Hustedt) H.Kobayashi, together with *F. radians*, *F. microvaucheriae* C.E. Wetzel et Ector and *Diatoma vulgare* Bory. Apart from these dominant species, the flora is also composed of *Amphora indistincta* Levkov, *Navicula gregaria* Donkin, *N. cryptotenella* Lange–Bertalot, *Gomphonema parvulum*, *Encyonema* cf. *brevicapitatum* Krammer, *E. ventricosum*

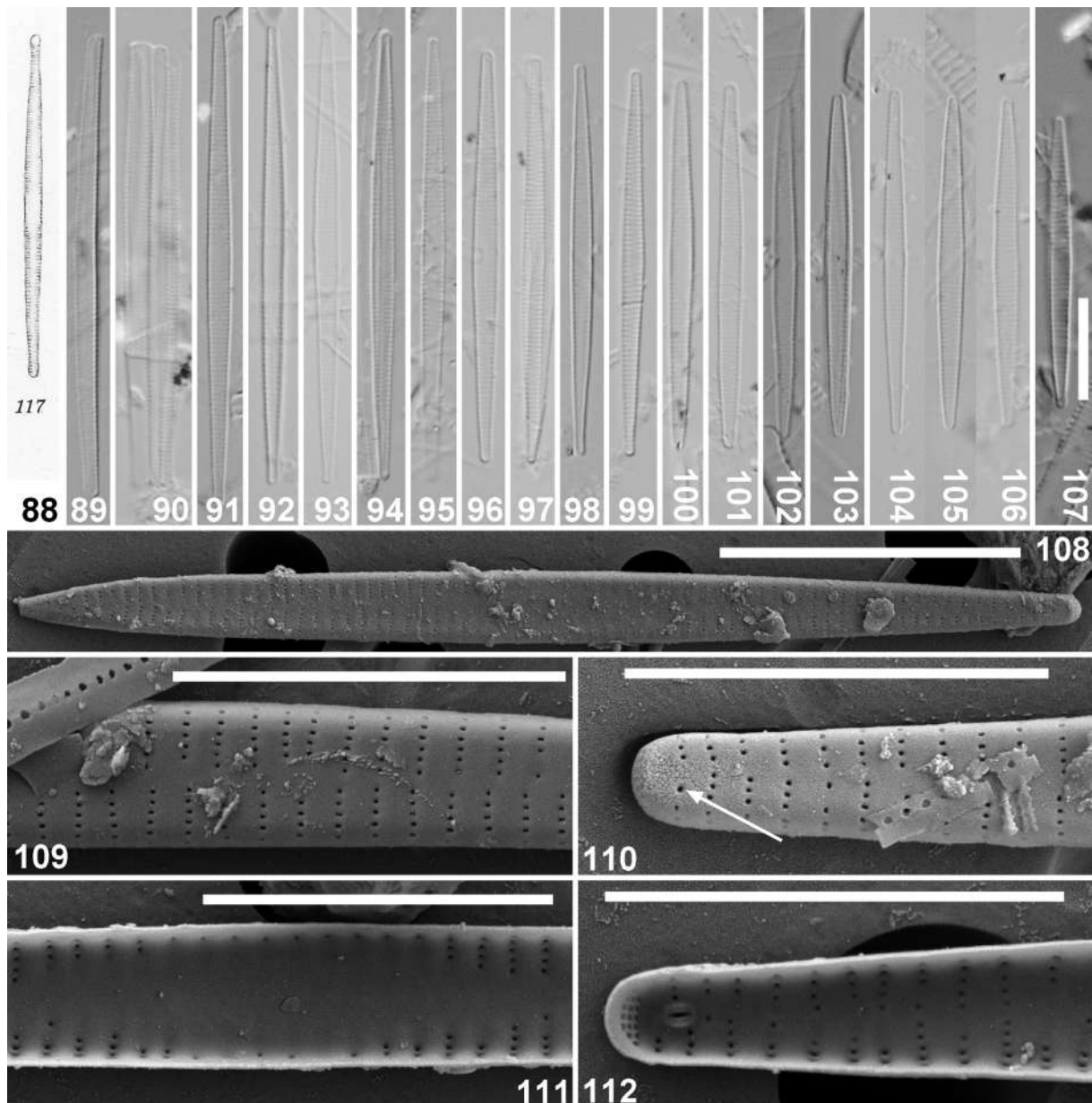
(C. Agardh) Grunow, *Reimeria sinuata* (Gregory) Kociolek et Stoermer and *Nitzschia dissipata* (Kützing) Grunow. This composition is a mixture of more mesotrophic and meso–eutrophic taxa with low to moderate saprobity levels and higher electrolyte contents (LANGE–BERTALOT et al. 2017). A better analysis of the *Fragilaria radians* populations in Europe will be necessary to establish the correct ecological preferences of this taxon.

***Fragilaria gracilis* Østrup 1910 (Figs 88–112)**

Original description: *Fragilaria gracilis* Østrup (1910), Danske Diatomeer p. 190, pl. V, fig. 117 (represented by our Fig. 88) \equiv *Fragilaria capucina* var. *gracilis* (Østrup) Hustedt 1950

LM (Figs 89–107): Frustules in girdle view rectangular, narrow, solitary or two cells connected to each other. Ribbon–like colonies of more than 3 cells together not observed. Valves linear to narrowly lanceolate with weakly but gradually tapering margins from central area to apices. Apices almost not protracted, occasionally very slightly rostrate, usually acutely rounded. Valve dimensions ($n=20$): length 29–48 μm , width 2.0–2.5 μm . Sternum very narrow but discernible in LM, linear, slightly widening near the central area. Central area moderately large, forming a clear rectangular hyaline area. Marginal striae in the central area unilaterally present in smaller specimens. Striae alternating or opposite (mostly near the apices), parallel throughout entire valve, 21–24 in 10 μm . Areolae not discernible in LM.

SEM (Figs 108–112): sternum clearly present, separating both sides of the striation, linear (Figs 108, 109) becoming narrower at the apices (Fig. 110). Spines, or vestiges of spines, not observed (Fig. 108). Ghost striae barely visible in the central area (Figs 108, 111). Valve face flat, virgae not raised (Fig. 108). Striae uniseriate, composed of very small, rounded to squarish areolae (Fig. 109). Apical pore field of the ocellulimbus type, covering the entire apex mantle, composed of 3–4 rows of very



Figs 88–112. *Fragilaria gracilis* Østrup. LM and SEM images taken from the lectotype material (ØSTRUP 1342): (88) original drawing taken from ØSTRUP (1910); (89–90) LM views of several frustules in girdle view, solitary or arranged in pairs; (91–107) LM views of the population arranged in decreasing length; (108) SEM external view of entire valve; (109) SEM external detail of the striae near the central area. Both opposite and alternating striae are present. (110) SEM external detail of the valve apex with the rimoportula (arrow); (111) SEM internal detail of central area; (112) SEM internal detail of a valve apex showing the rimoportula. Scale bar 10 µm (88–108) and 5 µm (109–112).

large, rounded poroids (Fig. 110). External rimoportula opening small, rounded, rimmed, replacing one areola in one of the last striae (Fig 110, arrows). Internally, central area clearly very large, bordered by only a few very short striae (Fig. 111). Rimoportula transapically elongated (Fig. 112).

Lectotype: C–A–9908, Østrup sample 1342, Botanic Garden Copenhagen, Denmark (lectotypified in KRAMMER & LANGE–BERTALOT 1991, p. 450), archived at C!. Figure 94 represents the lectotype.

Associated diatom flora: The lectotype sample of

F. gracilis was collected from a pool in the Botanic Garden of Copenhagen. The sample is dominated by (in decreasing order of abundance) *Fragilaria aequalis* Heiberg, *Diatoma problematica* Lange–Bertalot, *Navicula gregaria*, *Nitzschia dissipata*, *F. radians* (formerly *F. gracilis*) and *Achnanthisdium* cf. *jackii* Rabenhorst. Other taxa that were frequently observed in the lectotype slide, include *Navicula slesvicensis* Grunow, *Nitzschia paleacea* (Grunow) Grunow and *Gomphonella olivacea*. This species composition is typical for (meso–) eutrophic running waters with higher organic pollution and, especially, high electrolyte content, which contradicts the currently accepted idea that *Fragilaria radians* is

typical in oligo- to mesotrophic, oligosaprobic rivers (LANGE-BERTALOT et al. 2017).

Taxonomic remarks: For a long time, *Fragilaria gracilis* Østrup (ØSTRUP 1910) was considered to be part of the morphological variation of *F. capucina*. HUSTEDT (1932) raised doubts on the identity of *F. gracilis* basing his decision on the original description ØSTRUP published in 1910. In 1950, HUSTEDT finally recombined the taxon as *F. capucina* var. *gracilis* Hustedt but the single illustrated valve does not correspond to the type of *F. gracilis* as discussed later in TUJI (2007). Authors such as PATRICK & REIMER (1966) and LANGE-BERTALOT (1980) did not mention *F. gracilis* in their revisions and it was only KRAMMER & LANGE-BERTALOT (1991, p. 123) who added the ‘*gracilis*-Sippen’ to their *F. capucina* complex and lectotypified the species using Østrup sample 1342, suggesting it may indeed represent an independent species. Additionally, KRAMMER & LANGE-BERTALOT (1991) indicated that the species may have been found before but under different names. Comparison of the lectotype material of *F. gracilis* with the lectotype of *F. radians* showed that both are likely conspecific making *F. gracilis* a younger synonym of *F. radians*. Due to changes in the correct concept for *F. radians* in the nineteenth century (see above) and confusion with other narrow, linear *Fragilaria* species such as *F. famelica*, the species seems almost entirely absent from older literature prior to 1910. The illustrated valves in KRAMMER & LANGE-BERTALOT (1991, plate 111, figs 1–3) were taken from Kützing sample 189 (slide BM 18185), a sample collected near Kølma (Finland) and seem to be conspecific with *F. gracilis*. The sample, however, is listed in the handwritten Kützing catalogues kept in BR and BM as being dominated by *Synedra famelica* (B. VAN DE VIJVER, pers. obs.). Finally, TUJI (2007) studied the type material of *F. gracilis* but published only a few LM images of the type and did not compare his observations with the morphology of other taxa.

***Fragilaria pseudolaevissima* VanLandingham 1971 (Figs 113–139)**

Original description: ØSTRUP (1910), Danske Diatomeer p. 191, pl. V: fig. 119, cited by VANLANDINGHAM (1971), who provided a new name: Catalogue of the fossil and recent genera and species of diatoms and their synonyms, Part IV, p. 1816. (represented by our Fig. 113) ≡ *Fragilaria laevissima* Østrup 1910, nom. illeg., non *Fragilaria laevissima* Cleve 1898

LM (Figs 114–134): Valves linear to narrowly lanceolate with almost parallel to gradually narrowing margins and very weakly protracted, acutely rounded to slightly rostrate apices. Valve dimensions (n=20): length 25–42 µm, width 2.0–2.5 µm. Sternum narrow but distinct in LM, linear, gradually widening from the apices towards the central area. Central area rather small, forming an unclear hyaline area, usually bordered by several marginal striae. Striae usually alternating, becoming opposite near the apices, parallel throughout entire valve, 19–20 in 10

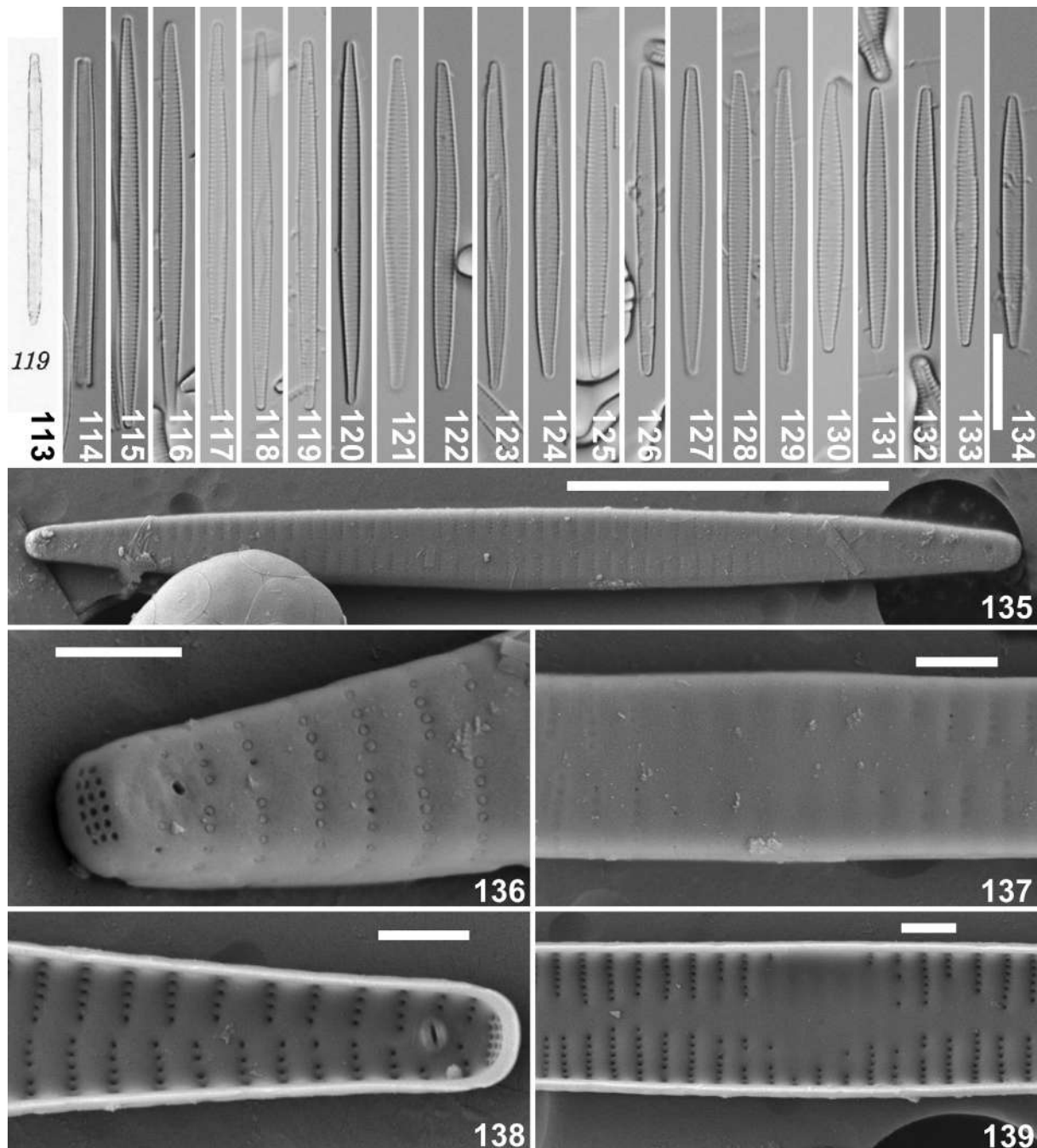
µm. Areolae not discernible in LM.

SEM (Figs 135–139): sternum narrow but distinct, lanceolate (Figs 135, 136) becoming narrower at the apices (Fig. 136). Spines, or vestiges of spines, not observed (Fig. 137). Ghost striae only weakly visible in the central area (Fig. 139). Valve face flat, virgae only weakly raised (Fig. 135). Striae uniseriate, composed of very small, rounded areolae (Fig. 136), externally covered by individual vola (Fig. 136). Apical pore field of the ocellulimbus type, moderately large, composed of 3 rows of very large, rounded poroids (Fig. 136). External rimoportula opening small, rounded, replacing one areola in one of the last striae, positioned close to the sternum (Figs 136, 137, arrows). Internally, rimoportula oblique (Fig. 138). Central area clearly large, unilateral, bordered by a few shortened striae (Fig. 139).

Analysed material: BR-4695, slide made from sample 8681, Kandestederne, Jutland, Denmark, (type material *F. laevissima*) archived at C! Figure 119 represents the lectotype.

Associated diatom flora: The type slide for *F. pseudolaevissima* is dominated by three *Fragilaria* species: *F. radians* (as *F. pseudolaevissima*), *F. heudreana* Van de Vijver, C.E. Wetzel et Ector, sp. nov. and *F. cf. henryi*. Other important species in the sample include *Meridion circulare* (Greville) C. Agardh, *Cymboplectra cf. naviculiformis* (Auerswald) Krammer, *Navicula eidrigiana* Carter, *Stauroneis producta* Grunow and several *Neidium* and *Pinnularia* species. This assemblage may point to a freshwater habitat with higher electrolyte content as some of the prominent species (e.g. *S. producta*, *F. cf. henryi*) can even be found in brackish conditions (LANGE-BERTALOT et al. 2017).

Taxonomic remarks: ØSTRUP (1910) described a second narrow-celled *Fragilaria* species, *F. laevissima* Østrup in the same publication where he described *F. gracilis* (Figs 88–112). As this name was a younger homonym for a species earlier described by CLEVE in 1898 as *F. laevissima* Cleve and later transferred to the raphid genus *Humidophila* as *H. laevissima* (Cleve) R.L. Lowe et al. (LOWE et al. 2014), the species was renamed *Fragilaria pseudolaevissima* VanLandingham (VANLANDINGHAM 1971). ØSTRUP (1910) only reported the species from one sample, collected in Kandestederne, near Skagen (Jutland, Denmark). The drawing that accompanied the description shows a very narrow linear valve with parallel margins and hardly protracted, weakly rostrate apices. In the type material, three different *Fragilaria* taxa were found in high abundances but none of the observed populations shows some similarity with the drawing in ØSTRUP (1910, pl. 5, fig. 119). One of the populations, composed of valves with a valve width > 4 µm, is described here below as *F. heudreana* Van de Vijver, C.E. Wetzel et Ector sp. nov. (Figs 438–476). Most likely KRAMMER & LANGE-BERTALOT (1991, p.



Figs 113–139. *Fragilaria pseudolaevissima* VanLandingham. LM and SEM images taken from the lectotype material (ØSTRUP 8681): (113) original drawing taken from ØSTRUP (1910); (114) LM view of a frustule in girdle view; (115–134) LM views of the population arranged in decreasing length; (135) SEM external view of entire valve; (136) SEM external detail of the valve apex with the rimoportula and the apical pore field; (137) SEM external detail of the central area with the faint ghost striae; (138) SEM internal detail of a valve apex showing the rimoportula; (139) SEM internal detail of central area. Scale bar 10 µm (113–135) and 1 µm (136–139).

122) based their decision to consider *F. pseudolaevissima* as a synonym for *F. rumpens* on this population. Since these valves cannot be conspecific with the drawing in ØSTRUP (1910), this synonymizing should not be considered correct. A second taxon, having distinct, in LM very discernible areolae, shows some similarity with *F. henryi* Lange–Bertalot. The third population (Figs 113–134) corresponds to the drawing in ØSTRUP (1910). However, analysis of the population shows all

morphological features of the type of *F. radians*, and based on these observations, it is highly likely that both taxa are conspecific. Therefore *F. pseudolaevissima* is added as a heterotypic synonym of *F. radians*.

***Fragilaria utermoehlii* (Hustedt) Lange–Bertalot 1993 (Figs 140–165)**

Basionym: *Synedra utermoehlii* Hustedt (HUSTEDT 1932): Die Kieselalgen Deutschlands, Österreichs und der Schweiz unter Berücksichtigung der übrigen Länder Europas sowie der angrenzenden Meeresgebiete.

Vol. VII. Teil 2. Lieferung 2, p. 185, fig. 687.

LM (Figs 140–159, 163): Frustules rectangular, not linked to each to form ribbon-like colonies. Frustules joined in bundle-like aggregates (Fig. 163). Valves linear to linear-lanceolate with weakly convex margins and non-protracted, acutely rounded apices. Valve dimensions (n=25): length 10–37 µm, width 2–3 µm. Sternum very narrow, linear, not to very weakly widening near the central area. Central area asymmetrical, often forming a rectangular to unilateral hyaline area. Shortened striae often present bordering on one side the central area. Striae parallel, usually opposing throughout the entire valve, alternating striae occasionally present (Fig. 115), 20–22 in 10 µm. Areolae not discernible in LM.

SEM (Figs 160–162, 164–165): Spines, or vestiges of spines, not observed. Valve face flat, virgae not to very weakly raised (Fig. 160). Striae uniseriate, composed of very small, rounded to weakly apically elongated areolae (Figs 160, 161). Ghost striae present in the central area (Figs 161, 164). Apical pore field of the ocellulimbus type, moderately large, composed of 3 rows of large, rounded poroids (Fig. 162). External rimoportula opening isolated, rounded, located at the sternum at one apex (Fig. 162). Internally, rimoportula straight, large, isolated, aligned with striae (Fig. 165).

Holotype (according to SIMONSEN 1987, p. 132): BRM K1/10, sample E4360, Dobersdorfer See, Schleswig-Holstein, Germany, coll. date 12.V.1921, leg. F. Hustedt, conserved in BRM! The type is represented by pl. 217: figs 1, 2 in SIMONSEN (1987).

Associated diatom flora: The type sample of *F. utermoehlii*, collected in a small lake not far from the German harbour of Kiel (Schleswig-Holstein) is almost entirely dominated by *F. crotonensis* Kitton, a very typical planktonic species, usually found in larger, meso- to eutrophic, weakly alkaline, moderately electrolyte-rich lakes and larger rivers (KRAMMER & LANGE-BERTALOT 1991). Only *F. utermoehlii* is present with a few valves. Dobersdorfer See is considered a calcareous, eutrophic lake with a high pH between 8 and 8.5 and a higher electrolyte content (LANDESAMT FÜR WASSERHAUSHALT UND KÜSTEN SCHLESWIG-HOLSTEIN 1995).

Taxonomic remarks: HUSTEDT (1932) described a colony-forming, rather finely striated species, *Synedra utermoehlii* Hustedt, from the Dobensdorfer See in Holstein (Germany) and classified the species together with *Synedra berolinensis* Lemmermann in the subgenus *Belonastrum*. The only feature combining these two taxa was the bundle-starshaped colonies he observed. LANGE-BERTALOT (in KRAMMER & LANGE-BERTALOT 1991, p. 127) invalidly transferred the species to the genus *Fragilaria* by forgetting to add the basionym. In 1993, LANGE-BERTALOT validated the transfer as *F. utermoehlii* (Hustedt) Lange-Bertalot. *Fragilaria utermoehlii* is

rarely reported in Europe and is generally considered to be planktonic (KRAMMER & LANGE-BERTALOT 1991). The most characteristic feature of the species is the presence of typical, bundle-shaped colonies, that, according to KRAMMER & LANGE-BERTALOT (1991, p. 127) seem to be the only discriminating feature to separate the species from *F. radians* (reported under the name *F. gracilis*). Following the morphological description in KRAMMER & LANGE-BERTALOT (1991), both species seem to differ also by the larger central area in *F. radians* (as *F. gracilis*), the longer, more elongate valves and the more acutely ending apices in the latter and the alternating striae, whereas *F. utermoehlii* has opposing striae.

Analysis of the type material of *F. utermoehlii*, revealed, however, a high similarity to *Fragilaria radians*. In the type of *F. utermoehlii*, valves with alternating striae could be observed. On the other hand, other *F. radians* populations showed smaller, less elongate valves, similar to the valves observed in the type material of *F. utermoehlii*. It is not clear whether the species really produces star-shaped colonies or whether the observed aggregates of frustules only represent bundles of frustules formerly attached to aquatic plants of macroalgae and detached during sampling. Since these differences are rather variable, we consider the species to be a heterotypic synonym of *F. radians*.

***Fragilaria aquaplus* Lange-Bertalot et S.Ulrich 2014**

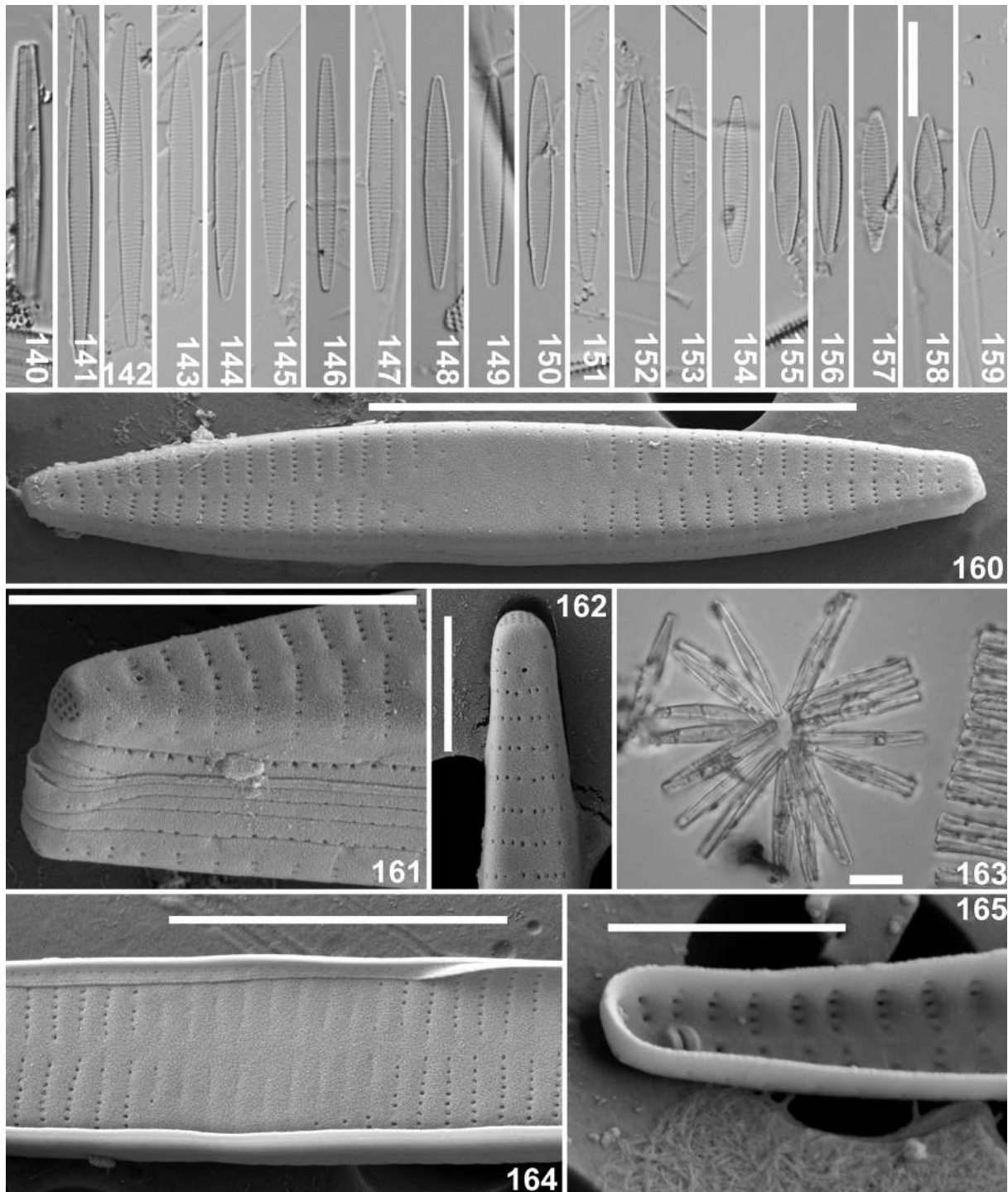
Fragilaria aquaplus is described based on a small population observed in a sample FRIEDRICH MEISTER collected in August 1905 from Lago della Crocetta (currently named Lagh da la Cruseta) in the Bernina Alps (canton of Graubünden, Switzerland). This sample, Meister 624, is the type material for another *Fragilaria* species, described as *Synedra nana* F.Meister (MEISTER 1912; LANGE-BERTALOT & ULRICH 2014). MEISTER originally did not separate *F. aquaplus*. It was only in 2014 that LANGE-BERTALOT & ULRICH described it, naming the species after the company Aquaplus in Switzerland who helped with getting access to the MEISTER collection. In the present paper, the original MEISTER material was investigated but only a handful of valves could be found (Figs 166–176). Therefore, a recent sample from Lagh da la Cruseta was kindly provided by Dr J. HÜRLIMANN (Aquaplus, Zug, Switzerland) containing a large population of *F. aquaplus*. As the analysis of this population provided important additions to our understanding of the species, the sample is formally added as epitype to the holotype assigned in LANGE-BERTALOT & ULRICH (2014, p. 32).

***Fragilaria aquaplus* Lange-Bertalot et S.Ulrich 2014 (Figs 166–215)**

Original description: *Fragilaria aquaplus* Lange-Bertalot et S.Ulrich (2014), p. 32, pl. 13, figs 15–19, pl. 14, figs 9–14.

Registration: <http://phycobank.org/102955>

LM (Figs 166–209): Frustules in girdle view rectangular, narrow, solitary or two cells connected to each other.

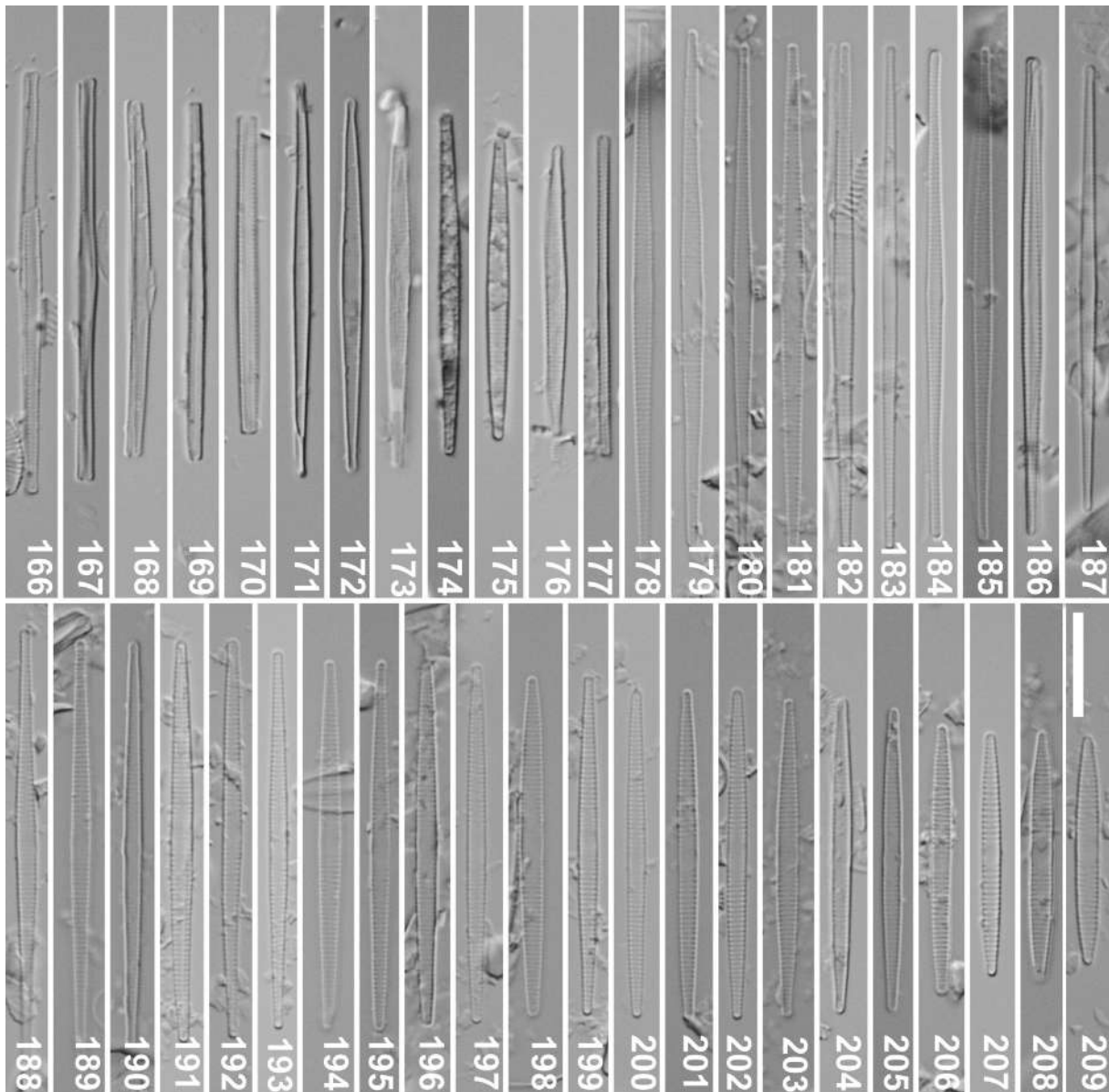


Figs 140–165. *Fragilaria utermoehlii* (Hustedt) Lange–Bertalot. LM and SEM images taken from the lectotype material (HUSTEDT E4360): (140) LM view of a frustule in girdle view; (141–159) LM views of the population arranged in decreasing length; (160) SEM external view of entire valve; (161) SEM external view of an entire frustule in oblique view; (162) SEM external detail of the valve apex with the rimoportula and the apical pore field; (163) LM image of a bundle-shaped colony; (164) SEM external detail of the central area with the distinct ghost striae; (165) SEM internal detail of a valve apex showing the rimoportula. Scale bar 10 μm (140–161, 163), 5 μm (164) and 1 μm (162, 165).

Ribbon-like colonies of more than 3 cells not observed. Valves needle-shaped, narrowly lanceolate with weakly but gradually tapering margins from central area to apices. Apices weakly to not protracted, slightly rostrate to acutely rounded. Valve dimensions (n=30): length 20–50 μm , width 1.5–2.5 μm . Sternum not visible at the apices,

only very slightly formed at the central area. Central area large, rectangular, occasionally weakly expanded. Ghost striae occasionally present. Striae opposite, parallel throughout entire valve, 22–24 in 10 μm . Areolae not discernible in LM.

SEM (Figs 210–215): sternum slightly, but visibly



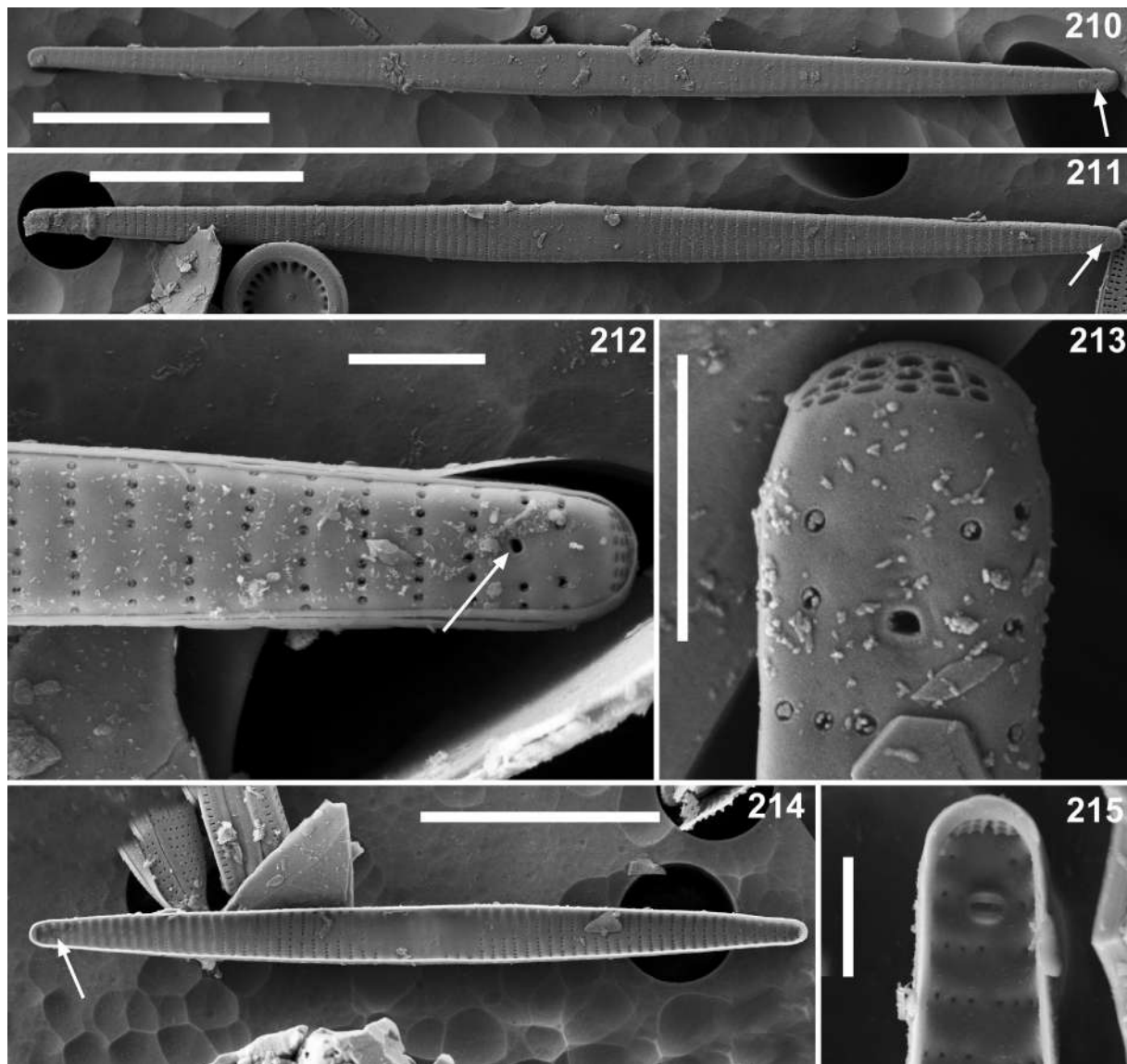
Figs 166–209. *Fragilaria aquaplus* Lange–Bertalot et S.Ulrich. LM images taken from the lectotype material (MEISTER sample 624, Figs 166–176) and the epitype material (HÜRLIMANN 5236, BR–4696, Figs 177–209): (166–170, 177) LM views of several solitary frustules in girdle view; (171–176, 178–209) LM views of the population arranged in decreasing length. Scale bar 10 μ m.

widening at valve centre (Figs 210, 211) to almost completely non-existing at the apices (Fig. 212), almost not discernible. Spines, or vestiges of spines, not observed (Fig. 210). Ghost striae visible in the central area (Fig. 210). Valve face entirely flat, virgae not raised (Fig. 210). Striae uniseriate, composed of very small, rounded areolae (Figs 211, 212), externally occluded by individual vela (Fig. 213). Apical pore field of the ocellulimbus type, moderately large, composed of 3 rows of large, rounded poroids (Fig. 213). External rimoportula opening large, rounded, replacing one areola in the before last stria, close to sternum at one apex (Figs 210–213, arrows). Internally, central area clearly very large, bordered by only a few very short striae (Fig. 214). rimoportula straight, aligned with virga (Figs 214, arrow, 215).

Holotype: Eu–CH–53 in coll. Lange–Bertalot (FR), assigned in LANGE–BERTALOT & ULRICH (2014), p. 35, slide made from sample Meister 624 (Lago della Crocetta, Switzerland, coll. date 11.VIII.1905, leg. F. Meister) in Coll. Meister (Z!).

Epitype (here designated for the above-mentioned holotype of *F. aquaplus*): BR–4696 prepared from sample Hürlimann 5236 (Lagh da la Cruceta, canton Graubünden, Switzerland northern shore, alt. 2307 m a.s.l., coll. date 04.VIII.2015, leg. J. Hürlimann), material archived in the Van Heurck collection (BR!). Figure 195 represents the epitype.

Associated diatom flora: Lago della Crocetta, the small lake from where *Fragilaria aquaplus* was described,



Figs 210–215. *Fragilaria aquaplus* Lange–Bertalot et Ulrich. SEM images taken from the epitype material (HÜRLIMANN 5236, BR–4696): (210, 211) SEM external views of an entire valve. The arrows indicate the position of the rimoportulae. (212) SEM external detail of the valve apex with the rimoportula (arrow). Note the almost absence of a sternum at the apices and the typically opposite striae. (213) SEM external detail of the valve apex with the rimoportula and an apical pore field. (214) SEM internal view of an internal valve. The arrow indicates the rimoportula. (215) SEM internal detail of a valve apex showing the rimoportula. Scale bar 10 μm (210–211, 214) and 1 μm (212, 213, 215).

has a diatom flora composed of several cymbelloid taxa such as *Cymbella langebertalotii* Krammer, *C. vulgata*, *Delicatophycus delicatulus* (Kützing) M.J. Wynne and *Encyonopsis subminuta*, several *Achnanthisidium* species, *Denticula tenuis*, *Fragilaria tenera* var. *nana* (F. Meister) Lange–Bertalot, *Navicula radiosa* Kützing and *Tryblionella brunoi* (Lange–Bertalot) Cantonati et Lange–Bertalot. This diatom composition is typical for oligo–mesotrophic, oligosaprobic, calcium–bicarbonate rich, alkaline lakes and rivers (LANGE–BERTALOT et al. 2017).

Taxonomic remarks: *Fragilaria aquaplus* resembles *F. radians* but can be separated based on several morphological criteria: 1. due to very narrow, almost non–existing sternum, the opposing striae in *F. aquaplus* seem to be

continue from margin to margin, which is never the case in *F. radians* where the striae are alternating with a broader sternum; 2. *F. aquaplus* has a slightly narrower valve width (1.5–2.5 μm) compared to *F. radians* (2.0–3.0 μm). The newly described *F. neglecta* has linear valves with strictly parallel margins whereas *F. aquaplus* has narrowly lanceolate valves with gradually narrowing margins from the central area to the apices. Moreover, *F. aquaplus* possesses a well–developed central area whereas the latter is absent in *F. neglecta*. *Fragilaria acerosa*, another new species from Sweden (see below), has shorter, narrower valves with acutely ending, never protracted apices. *Fragilaria aquaplus* also shows some resemblance to *F. huerlimannii* Van de Vijver sp. nov., especially when comparing the valve dimensions. The

latter, however, can be separated in possessing a distinct sternum reaching almost the apices, a slightly swollen central area and more distinctly protracted apices.

***Fragilaria huerlimannii* Van de Vijver sp. nov.**

A large population of a narrow-celled *Fragilaria* species was recorded in a sample from the Fiume Ticino, in the Riviera region near the town of Biasca (canton Ticino, Switzerland). Although the observed valves initially would have been identified as *F. gracilis* (now *F. radians*), the valves would represent the narrowest of all *radians*-populations with valves often narrower than the minimum valve width (2.0 µm) given for *F. radians*. Moreover, almost all observed specimens possessed clearly protracted, weakly capitate apices and a slightly swollen central area. Comparison with all examined *F. radians* populations excluded all conspecificity and therefore this Swiss population is described as a new species: *F. huerlimannii* Van de Vijver sp. nov.

***Fragilaria huerlimannii* Van de Vijver sp. nov. (Figs 216–243)**

Registration: <http://phycobank.org/102956>

LM (Figs 216–238): Frustules in girdle view rectangular, solitary. Ribbon-like colonies with more than 2 cells not observed. Valves needle-shaped, narrowly lanceolate with gradually tapering margins towards the protracted, rostrate to weakly capitate apices. Valve dimensions (n=30): length 20–50 µm, width 1.5–2.0 µm. Sternum narrow but clearly discernible in LM, gradually widening from apices to central area. Central area large, forming a clear hyaline zone, weakly, occasionally distinctly swollen. Ghost striae not visible in the central area. Striae opposite or alternate, parallel throughout the entire valve, 20–21 in 10 µm. Areolae not discernible in LM. **SEM** (Figs 239–243): Valve face flat, virgae not raised above the valve surface (Fig. 240). Spines entirely absent (Fig. 239). Striae uniseriate, composed of small, rounded areolae, externally covered by individual vela (Figs 240, 242). Central area lacking (Fig. 240) or with very faint ghost striae (Fig. 241). Apical pore field of the ocellulimbus type, rather small, composed of 3 short rows of large, rounded poroids (Fig. 242). External rimoportula opening located at one apex on the sternum between the before last striae, small, rounded, distinctly rimmed and surrounded by shallow ridges (Figs 240, 242). Internally, virgae only very weakly raised. Rimoportula straight, perpendicular on the sternum, large, isolated (Fig. 243).

Holotype: BR-4697 (BR, Meise Botanic Garden, Belgium), slide made from Hürlimann Sample 6671. Figure 227 represents the holotype.

Isotype: Slide-394 (University of Antwerp, Belgium)

Type locality: sample Hürlimann 6671 (Fiume Ticino, canton Ticino, Switzerland, alt. 305 m a.s.l., coll. date 08.VII.2020, leg. J. Hürlimann), material kept in BR!

Etymology: The new species is named after our dear

colleague Joachim Hürlimann (Aquaplus, Zug, Switzerland) in honour of his significant contributions on the Swiss freshwater diatom flora.

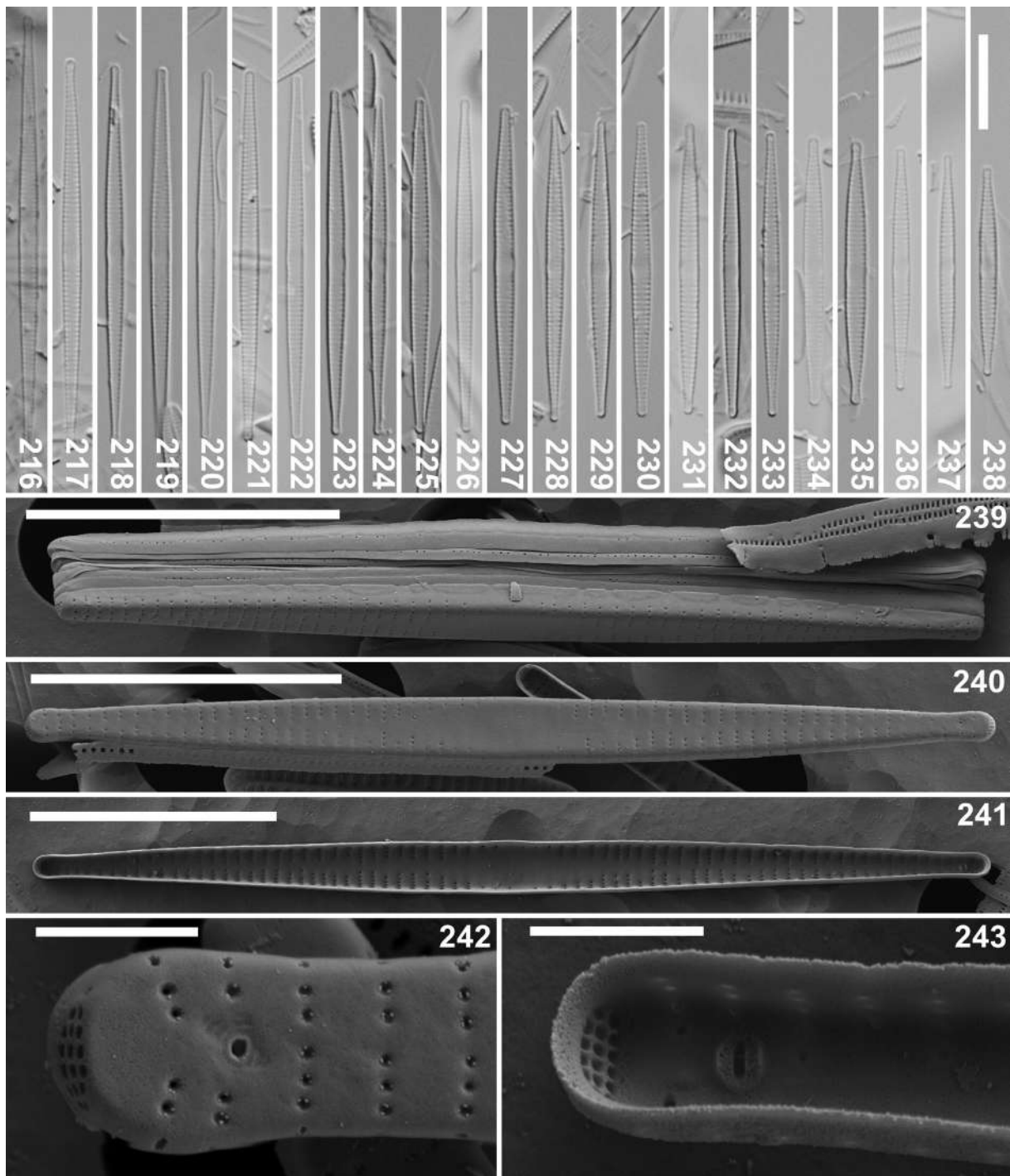
Associated diatom flora: The type sample is dominated by *Fragilaria huerlimannii*, *Achnantheidium pyrenaicum* (Hustedt) H.Kobayasi (including *A. rostrypyrenaicum* Jüttner et E.J.Cox), *A. delmontii* Pérès et al., *A. cf. microcephalum*, *Diatoma ehrenbergii* Kützing, *Encyonema silesiacum* (Bleisch) D.G.Mann with minor abundances of *Cocconeis lineata* Ehrenberg, *Reimeria sinuata*, *Ulnaria cf. ulna* (Nitzsch) Compère and *Gomphonema tergestinum* (Grunow) M.Schmidt. The sample was taken from a small, shallow river in a limestone area and was characterized by a rather medium-low conductivity (178 µS.m⁻¹) (HÜRLIMANN, pers. comm.). Based on the species composition, especially the presence of *D. ehrenbergii* and *Achnantheidium pyrenaicum*, the sample would be classified as moderately calcium-bicarbonate enriched, oligo- to mesotrophic with low levels of organic pollution (LANGE-BERTALOT et al. 2017).

Taxonomic remarks: *Fragilaria huerlimannii* differs from *F. radians* in having narrower, more linear-lanceolate valves (max. 2 µm in width compared to 2–3 µm in *F. radians*), a consistently slightly swollen, distinct central area and almost always protracted, rostrate to capitate apices. *Fragilaria radians* has a more linear, very gradually tapering valve outline and lacks the protracted apices and instead possesses acutely rounded, rarely rostrate apices. *Fragilaria aquaplus* differs in less protracted, more linear valves, distinctly lacking a sternum and with a less inflated central area. The newly described *F. acerosa* Van de Vijver et al. sp. nov. and *F. neglecta* Van de Vijver et al. sp. nov. (see below) can be separated by their smaller to even absent central area, the often not-protracted, very acutely rounded apices and the lack of a central inflation.

Two *Fragilaria* taxa related to *F. radians* from oligotrophic rivers in northern Europe

In northern Europe, populations of narrow-celled, finely striated *Fragilaria* species are often observed and usually identified as *F. gracilis* (now *F. radians*). These populations are mostly found in very oligotrophic, slightly acidic to almost circumneutral environments and differ from the type material of *F. radians* as illustrated and discussed hereabove. Within these populations, two well separable taxa can be distinguished, showing a consistent set of morphological features to allow the characterization of these two taxa. Since we were unable to identify known taxa in literature, conspecific with the two Nordic taxa, they are described as new species: *Fragilaria acerosa* Van de Vijver, C.E.Wetzel, Jarlman et Ector sp. nov. and *F. neglecta* Van de Vijver, C.E.Wetzel, Jarlman et Ector sp. nov.

The first taxon, *F. acerosa*, is the most variable in



Figs 216–243. *Fragilaria huerlimannii* Van de Vijver sp. nov. LM and SEM images taken from the holotype material (HÜRLIMANN 6671, BR–4697): (216–238) LM views of the population arranged in decreasing length; (239) SEM external view of entire frustule in oblique view. Note the mantle plaques. (240) SEM external view of an entire valve; (241) SEM internal view of an internal valve; (242) SEM external detail of the valve apex with the rimoportula and the apical pore field; (243) SEM internal detail of a valve apex showing the rimoportula. Scale bar 10 μm (216–241) and 1 μm (242–243).

outline and size ranges. Therefore, several populations collected from Swedish rivers are presented, showing the broad variability of the species. Since it is impossible to separate the different populations and since they are always found in mixed morphologies under the same ecological conditions, they are considered to belong to the same species. The second species, however, *F.*

neglecta, shows a constant morphology in all samples where it was encountered, and clearly differs from all *F. acerosa*–populations. Although both species were occasionally found in the same samples, intermediate valves between both taxa could at present not be observed and therefore, these populations are split off as a separate species.

***Fragilaria acerosa* Van de Vijver, C.E.Wetzel, Jarlman et Ector sp. nov. (Figs 244–410)**Registration: <http://phycobank.org/102957>

LM (Figs 244–291): Frustules in girdle view rectangular, very narrow, solitary or two cells connected to each other. Ribbon-like colonies with more than 2 cells not observed. Longer valves elongated, needle-shaped, linear to very narrowly lanceolate with weakly protracted, acutely rounded apices. Shorter valves more lanceolate, with gradually narrowing margins towards the weakly protracted, very acutely rounded apices. Valve dimensions (n=100): length 13–70 µm, width 1.5–2.5 µm. Sternum narrow but distinct, gradually widening from apices to the central area. Central area very small due to irregular shortening of a few central striae. Striae alternating, parallel throughout entire valve, 18–22 in 10 µm. Areolae not discernible in LM.

SEM (Figs 292–298): Spines, or vestiges of spines, not observed (Figs 292, 293). Valve face flat, virgae not to very weakly raised (Fig. 294, 297). Striae uniseriate, composed of small, rounded areolae (Figs 294–296). Apical pore field of the ocellulimbus type, moderately large, composed of only 3 rows of large, rounded poroids (Fig. 295). External rimoportula opening isolated, rounded, close to sternum at one apex (Fig. 296), rimmed. Internally, rimoportula straight, almost rounded, isolated, aligned with virga (Fig. 298).

Holotype: BR-4698 (BR, Meise Botanic Garden, Belgium), slide made from sample Haraldsjöån. Figure 264 represents the holotype.

Isotype: Slide-395 (University of Antwerp, Belgium)

Type locality: Haraldsjöån, Västmanlands län, Sweden (coll. date 06.IX.2005, leg. A. Jarlman).

Analysed material: various Swedish rivers, all leg. A. Jarlman: Haraldsjöån (Sandån Övre, Skinnskatteberg, Sweden, coll. date 30.IX.2004), Hammarbäcken (Härjedalen, Sweden, coll. date 10.IX.2005, BR-4699), Stridbäcken (Nordmaling, Sweden, coll. date 24.IX.2004, BR-4700), Norrhultsbäcken (Åseda, Sweden, coll. date 04.X.2004, BR-4701) and Bjurbäcken (Burträsk, Sweden, coll. date 23.IX.2004, BR-4702), all material kept in BR!

Associated diatom flora: The type sample for *F. acerosa* was collected from a small river (Haraldsjöån) that flows out of Lake Haraldsjön. The river has a slightly acid pH (6.3), a low conductivity (<30 µS.cm⁻¹) with low nutrient concentrations. The sample is dominated by *Achnanthydium minutissimum* (Kützing) Czarnecki, *Brachysira microcephala* (Grunow) Compère, *Encyonopsis subminuta* Krammer, *Eunotia incisa* W.Gregory, *F. acerosa*, *Frustulia crassinervia* (Brébisson ex W.Smith) Lange-Bertalot et Krammer and *Tabellaria flocculosa*. Another large population of *F. acerosa* was collected from Hammarbäcken (Sweden) (Figs 299–345). The latter sample is dominated by *Achnanthydium minutissimum*, *F. acerosa*, *Rossethidium pusillum* (Grunow)

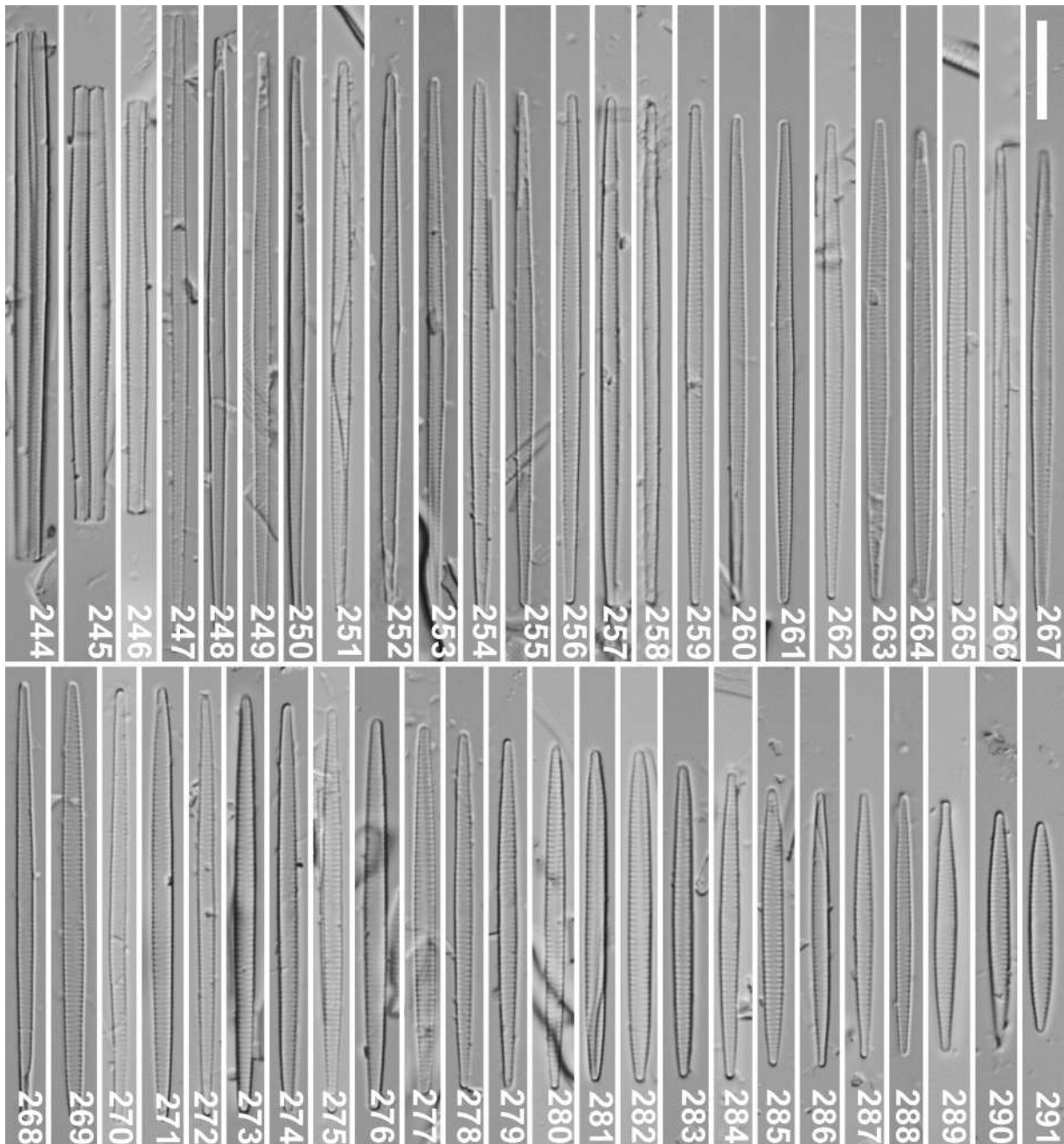
Round et Bukhtiyarova, several *Eunotia* taxa such as *E. paratridentula* Lange-Bertalot et Kulikovskiy, *E. incisa*, *E. minor* (Kützing) Grunow and *E. implicata* Nörpel, Lange-Bertalot et Alles, along with *Tabellaria flocculosa* and *Frustulia erifuga* Lange-Bertalot et Krammer. Measured pH was 6.3. Other measured parameters include a conductivity of <25 µS.cm⁻¹, a TN of 265 µg.l⁻¹ and a TP of 14 µg.l⁻¹. The species composition in both samples point to dystrophic to oligotrophic, very electrolyte poor, acidic to circumneutral running water environments on siliceous bedrock (LANGE-BERTALOT et al. 2017).

Taxonomic remarks: *Fragilaria acerosa* has commonly been identified as *F. gracilis* (now *F. radians*) in northern European rivers and shows a broad range in morphological variability. The illustrated populations from Haraldsjöån (Figs 244–298), Hammarbäcken (Figs 299–345), Bjurbäcken (Figs 346–366), Norrhultsbäcken (Figs 367–387) and Stridbäcken (Figs 388–410) all show part of the cell diminution series of this species. Some populations (Haraldsjöån, Stridbäcken) have, besides the more common smaller valves, some large specimens, whereas other sites (Hammarbäcken, Norrhultsbäcken) only have smaller valves. Similar observations have also been made for *Fragilaria radians*, highlighting the importance of a good analysis on and above the population level.

The new species can be separated from *Fragilaria radians* in having a typical needle-shaped valve outline with very acutely ending apices, a lower valve width never exceeding 2.5 µm with most valves remaining below 2.0 µm in width, and by its very small central area. In contrast *F. radians* has a rather large, rectangular central area, a feature never observed in *F. acerosa*, and on average a higher valve width (>2.5 µm). *Fragilaria neglecta* is longer (up to 70 µm), has strictly parallel (not convex, lanceolate) margins, more bluntly rounded apices and lacks almost completely a central area. *Fragilaria aquaplus* has a more lanceolate valve outline, lacks a distinct sternum, has opposite striae and less acutely rounded apices. *Fragilaria huerlimannii*, described from Switzerland, has a distinct, slightly swollen central area and always protracted, weakly capitate apices contrary to the almost absent central area in *F. acerosa*.

***Fragilaria neglecta* Van de Vijver, C.E.Wetzel, Jarlman et Ector sp. nov. (Figs 411–437)**Registration: <http://phycobank.org/102958>

LM (Figs 411–432): Frustules in girdle view rectangular, solitary or two cells connected to each other. Ribbon-like colonies not observed. Valves linear with strictly parallel margins and not protracted, broadly rounded apices throughout entire cell diminution series. Valve dimensions (n=30): length 30–70 µm, width 1.5–2.0 µm. Sternum narrow but distinct, lanceolate throughout the entire valve length. Central area absent to very small due to unilateral shortening of a few central striae



Figs 244–291. *Fragilaria acerosa* Van de Vijver, Jarlman, C.E.Wetzel et Ector sp. nov. LM images taken from the holotype material (Haraldsjöän, Sweden, BR-4698): (244–246, 277) LM views of several frustules in girdle view, solitary or in pairs; (247–291) LM views of the population arranged in decreasing length. Scale bar 10 μ m.

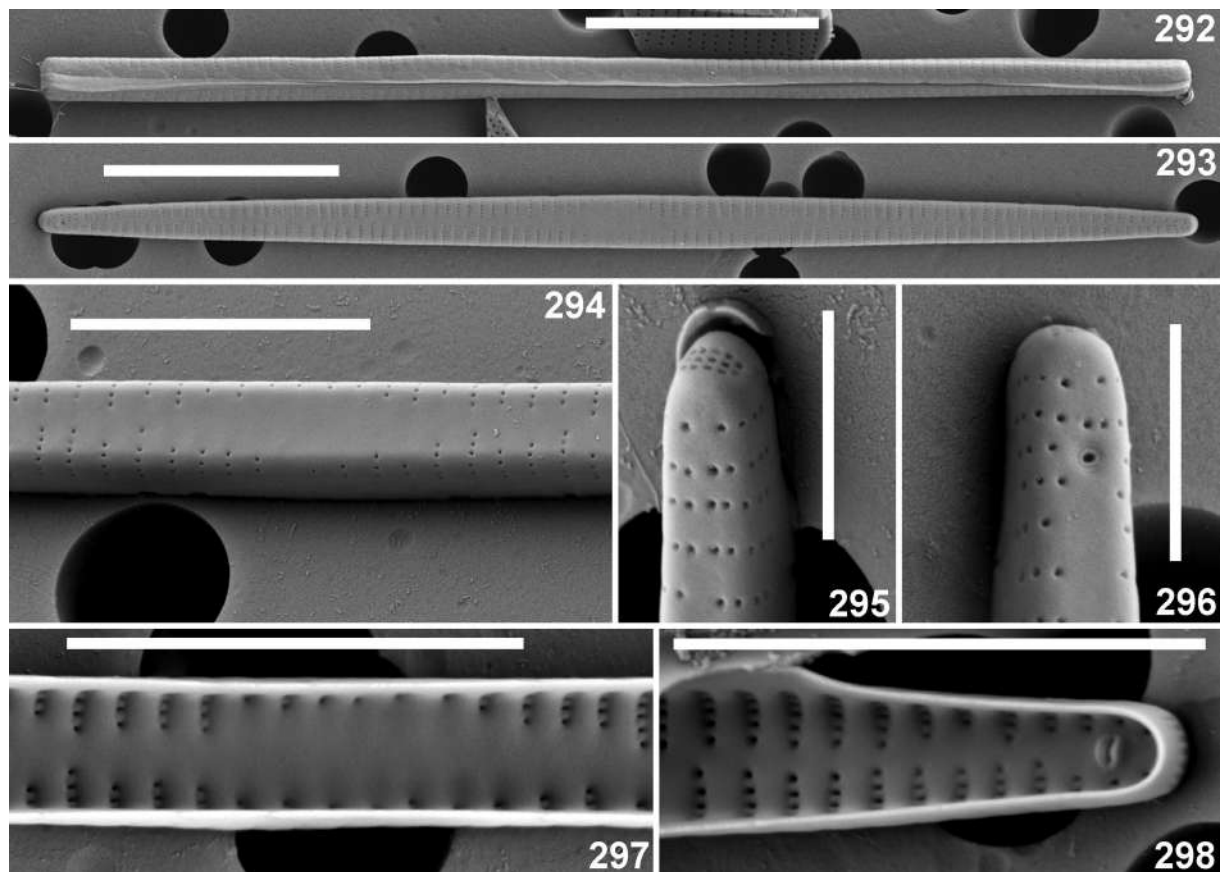
(Fig. 429). Striae alternating, parallel to weakly radiate throughout entire valve, 20–21 in 10 μ m. Areolae not discernible in LM.

SEM (Figs 433–437): Very large (elongated) plaques present at the mantle edge along the entire valve length (Fig. 433). Spines, or vestiges of spines, not observed. Valve face entirely flat, virgae not raised (Figs 434, 436). Striae uniseriate, composed of very small, rounded to transapically elongated areolae (Figs 434, 435), externally occluded by individual vela (Fig. 435). Apical pore field of the ocellulimbus type, moderately large, composed of 4 rows of large, rounded poroids (Fig.

435). External rimoportula opening rounded, rimmed, replacing one areola in last stria, close to sternum at one apex (Fig. 435). Internally, rimoportula straight, aligned with virga (Fig. 437).

Holotype: BR-4703 (BR, Meise Botanic Garden, Belgium), slide made from sample Mälskarbäcken. Figure 420 represents the holotype.

Isotype: Slide-396 (University of Antwerp, Belgium)
Type locality: Mälskarbäcken, Vilhelmina Kommun, Västersbotten, Sweden (coll. date 12.IX.2005, leg. A. Jarlman).

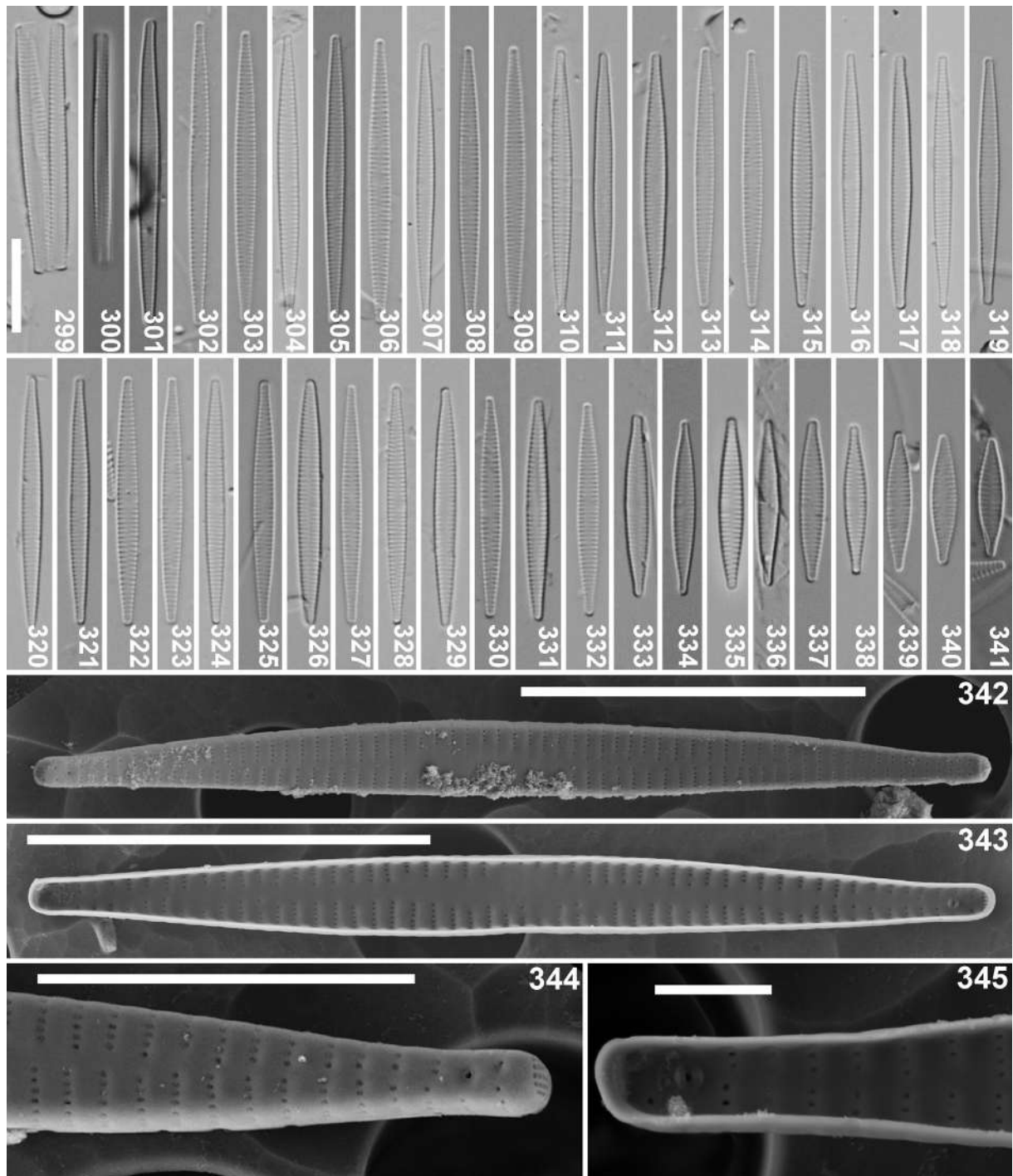


Figs 292–298. *Fragilaria acerosa* Van de Vijver, Jarlman, C.E.Wetzel et Ector sp. nov. SEM images taken from the holotype material (Haraldsjöån, Sweden, BR-4698): (292) SEM external view of an entire frustule in oblique view; (293) SEM external view of an entire valve; (294) SEM external detail of the central area; (295) SEM external detail of the valve apex with the apical pore field without a rimoportula; (296) SEM external detail of the valve apex with the rimoportula; (297) SEM internal detail of the central area; (298) SEM internal detail of a valve apex showing the rimoportula. Scale bar 10 μm (292, 293), 5 μm (294, 297, 298) and 2 μm (295, 296).

Associated diatom flora: The type sample for *F. neglecta* is dominated (in decreasing abundance) by *Brachysira microcephala*, *Tabellaria flocculosa* (Roth) Kützing, *F. neglecta*, *Frustulia crassinervia*, *Eunotia bilunaris* (Ehrenberg) Schaarschmidt, *Encyonema neogracile* Krammer, *Kobayasiella pseudostauron* (Lange–Bertalot) Lange–Bertalot, and *Gomphonema* cf. *exilissimum* (Grunow) Lange–Bertalot et E.Reichardt. This is a diatom community typical for very oligotrophic, oligosaprobic, electrolyte–poor, mildly acidic water bodies (LANGE–BERTALOT et al. 2017), indicating a high level of water quality. Measured chemical parameters for the river in September 2005 indicate a pH of 6.5, low TP (11 $\mu\text{g.l}^{-1}$) and TN (228 $\mu\text{g.l}^{-1}$) concentrations.

Taxonomic remarks: *Fragilaria neglecta* is one of the species that always has been identified as *F. gracilis* (JARLMAN, pers. obs.), mostly given its thin, slender outlook and high stria density. Similar valves have at present not been illustrated in the literature. The valve depicted in KRAMMER & LANGE–BERTALOT (1991, plate 111, fig. 6) has a similar outline but individual areolae are discernible in LM, which is never the case in *F. neglecta*. The new species differs from the type population of *F.*

radians in having a linear valve outline with strictly parallel margins (contrary to the more linear–lanceolate outline of *F. radians*), non–protracted apices (*F. radians* has weakly rostrate to subcapitate apices), an almost absent central area (the latter clearly present in *F. radians*) and a slightly lower valve width (1.5–2.0 μm vs. 2.0–2.5 μm in *F. radians*). *Fragilaria aquaplus* possesses similar valve dimensions with a valve width never exceeding 2.0 μm but can be separated based on the presence of a distinct central area, less parallel valves giving *F. aquaplus* a narrowly lanceolate (and not a linear) valve outline, a higher stria density (21–23 in 10 μm versus 20–21 in 10 μm for *F. neglecta*). Moreover, the sternum in *F. aquaplus* is almost non–existing giving the non–alternating striae the impression of continuing from margin to margin, a feature never observed in *F. neglecta*. *Fragilaria acerosa*, also described in this paper, has smaller valves in its cell diminution series (length down to 13 μm) with a more lanceolate valve outline (lacking parallel margins), a distinct, though small, central area and very acute apices.

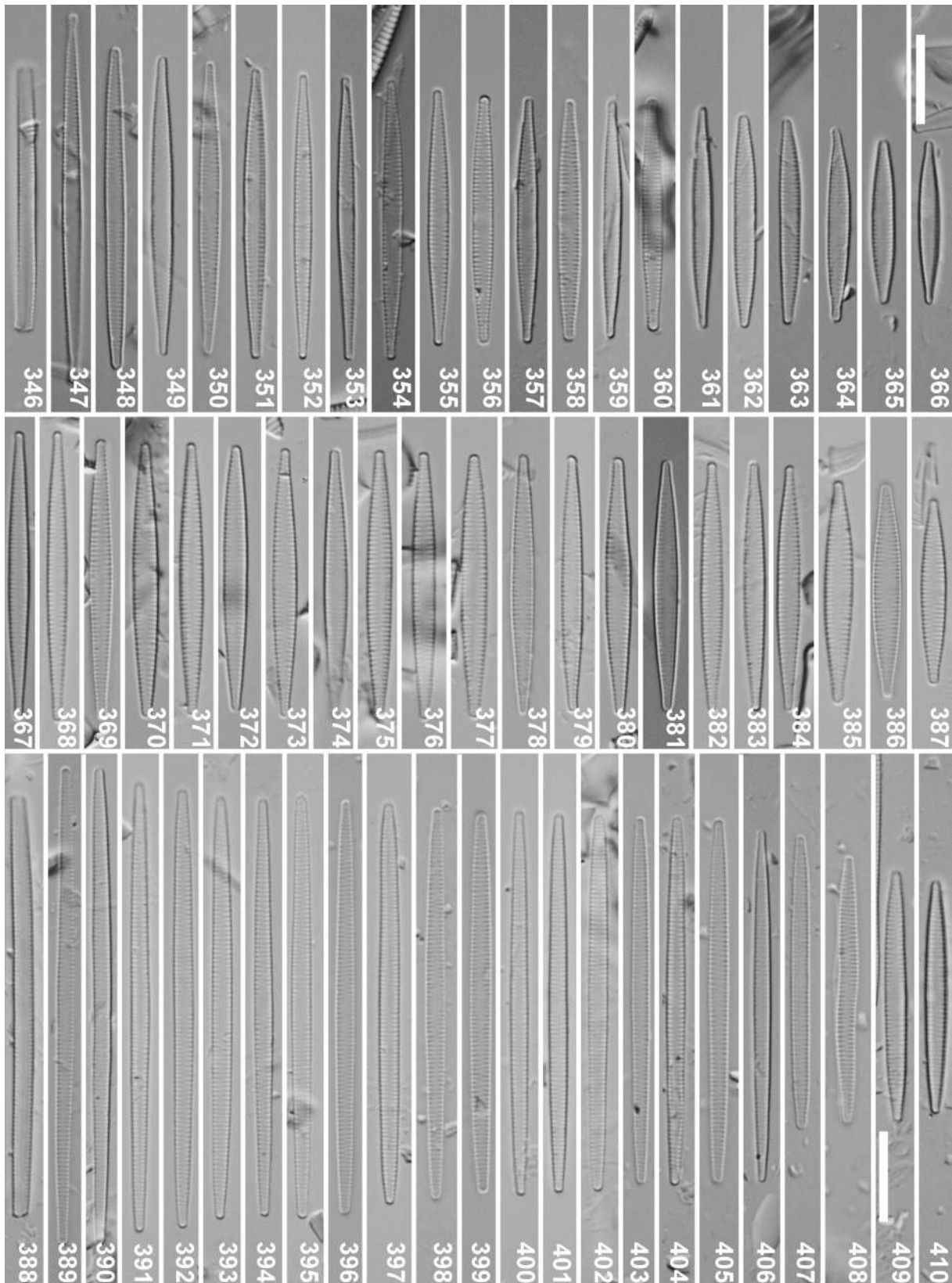


Figs 299–345. *Fragilaria acerosa* Van de Vijver, Jarlman, C.E.Wetzel et Ector, sp. nov. LM images taken from Hammarsbäcken, Sweden (BR-4699): (299, 300) LM views of entire frustules in girdle view; (301–341) LM views of the population arranged in decreasing length; (342) SEM external view of an entire valve; (343) SEM internal view of an entire valve; (344) SEM external detail of the valve apex with the apical pore field and the rimoportula; (345) SEM internal detail of a valve apex showing the rimoportula. Scale bar 10 μ m (299–343), 5 μ m (344) and 1 μ m (345).

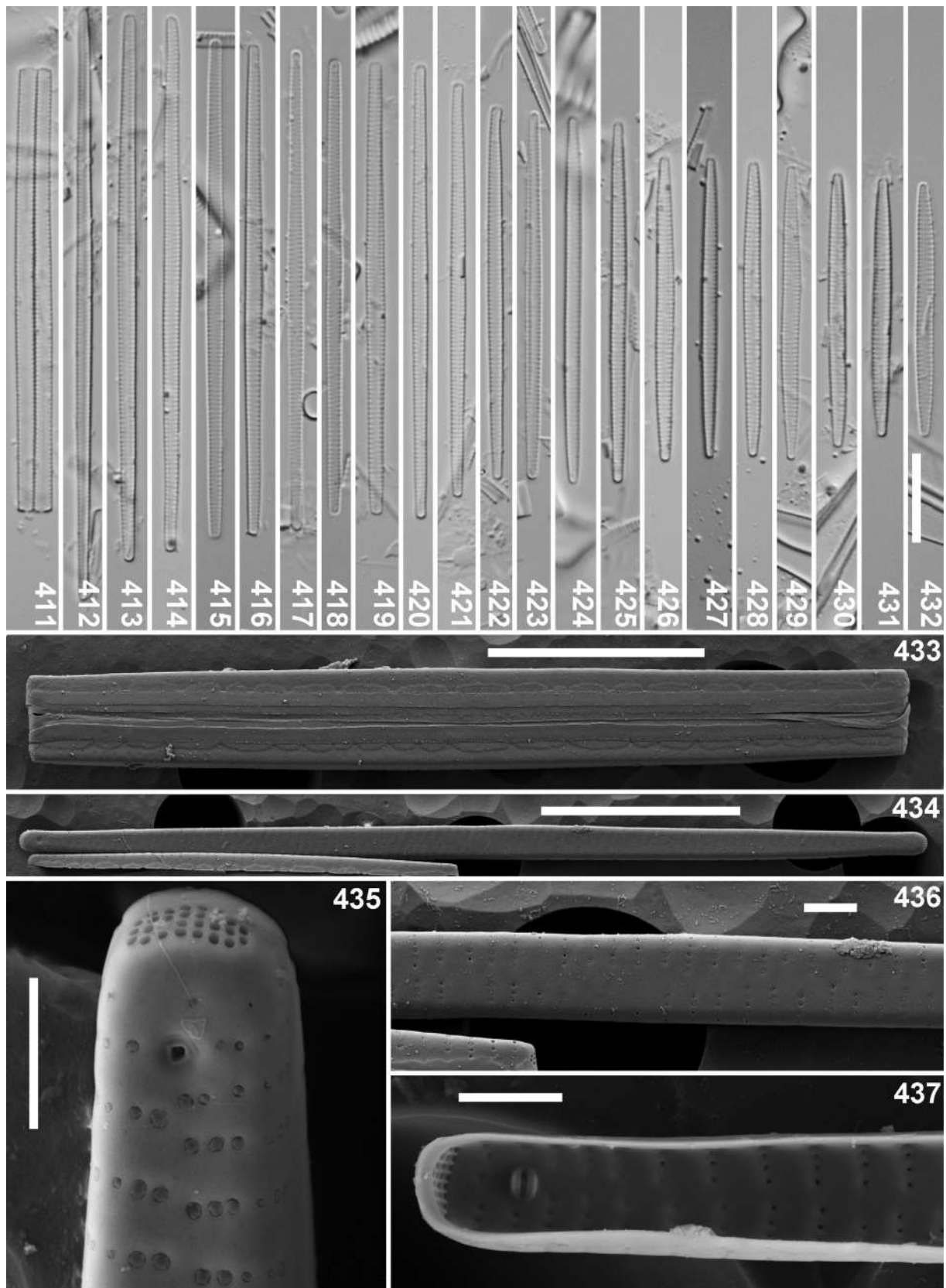
***Fragilaria heudreana* Van de Vijver, C.E.Wetzel et Ector sp. nov.**

In the type material for *Fragilaria pseudolaevissima* VanLandingham (illegitimately published as *F. laevissima* Østrup 1910), two *Fragilaria* taxa showing some similarity to *F. radians* could be identified. A first, with very narrow valves, was identified as *F. pseudolaevissima*

and is now considered being a heterotypic synonym of *F. radians* (see above). The second, however, has broader valves and shows a higher similarity to *F. rumpens* than to *F. radians*, due to its broader valves and slightly rostrate apices. This taxon was illustrated in KRAMMER & LANGE-BERTALOT (1991, pl. 110, fig. 4) as a valve belonging to *F. laevissima*, a species they considered as a synonym



Figs 346–410. *Fragilaria acerosa* Van de Vijver, Jarlman, C.E.Wetzel et Ector sp. nov. LM images taken from several Swedish rivers showing the variability in valve length: Stridbäcken, Sweden (BR–4700, Figs 346–366), Norrhultsbäcken, Sweden (BR–4701, Figs 367–387) and Bjurbäcken, Sweden (BR–4702, Figs 388–410): (346, 388) represent frustules in girdle view. All other Figs: LM views of the population arranged in decreasing length. Scale bar 10 μ m.



Figs 411–437. *Fragilaria neglecta* Van de Vijver, Jarlman, C.E. Wetzel et Ector sp. nov. LM and SEM images taken from the holotype population (Målskarbäcken, Sweden, BR–4703): (411) LM view of two connected frustule in girdle view; (412–432) LM views of the population arranged in decreasing length; (433) SEM external view of an entire frustule in girdle view; (434) SEM external view of an entire valve; (435) SEM external detail of the valve apex with the apical pore field and the rimoportula; (436) SEM external detail of the central part of the valve showing the absence of a distinct central area; (437) SEM internal detail of a valve apex showing the rimoportula. Scale bar 10 μm (411–434) and 1 μm (435–437).

of *F. rumpens* (KRAMMER & LANGE–BERTALOT 1991, p. 122). However, ribbon-like colonies, one of the typical features of *F. rumpens* have so far not been observed in the Østrup material and hence conspecificity with *F. rumpens* should be doubted. As the observed population also showed important differences with the type of *F. radians* and other similar taxon could not be found in literature, the population from Østrup sample 8681 is described as a new taxon: *Fragilaria heudreana* Van de Vijver, C.E. Wetzel et Ector sp. nov.

***Fragilaria heudreana* Van de Vijver, C.E. Wetzel et Ector sp. nov. (Figs 438–476)**

Registration: <http://phycobank.org/102959>

LM (Figs 438–471): Frustules in girdle view rectangular, solitary or with two cells connected to each other. Ribbon-like colonies with more than 2 cells not observed. Valves linear to narrowly lanceolate with almost parallel margins, only very gradually tapering towards the protracted, rostrate apices. Valve dimensions (n=40): length 12–50 µm, width 3.0–5.0 µm. Sternum narrow to occasionally moderately broad (Figs 462, 464), distinct, gradually widening from apices to central area. Central area unilateral, forming a large, irregularly shaped hyaline area, bordered by several shortened striae. Ghost striae very prominently present in the central area. Striae distinctly alternating, parallel becoming more radiate near the apices, 18–21 in 10 µm. Areolae not discernible in LM. **SEM** (Figs 472–476): Regular series of small, conical spines present on the valve face/mantle junction (Figs 472, 473). At the apices, several blunt spines present (Figs 472–474). Valve face flat, virgae distinctly raised (Fig. 472). Striae uniseriate, composed of small weakly apically elongated areolae, externally covered by individual vela (Figs 472, 474). Ghost striae present in the central area (Fig. 473). Apical pore field of the ocellulimbus type, distinct, large, composed of 3 long rows of large, rounded, rimmed poroids (Fig. 474). External rimoportula opening small, rounded, located at one apex on the sternum between the last striae, small, rounded (Figs 472, 474, arrows). Internally, virgae likewise raised (Fig. 476). Rimoportula clearly oblique, large, isolated, replacing some areolae in the last stria (Fig. 475).

Holotype: BR–4695 (BR, Meise Botanic Garden, Belgium), slide made from Østrup sample 8681. Figure 443 represents the holotype.

Isotype: Slide–397 (University of Antwerp, Belgium)

Type locality: Kandestederne, Jutland, Denmark, Østrup sample 8681 archived at C!

Etymology: The new species is named after our dear colleague David Heudre (DREAL Grand Est, France) in honour of his significant contributions on the European freshwater diatom flora.

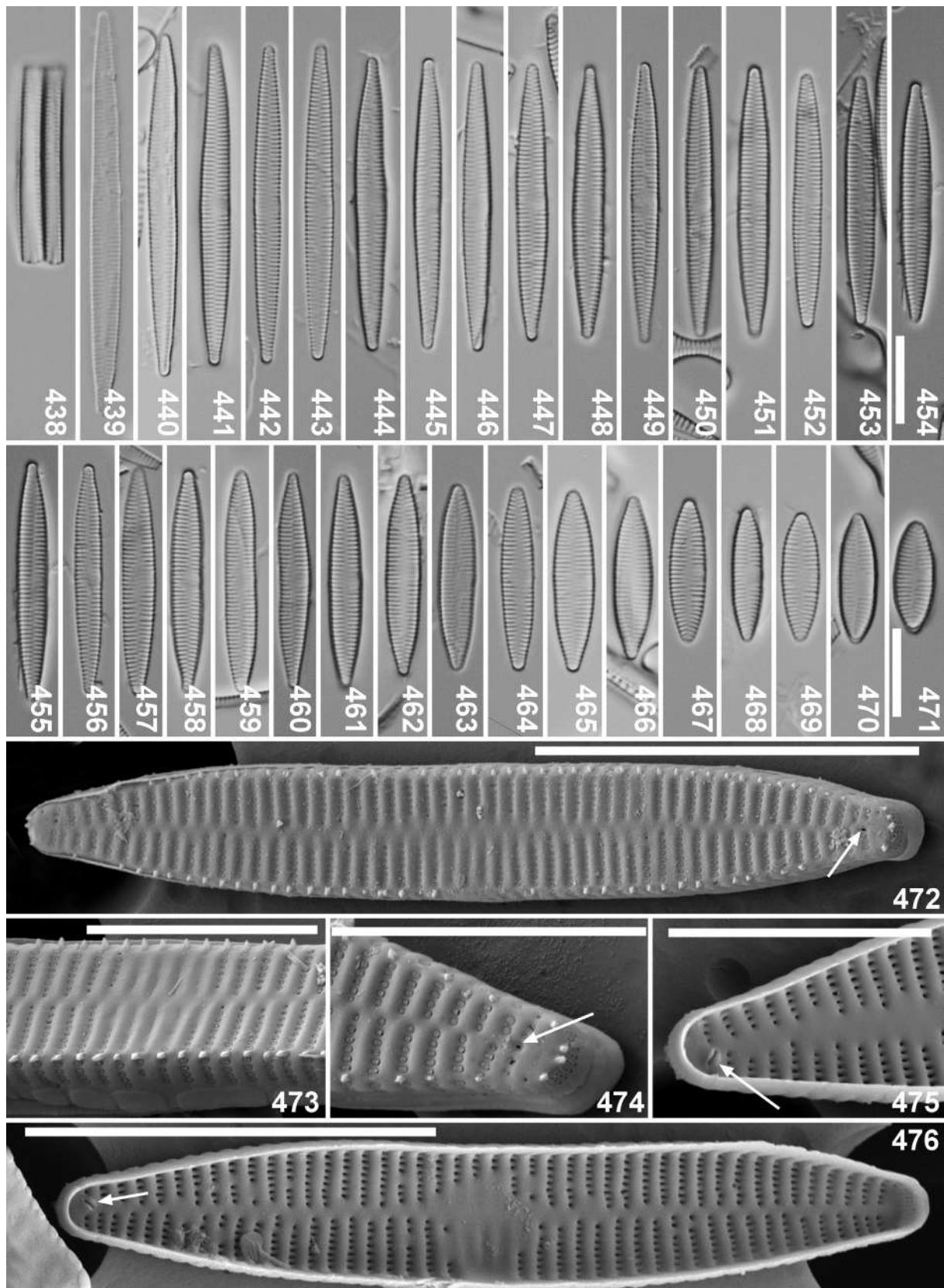
Associated diatom flora: The type sample is dominated

by three *Fragilaria* species: *F. radians*, *F. heudreana*, and *F. cf. henryi*. Other important species in the sample include *Meridion circulare* (Greville) C. Agardh, *Cymboplectra cf. naviculiformis* (Auerwald) Krammer, *Navicula eidrigiana* J.R. Carter, *Stauroneis producta* Grunow, and several *Neidium* and *Pinnularia* species. This assemblage may point to a freshwater habitat with higher electrolyte content as some of the dominant species (e.g. *S. producta*, *F. cf. henryi*) can even be found in brackish conditions (LANGE–BERTALOT et al. 2017).

Taxonomic remarks: *Fragilaria heudreana* differs from *F. radians* in having broader valves (up to 5 µm in width compared to 2–3 µm in *F. radians*), a typical but distinct asymmetrical central area, distinct but small marginal non-linking spines, entirely surrounding the valve margin (*F. radians* does not possess spines), more robust looking, less lanceolate valves. The main difference with *F. rumpens* is the total absence of ribbon-like colonies, despite the presence of small, conical spines that should, however, not be considered as linking spines. The newly described *F. eutrappenta* Van de Vijver, Kusber et D.M. Williams sp. nov. (see below), can be separated based on its total lack of marginal spines, the longer valves and the larger hyaline central area.

Two new *Fragilaria* species formerly identified as *F. gracilis* or *F. rumpens* from eutrophic rivers in Belgium

In several (meso–)eutrophic rivers in Flanders, the northern part of Belgium, several large populations of at least two different *Fragilaria* taxa were observed, formerly identified as *F. gracilis* (now *F. radians*) or *F. rumpens*. Morphological analysis of both taxa excluded conspecificity with *F. rumpens* as none of them produces ribbon-like colonies, a typical feature for *F. rumpens* (VAN DE VIJVER et al. 2022). On the other hand, the morphology of these two new taxa also differ sufficiently from *F. radians* based on a higher valve width (> 3 µm), a consistently broader sternum or a different valve outline with clearly protracted, elongated, rostrate apices, justifying their separation as independent taxa. A first taxon, hereby described as *Fragilaria eutrappenta* Van de Vijver, C.E. Wetzel et Ector sp. nov., is widespread in Europe with records (usually reported as *F. gracilis* or *F. rumpens*) from Belgium (VAN DE VIJVER, unpubl. res.), Switzerland (HÜRLIMANN & STRAUB 1991), Italy (VAN DE VIJVER, unpubl. res.) and France (PEETERS & ECTOR 2017). The species is the largest of all taxa in the *F. radians* complex and is characterized by its broad, almost linear valves with weakly protracted, cuneately ending to rostrate apices. The second species, *F. mertensiana* Van de Vijver, C.E. Wetzel et Ector sp. nov., possesses a large central area, a relatively broad, lanceolate sternum and protracted, very distinctly elongated, rostrate apices, features not observed so far in *F. radians* (see above).



Figs 438–476. *Fragilaria heudreana* Van de Vijver, C.E.Wetzel et Ector sp. nov. LM and SEM images taken from holotype material (ØSTRUP 8681, BR–4695): (438) LM view of two connected frustule in girdle view; (439–471) LM views of the population arranged in decreasing length; (472) SEM external view of an entire valve. Note the presence of the marginal spines, the distinctly raised virgae and rimoportula (arrow). (473) SEM external detail of the central area with the ghost striae; (474) SEM external view of the valve apex with the apical pore field and the rimoportula (arrow). Note also the larger spines on the apex. (475) SEM internal detail of a valve apex showing the rimoportula (arrow); (476) SEM internal view of an entire valve showing the position of the rimoportula (arrow). Scale bar 10 μm (438–472, 476) and 5 μm (473–475).

***Fragilaria eutrappenta* Van de Vijver, Kusber et D.M. Williams sp. nov. (Figs 477–520)**Registration: <http://phycobank.org/102960>

LM (Figs 477–514): Frustules in girdle view narrow, rectangular, solitary or very occasionally two cells connected to each other. Ribbon-like colonies with more than 2 cells not observed. Valves almost linear to narrowly lanceolate with parallel margins, only very gradually tapering towards the slightly protracted, weakly rostrate apices. Valve dimensions (n=50): length 20–75 µm, width 3.0–4.0 µm. Sternum moderately narrow, distinct, gradually widening from apices to central area. Central area forming a large, irregularly shaped hyaline area, occasionally irregularly bordered by several shortened striae. Striae alternating, parallel throughout entire valve, 18–20 in 10 µm. Areolae not discernible in LM.

SEM (Figs 515–520): Valve face entirely flat, virgae not raised (Fig. 515). Spines, or vestiges of spines, not observed on the valve face (Figs 515, 516). Striae uniseriate, composed of very small, rounded areolae (Figs 515, 516), externally occluded by individual vela (Fig. 517). Central area large, hyaline, ghost striae absent. Sternum near the central area distinctly widening (Fig. 516). Apical pore field of the ocellulimbus type, rather small, composed of 4 rows of large, rounded poroids (Fig. 517). External rimoportula opening rounded, almost in the middle of or very close to the sternum, at one apex (Fig. 517). Internally, virgae weakly raised (Figs 519, 520). Rimoportula internally straight to weakly oblique, positioned in the middle of the sternum (Fig. 520).

Holotype: BR–4704 (BR, Meise Botanic Garden, Belgium), slide made from sample RIKA_DE_BIE_017. Figure 487 represents the holotype.

Isotype: Slide–398 (University of Antwerp, Belgium)

Type locality: River Grote Nete, Balen, Province of Antwerp, Belgium, sample RDB–17, (51°9′29.63″N, 05°11′25.19″E, coll. date 03.V.1995, leg. B. Van de Vijver)

Associated diatom flora: The type sample for *F. eutrappenta* is dominated by *Gomphonema parvulum*, *Fragilaria* cf. *pectinalis* (O.F.Müller) Lyngbye, *F. eutrappenta*, *Navicula rhynchocephala* Kützing, *N. cryptocephala* Kützing, and *Frustulia vulgaris* (Thwaites) De Toni. Small numbers of *Fragilariforma virescens* (Ralfs) D.M. Williams et Round and *Eunotia bilunaris* were observed. The new species was, however, observed in a large number of lowland rivers in Flanders. All samples were dominated by species that, according to LANGE–BERTALOT et al. (2017), point to higher trophic conditions with moderate saprobity (up to β–mesosaprobic) and circumneutral to slightly acidic conditions.

Taxonomic remarks: *Fragilaria eutrappenta* is most similar to *Fragilaria rumpens* based on valve dimensions, but differs in not forming ribbon-like colonies, the absence of linking spines, and a more linear, less

lanceolate valve outline (VAN DE VIJVER et al. 2022). Similarly, the new species can also be distinguished from *Fragilaria capucina* based on the absence of linking spines and hence the absence of colony-formation. Moreover, *F. capucina* possesses one rimoportula at each apex, contrary to *F. eutrappenta* that only has a rimoportula at one apex (VAN DE VIJVER et al. 2021b). *Fragilaria radians* has narrower valves (max. valve width < 3 µm) giving them a slender outlook, less protracted, almost not rostrate apices, a narrower sternum, especially near the central area and usually opposite, less alternating striae (see above).

***Fragilaria mertensiana* Van de Vijver, C.E. Wetzel et Ector sp. nov. (Figs 521–546)**Registration: <http://phycobank.org/102961>

LM (Figs 521–545): Frustules solitary or very occasionally two cells connected to each other. Ribbon-like colonies with more than 2 cells not observed. Valves (narrowly) lanceolate with clearly convex, never parallel margins. Margins at valve centre even weakly convex. Apices distinctly protracted, subcapitate to rostrate. Valve dimensions (n=20): length 15–40 µm, width 2.5–3.0 µm. Sternum broad, distinct, clearly widening at the central area. Central area forming a large, rectangular hyaline area, occasionally irregularly bordered by several shortened striae. Striae rather short, alternating or opposite, parallel throughout entire valve, 17–20 in 10 µm. Areolae not discernible in LM.

SEM (Fig. 546): Valve face flat, virgae hardly raised and much wider than the areolae (Fig. 546). Marginal spines absent. Sternum very broad. Striae uniseriate, composed of rather small, rounded areolae and towards the axial area by one very shallow surface depression (Fig. 546). Rimoportula rimmed, rounded, located almost on the sternum (Fig. 546, arrow). Apical pore field of the ocellulimbus type, composed of 4 rows of large, rounded pores. Internal structure not observed due to the rarity of the species in the sample.

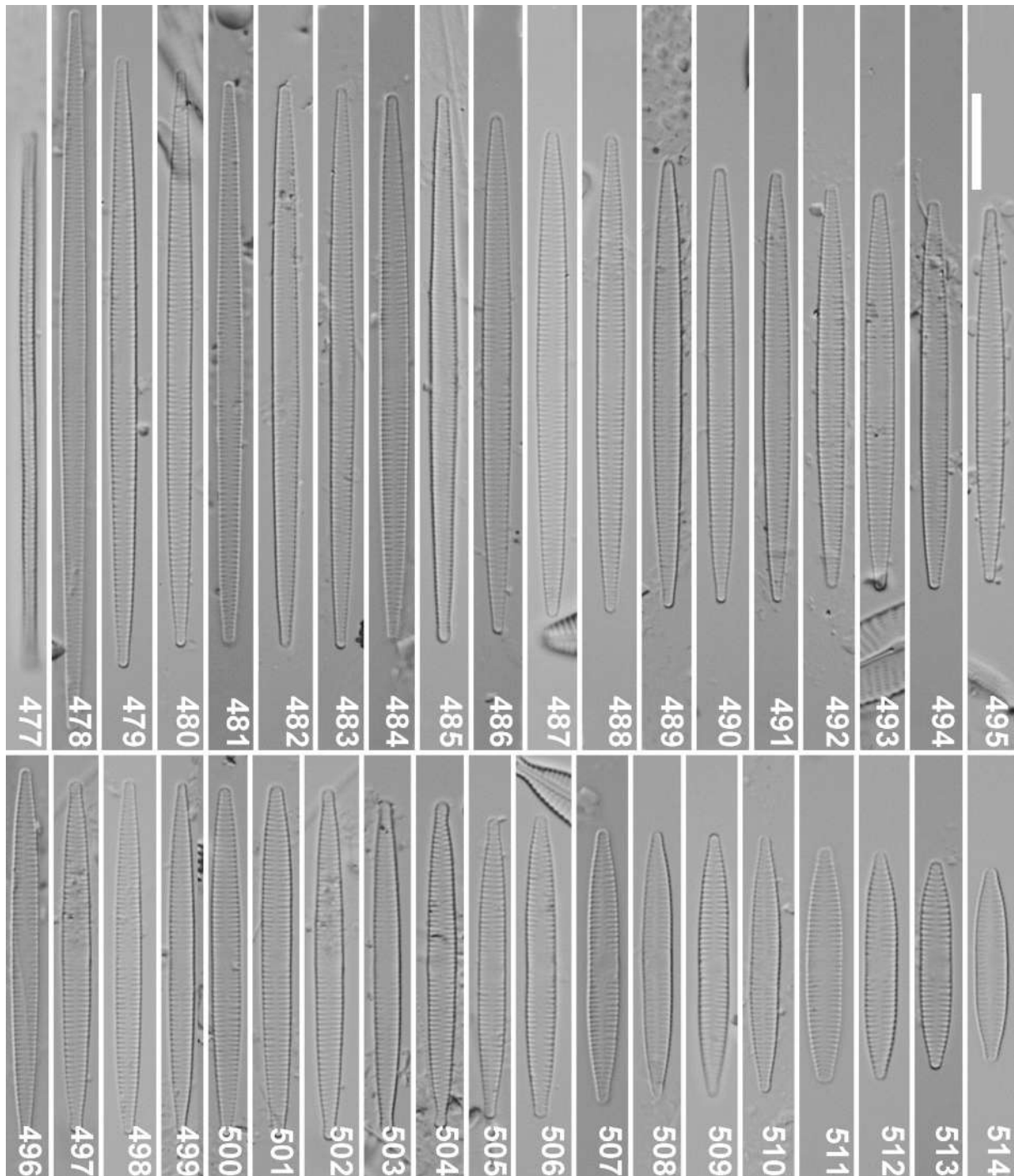
Holotype: BR–4705 (BR, Meise Botanic Garden, Belgium), slide made from sample APM17–98. Figure 528 represents the holotype.

Isotype: Slide–399 (University of Antwerp, Belgium)

Type locality: River Molse Neet, Geel (Prov. Antwerp), Belgium, sample APM17–98 (51°8′51.49″N, 05°0′13.52″E, coll. date 10.V.2017, leg. Vlaamse Milieu Maatschappij, VMM).

Etymology: The new species is named after our dear colleague Ir. Adrienne Mertens (Diatomella, The Netherlands) in honour of her important contributions to the knowledge of the diatoms of the Low Countries (Belgium and The Netherlands).

Associated diatom flora: The type sample for *F. mertensiana* is dominated by a very diverse diatom flora dominated by (in decreasing order of abundance) *Sellaphora nigri*

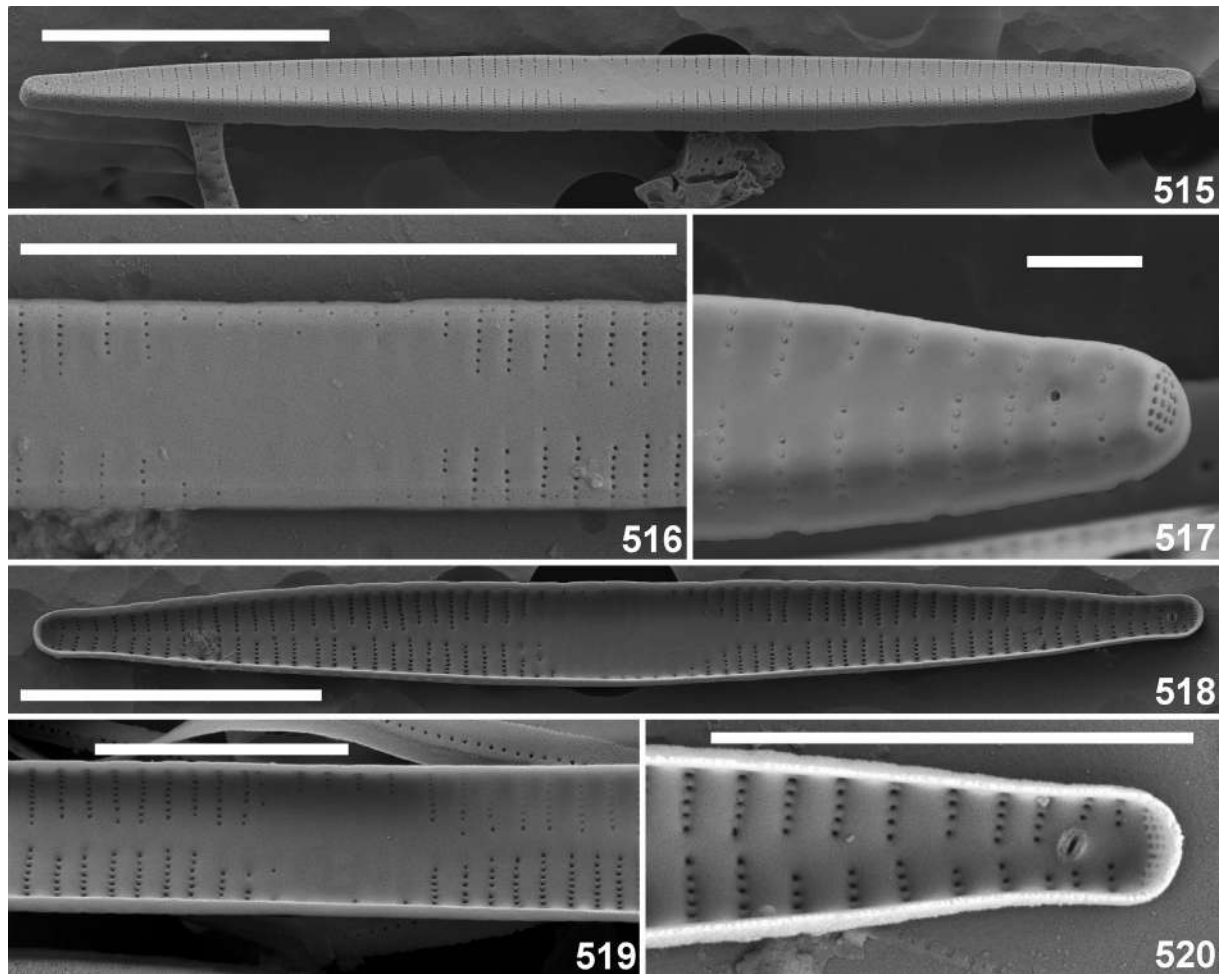


Figs 477–514. *Fragilaria eutrappenta* Van de Vijver, Kusber et D.M.Williams sp. nov. LM images taken from the holotype material (RIKA DE BIE17, BR-4704): (477) LM view of a frustule in girdle view, solitary or in pairs; (478–514) LM views of the population arranged in decreasing length. Scale bar 10 μm .

(De Notaris) C.E.Wetzel et Ector, *Fragilaria campyla*, *F. eutrappenta*, *F. mertensiana*, *Gomphonema parvulum*, *Luticola goeppertiana* (Bleisch) D.G.Mann, *Surirella brebissonii* var. *kuetzingii* Krammer et Lange–Bertalot, *Nitzschia minuta* Bleisch and *Amphipleura pellucida* (Kützing) Kützing. This species composition points to a eutrophic, α -meso- to polysaprobic environment with higher electrolyte content (LANGE–BERTALOT et al. 2017), often indicating increased levels of pollution.

Physical and chemical measurements for the sampling spot, collected at the sampling date indicate a pH of 7.6, a conductivity of 535 $\mu\text{S}\cdot\text{cm}^{-1}$, TN of 1.5 $\text{mg}\cdot\text{l}^{-1}$, TP of 0.17 $\text{mg}\cdot\text{l}^{-1}$ and a SO_4^{2-} of 110 $\text{mg}\cdot\text{l}^{-1}$.

Taxonomic remarks: *Fragilaria mertensiana* shows some resemblance with several members of the former *F. gracilis* complex but the combination of distinctly protracted, capitate apices, the broad sternum and the



Figs 515–520. *Fragilaria eutraphenta* Van de Vijver, Kusber et D.M. Williams sp. nov. SEM images taken from the holotype material (RIKA DE BIE17, BR-4704): (515) SEM external view of an entire valve; (516) SEM external detail of the central area; (517) SEM external detail of the valve apex with the rimoportula; (518) SEM internal view of an entire valve; (519) SEM internal detail of the central area; (520) SEM internal detail of a valve apex showing the rimoportula. Scale bar 10 μm (515, 518), 5 μm (516) and 1 μm (517, 519, 520).

large central area, separates this new species from all others. *Fragilaria radians* has less protracted apices and a narrower sternum. *Fragilaria eutraphenta*, also present in the same sample as *F. mertensiana*, is wider (width 3.0–4.0 μm versus 2.5–3.0 μm), has more robust valves lacking distinctly protracted apices, and a narrower sternum. *Fragilaria huerlimannii* is narrower (max. 2.0 μm width) with a narrower sternum.

At present, the species was only observed in one sample but given its unique combination of morphological features, its description as a separate species is justified, especially as it was observed in quite different ecological conditions compared to all samples where *F. radians* was observed.

Two previously described species in the *F. gracilis* complex

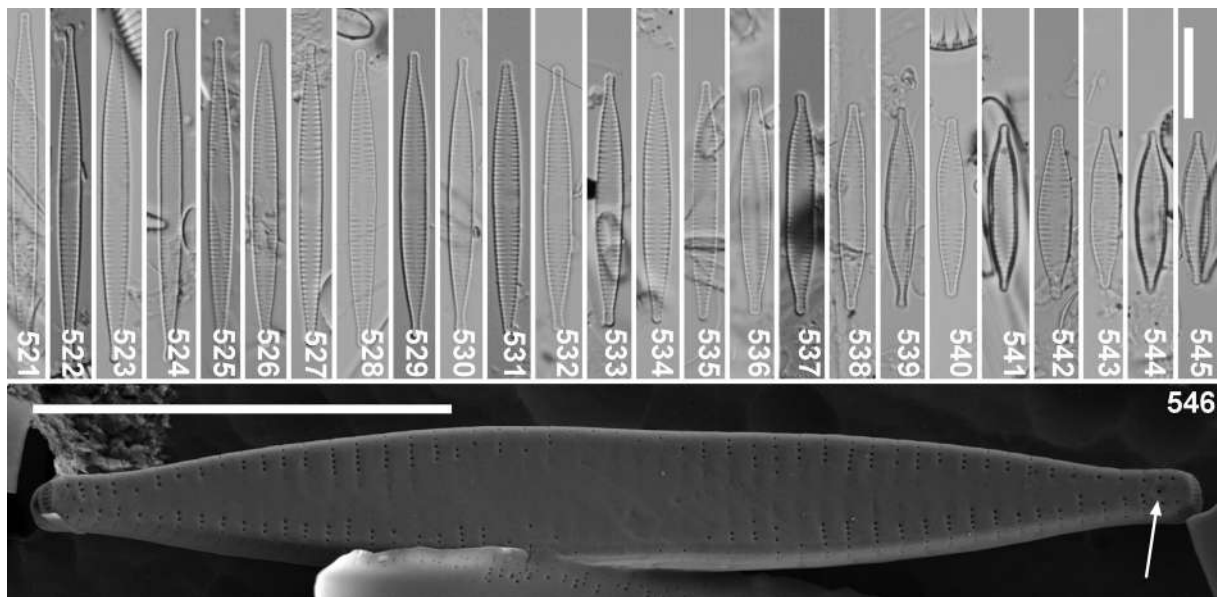
In the recent past, two small species, showing some similarity with *Fragilaria radians* (former *F. gracilis*) have been described from Siberia (KULIKOVSKIY et al. 2010) and the siliceous Italian south-eastern Alps (CANTONATI et al. 2019). Both are geographically very

localized but need to be discussed in the light of giving a good overview of the *F. radians* (former *F. gracilis*) complex. Therefore, a short discussion of the morphology of the type material is presented.

Fragilaria boreomongolica Kulikovskiy et al. (Figs 547–561)

Original description: *Fragilaria boreomongolica* Kulikovskiy, Lange-Bertalot, Witkowski et Dorofeyuk in KULIKOVSKIY et al. (2010), p. 36, pl. 9, figs 2–8, 22–23)

LM (Figs 547–559): Frustules in girdle view rectangular, solitary. Ribbon-like colonies with more than 2 cells at present not observed. Valves mostly linear with parallel margins, only narrowing near the slightly protracted, rostrate apices. Valve dimensions (n=15): length 15–30 μm (22–37 μm in KULIKOVSKIY et al. 2010), width 2.5–3.0 μm . Sternum distinct, gradually widening from apices to central area. Central area variable, occasionally absent, usually forming a large, unilateral hyaline area, irregularly bordered by a few shortened striae. Striae alternating or opposite, parallel throughout entire valve, 18–21 in 10



Figs 521–546. *Fragilaria mertensiana* Van de Vijver, C.E. Wetzel et Ector sp. nov. LM and SEM images taken from holotype material (APM17–98, BR–4705): (521–545) LM views of the population arranged in decreasing length: (546) SEM external view of an entire valve. The arrow indicates the rimoportula. Scale bars 10 μ m.

μ m. Areolae not discernible in LM.

SEM (Figs 560–561): Valve flat, lacking marginal spines (Figs 560, 561). Broad sternum well visible (Fig. 561). Striae uniseriate, composed of very small, rounded areolae (Figs 560, 561). Apical pore field of the ocellulimbus type, very small, composed of only a few short rows of large, rounded poroids (Fig. 560). External rimoportula opening very small, linear, hardly discernible from the areolae, positioned in the middle of the sternum (Figs 560, 561, arrow). Internal structure not observed due to rarity of species in the material.

Holotype: SZCZ slide n° 12529 in collection A. Witkowski, Institute of Marine Sciences, University of Szczecin, Poland

Isotype: IBIW slide n° 9 in collection M. Kulikovskiy, Institute for Biology of Inland Waters, Borok, Russia

Taxonomic remarks: The linear valve outline in *F. boreomongolica* is only rarely seen in the *Fragilaria radians* (formerly *F. gracilis*) complex. *Fragilaria eutrappenta* has a similar valve outline but the valves are always larger and wide. *Fragilaria radians* has a more linear–lanceolate valve outline with gradually tapering apices. Up to now, the species has not been observed in European waters.

***Fragilaria tridentina* Cantonati et Lange–Bertalot (Figs 562–587)**

Original description: *Fragilaria tridentina* (CANTONATI & LANGE–BERTALOT 2019, p. 268, figs 14–35, 76–81)

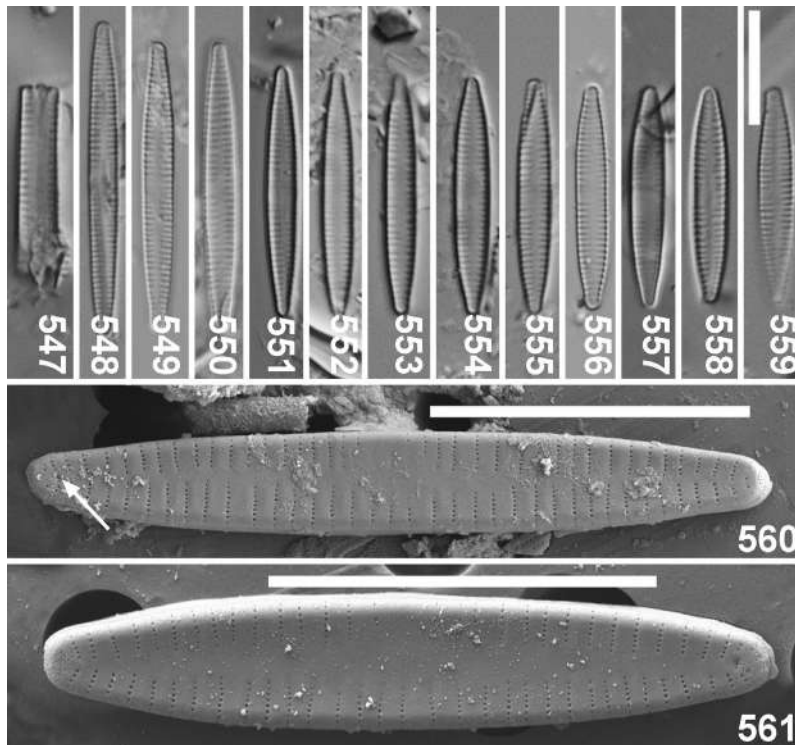
LM (Figs 562–585): Frustules in girdle view rectangular, usually solitary. Ribbon–like colonies with more than 2 cells at present not observed. Valves almost linear to

narrowly lanceolate, with weakly protracted, distinctly cuneate, not rostrate, apices. Valve dimensions (n=25): length 14–25 μ m (11–27 μ m according to CANTONATI et al. 2019), width 2.5–3.5 μ m (2.5–3.0 μ m according to CANTONATI et al. 2019). Sternum narrow, discernible in LM, almost not widening from apices to central area. Central area forming a small, unilateral hyaline area, bordered on one side by several, irregularly shortened striae. Striae opposite, parallel near the central area, becoming weakly radiate near the apices, 19–22 in 10 μ m. Areolae not discernible in LM.

SEM (Figs 586–587): Valve face flat. Virgae not raised (Fig. 586). Spines absent (Fig. 586). Striae uniseriate, composed of small, rounded areolae (Fig. 586). Central area small, unilateral. Sternum near the central area almost not widening (Fig. 586). Apical pore field of the ocellulimbus type, rather small, composed of only a few rows of large, rounded poroids (Fig. 586). External rimoportula opening small, rounded, almost not distinguishable from the areolae, positioned in the middle of the sternum (Fig. 586, arrow). Internally, virgae not raised (Fig. 587). Rimoportula internally small, usually straight to weakly oblique, positioned in the middle of the sternum (Fig. 587).

Holotype: TR cLIM004 DIAT 2513 (Diatom Collection of the MUSE–Museo delle Scienze, Trento, Italy)

Taxonomic remarks: In the analysed type material, frustules connected to each other forming ribbon–like colonies with more than 2 cells were not observed. CANTONATI et al. (2019, p. 268) noted the presence of more frustules connected to each other in band–like aggregations or in bundles attached to the substrate (see



Figs 547–561. *Fragilaria boreomongolica* Kulikovskiy et al. LM and SEM images taken from holotype material (SZCZ–12529): (547) LM view of a frustule in girdle view; (548–559) LM views of the population arranged in decreasing length; (560, 561) SEM external views of an entire valve. The rimoportulae are indicated by arrows. Scale bars 10 µm.

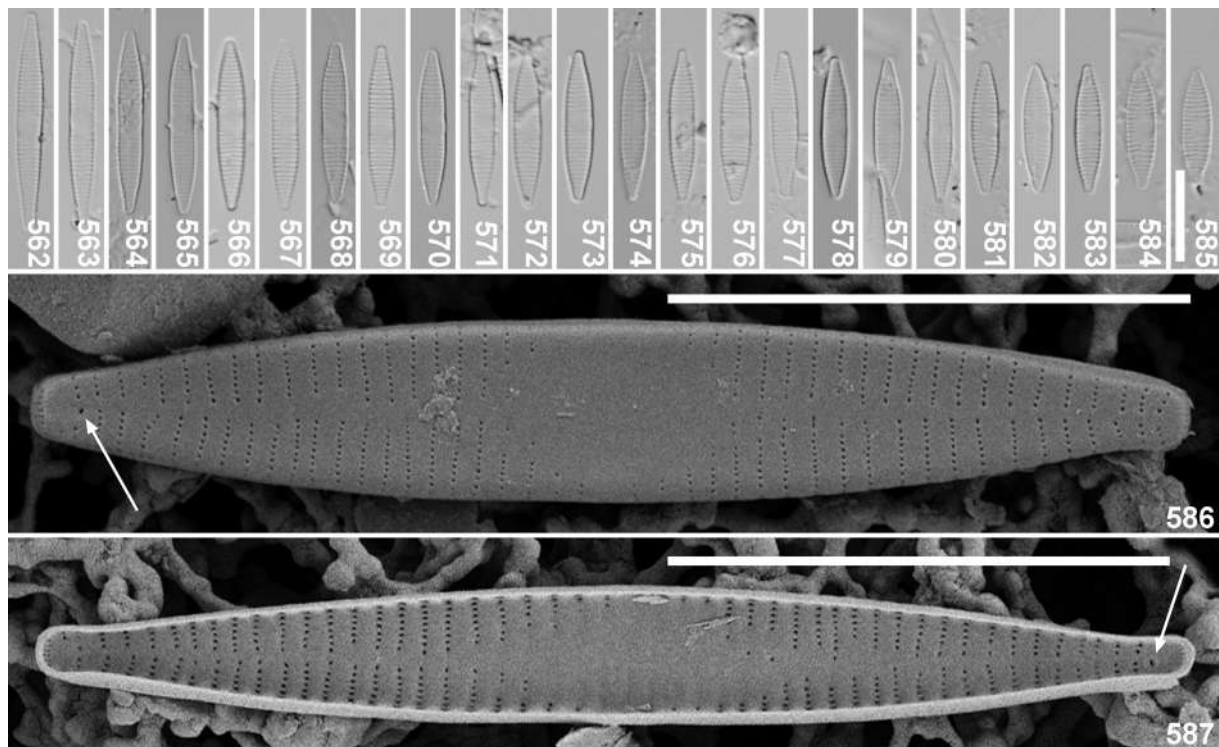
CANTONATI et al. 2019, fig. 35). *Fragilaria tridentina* is probably one of the shortest species in the *F. gracilis* complex, with valves never exceeding 30 µm. The species differs from *F. radians* in having more silicified, shorter valves, a smaller central area and typically cuneate apices, whereas *F. radians* usually has more protracted, weakly rostrate apices and a valve length up to 50 µm and a valve width between 2.0 and 3.0 µm. The valve width in *Fragilaria tridentina* is always more than 2.5 µm in the observed type population. *Fragilaria heudreana* possesses marginal spines and has much wider valves (up to 4.0 µm).

DISCUSSION

Our observations demonstrate that the ‘*F. gracilis*–complex’ is more diverse than currently recognized in the literature, primarily due to the lack of a precise morphological characterization of *F. gracilis*. Force–fitting populations with different ecological background into *F. gracilis* and subsequent taxonomic broadening of the original species concept increased the confusion. All taxa discussed in this paper, apart from *Fragilaria heudreana*, share some important features that are often clearly different from other *Fragilaria* taxa suggesting that this complex forms a distinct, separate group within the genus *Fragilaria*. In KAHLERT et al. (2019) all *F. gracilis*–strains grouped separately from the other *Fragilaria* taxa (see KAHLERT et al. 2019, fig. 1), confirming the morphological evidence found in the present paper of a separate *F. gracilis*–complex.

None of the analysed taxa seem to produce ribbon–like colonies. Instead, only individual cells or two cells joined together have been observed. This separates these taxa from the *F. capucina*–complex (VAN DE VIJVER et al. 2021b), *F. mesolepta* Rabenhorst (HEUDRE et al. 2019) and *F. rumpens* (VAN DE VIJVER et al. 2022), both typically forming (often very) long ribbon–like colonies, although other *Fragilaria* groups such as *F. perminuta* or *F. vaucheriae* are not producing such ribbon–like colonies (WETZEL & ECTOR 2015; VAN DE VIJVER & ECTOR 2020).

Apart of *Fragilaria heudreana* Van de Vijver, C.E.Wetzel et Ector sp. nov., none of the observed populations possess marginal spines as often observed in the genus *Fragilaria* (VAN DE VIJVER et al. 2020d, 2021b), most likely the reason for the absence of colony–formation as marginal linking spines are the principal way of colony–formation in *Fragilaria* (WILLIAMS 2019). Nevertheless, a lot of *Fragilaria* species possess small, acute spines, organized in long, marginal series, never contributing to the formation of colonies. Typical examples include *F. alpestris* Krasske (VAN DE VIJVER et al. 2020e), *F. austriaca* (Grunow) Lange–Bertalot (VAN DE VIJVER et al. 2020a), *F. campyla* (Hilse) Van de Vijver et al. (VAN DE VIJVER et al. in press) and *F. septentrionalis* (Østrup) Van de Vijver, C.E.Wetzel et Ector (VAN DE VIJVER et al. 2020f). Several other species, such as *F. vaucheriae*, have small marginal spinules and papilla–like structures (WETZEL & ECTOR 2015), but similar structures are also absent in the entire *F. gracilis*–complex. The only exception in the *F. gracilis*–complex is *Fragilaria heudreana*, a new species, possessing well–developed, though small, conical non–linking spines along its valve



Figs 562–587. *Fragilaria tridentina* Cantonati et al. LM and SEM images taken from holotype material (cLIM004 DIAT 1985): (562–585) LM views of the population arranged in decreasing length; (586) SEM external view of an entire valve. The rimoportula is indicated by an arrow. (587) SEM internal view of an entire valve showing the position of the rimoportula (arrow). Scale bars 10 μ m.

margins, hinting that the latter species may actually not belong to the *F. gracilis*-complex.

The external rimoportula opening is usually rounded, well separated from the areolae, rimmed, and positioned almost on the sternum. In several species, the area immediately surrounding the rimoportula is characterized by the presence of short, irregular ridges (see for instance Figs 213, 242, 296 & 435). A similar ornamentation around the rimoportulae was not observed in other *Fragilaria* taxa, even under high magnification. Moreover, in most other *Fragilaria* species, the rimoportula usually replaces several areolae in the last or before last stria at the apex (VAN DE VIJVER et al. in press). *Fragilaria heudreana* is again the exception to this observation as the latter has a small rimoportula, replacing some areolae in the last stria (Fig. 472).

All taxa, except *F. heudreana*, have relatively small to moderately large apical pore fields, composed of max. 4 short rows of large poroids, contrary to a lot of *Fragilaria* taxa showing larger apical pore fields, often with 5 or more long to moderately long rows of smaller poroids (VAN DE VIJVER et al. 2020d, 2021b).

The girdle structure of the *F. gracilis*-complex is composed of several open, perforated bands (see for instance Figs 161, 239).

All species also share some similar morphometric features: The maximum valve width usually does not exceed 3 μ m for all reported species in this paper, separating them from the taxa in the *F. rumpens*- and *F. capucina*-groups

(VAN DE VIJVER et al. 2021b, 2022). Exceptions include *F. eutrappenta* Van de Vijver et al. sp. nov. and *F. heudreana* that both have a valve width up to 4.0 and 5.0 μ m, respectively.

All observed taxa have a high stria density, usually between 17 and 25 striae in 10 μ m. Such a high stria density is often only observed in very long, needle-shaped *Fragilaria* species such as *F. ostensfeldii* (VAN DE VIJVER et al. 2021a). *Fragilaria rumpens* and some species related to *F. rumpens* also have a relatively high stria density that, however, only very rarely exceeds 20 in 10 μ m (VAN DE VIJVER et al. 2022). Moreover, the striae are composed of very small areolae, not discernible in LM, contrary to for instance the species-complex related to *Fragilaria famelica* (Kützing) Lange-Bertalot where the areolae are often very well visible in LM (LANGE-BERTALOT 1980; KRAMMER & LANGE-BERTALOT 1991).

ACKNOWLEDGEMENTS

The authors would like to thank Dr J. Hürlimann and Dr F. Straub for providing samples from Switzerland containing interesting *Fragilaria gracilis*-populations. Mrs Amelie Jarlman (Jarlman Konsult, Lund, Sweden) is thanked for providing us with the samples from the Swedish rivers. Dr M. Kulikovskiy (Borok, Russia) is thanked for providing us the type material of *Fragilaria boreomongolica*. Dr N. Lundholm and Dr C. Lange from the University of Copenhagen (Denmark), are thanked for sending us the type material of *Fragilaria gracilis* and *F. pseudolaevissima*. Dr E. Cesar (Natural History Museum, London, UK) is thanked for sending us the type material of *Synedra radians*. The type material of *Synedra utermoehlii* was kindly sent to us by Dr L. Eggers (Hustedt collection, Bremerhaven, Germany). Ir A. Mertens is thanked for her constructive advice on the *F. gracilis* populations

from the Low Countries. The Vlaamse Milieu Maatschappij (VMM) is thanked for the ecological data of the Molse Nete and for the permission to use sample APM17–98. The Service Public de Wallonie (SPW), Agriculture, Ressources naturelles et Environnement is thanked for permission to use sample BERW–03510. Dr A. Ball and the staff of the IAC laboratory at the Natural History Museum are thanked for their help with the scanning electron microscopy. This study was supported by an EU Synthesys grant (GP–TAF 5970) to BVDV to visit the National History Museum in London, UK. Funding for this research was partly provided to CEW and LE in the framework of the project DIATOMS (LIST – Luxembourg Institute of Science and Technology).

REFERENCES

- BOYER, C.S. (1927): Synopsis of North American Diatomaceae. Part I. Coscinodiscatae, Rhizosolenatae, Biddulphiatae, Fragilariatae. – Proceedings of the Academy of Natural Sciences of Philadelphia 78(Suppl.): 1–228.
- CANTONATI, M.; ANGELI, N. & LANGE–BERTALOT, H. (2019): Three new *Fragilaria* species (Bacillariophyta) from low–conductivity mountain freshwaters (Alps and Apennines). – Phytotaxa 404: 261–274. <https://doi.org/10.11646/phytotaxa.404.6.5>
- CLEVE, P.T. (1898): Diatoms from Franz Josef Land, collected by the Harmsworth–Jackson–Expedition. – Bihang till Kongliga Svenska Vetenskaps–Akademiens Handlingar, Afd. III 24: 1–26.
- CLEVE–EULER, A. (1953): Die Diatomeen von Schweden und Finnland. Teil II. Araphideae, Brachyraphideae. – Kungliga Svenska Vetenskapsakademiens Handlingar, ser. IV 4: 1–158.
- COX, E.J. & ROSS, R. (1981): The striae of pennate diatoms. – In: ROSS, R. (ed.): Proceedings of the Sixth Symposium on Recent and Fossil Diatoms. Budapest, September 1–5, 1980. Taxonomy · Morphology · Ecology · Biology. – pp. 267–278, Otto Koeltz, Koenigstein.
- DELGADO, C.; NOVAIS, M.H.; BLANCO, S. & ALMEIDA, S.F.P. (2015): Examination and comparison of *Fragilaria candidagilae* sp. nov. with type material of *Fragilaria recapitellata*, *F. capucina*, *F. perminuta*, *F. intermedia* and *F. neointermedia* (Fragilariales, Bacillariophyceae). – Phytotaxa 231: 1–18. <https://doi.org/10.11646/phytotaxa.231.1.1>
- DELGADO, C.; NOVAIS, M.H.; BLANCO, S. & ALMEIDA, S.F.P. (2016): *Fragilaria rinoi* sp. nov. (Fragilariales, Fragilariophyceae) from periphytic river samples in Central Portugal. – European Journal of Taxonomy 248: 1–16. <https://doi.org/10.5852/ejt.2016.248>
- GRUNOW, A. (1862): Die österreichischen Diatomaceen nebst Anschluss einiger neuen Arten von andern Lokalitäten und einer kritischen Uebersicht der bisher bekannten Gattungen und Arten. – Verhandlungen der kaiserlich–königlichen zoologisch–botanischen Gesellschaft in Wien 12: 315–472 [Abt 1], 545–588 [Abt. 2], 7 pls. <https://doi.org/10.5962/bhl.title.64361>
- HEUDRE, D.; WETZEL, C.E., MOREAU, L., VAN DE VIJVER, B. & ECTOR, L. (2019): On the identity of the rare *Fragilaria subconstricta* (Fragilariaceae), with *Fragilaria* species forming ribbon–like colonies shortly reconsidered. – Plant Ecology and Evolution 152: 327–339. <https://doi.org/10.5091/pecevo.2019.1619>
- HÜRLIMANN, J. & STRAUB, F. (1991): Morphologische und ökologische Charakterisierung von Sippen um den *Fragilaria capucina*–komplex sensu Lange–Bertalot 1980. – Diatom Research 6: 21–47. <https://doi.org/10.1080/0269249X.1991.9705145>
- HUSTEDT, F. (1930): Bacillariophyta (Diatomeae) Zweite Auflage. In: Die Süßwasser–Flora Mitteleuropas. Heft 10. (Pascher, A. Eds), – pp. [i]–vii, [1]–466. Jena: Verlag von Gustav Fischer.
- HUSTEDT, F. (1932): Die Kieselalgen Deutschlands, Österreichs und der Schweiz unter Berücksichtigung der übrigen Länder Europas sowie der angrenzenden Meeresgebiete. Vol. VII. Teil 2. Lieferung 2. In: Rabenhorst’s Kryptogamen Flora von Deutschland, Österreich und der Schweiz. (Anon. Eds). – pp. 177–320, Akademische, Leipzig.
- HUSTEDT, F. (1950): Die Diatomeenflora norddeutscher Seen mit besonderer Berücksichtigung des holsteinischen Seengebiets. V.–VII. Seen in Mecklenburg, Lauenburg und Nordostdeutschland. – Archiv für Hydrobiologie 43: 329–458, Tafs 21–41.
- KAHLERT, M.; KELLY, M.G.; MANN, D.G.; RIMET, F.; SATO, S.; BOUCHEZ, A. & KECK, F. (2019): Connecting the morphological and molecular species concepts to facilitate species identification within the genus *Fragilaria* (Bacillariophyta). – Journal of Phycology 55: 948–970. <https://doi.org/10.1111/jpy.12886>
- KRAMMER, K. & LANGE–BERTALOT, H. (1991): Bacillariophyceae. 3 Teil: Centrales, Fragilariaceae, Eunotiaceae. – In: Ettl, H.; Gerloff, J.; Heynig, H. & Mollenhauer, D. (eds): Süßwasserflora von Mitteleuropa, Band 2/3. – 576 pp., Gustav Fischer Verlag, Stuttgart – Jena.
- KRAMMER, K. & LANGE–BERTALOT, H. (2000): Bacillariophyceae. 3. Teil: Centrales, Fragilariaceae, Eunotiaceae. – In: Ettl, H.; Gerloff, J.; Heynig, H. & Mollenhauer, D. (eds): Süßwasserflora von Mitteleuropa, Band 2/3 (2nd edition). – 599 pp., Spektrum Akademischer Verlag, Heidelberg.
- KULIKOVSKIY, M.S.; LANGE–BERTALOT, H.; WITKOWSKI, A.; DOROFYUK, N.I. & GENKAL, S.I. (2010): Diatom assemblages from *Sphagnum* bogs of the world. I. Nur bog in northern Mongolia. – Bibliotheca Diatomologica 55: 1–326.
- KÜTZING, F.T. (1844): Die kieselschaligen Bacillarien oder Diatomeen. – pp. 1–152, pls 1–30, Zu finden bei W. Köhne, Nordhausen. <https://doi.org/10.5962/bhl.title.64360>
- LANDESAMT FÜR WASSERHAUSHALT UND KÜSTEN SCHLESWIG–HOLSTEIN (1995): Der Dobersdorfer See. – Landesamt für Wasserhaushalt und Küsten Schleswig–Holstein. LW 631 – 5203.71–21, 123 pp.
- LANGE–BERTALOT, H. (1980): Zur systematischen Bewertung der bandförmigen Kolonien bei *Navicula* und *Fragilaria*. Kriterien für die Vereinigung von *Synedra* (subgen. *Synedra*) Ehrenberg mit *Fragilaria* Lyngbye. – Nova Hedwigia 33: 723–787.
- LANGE–BERTALOT, H. (1993): 85 neue Taxa und über 100 weitere neu definierte Taxa ergänzend zur Süßwasserflora von Mitteleuropa, Vol. 2/1–4. – Bibliotheca Diatomologica 27: 1–164.
- LANGE–BERTALOT, H. & ULRICH, S. (2014): Contributions to the taxonomy of needle–shaped *Fragilaria* and *Ulnaria* species. – Lauterbornia 78: 1–73.
- LANGE–BERTALOT, H.; HOFMANN, G.; WERUM, M. & CANTONATI, M. (2017): Freshwater Benthic Diatoms of Central Europe: Over 800 Common Species Used in Ecological Assessments. English edition with updated taxonomy and added species. – 942 pp., Koeltz Botanical Books, Schmittens–Oberreifenberg.
- LOWE, R.L.; KOCIOLEK, P.; JOHANSEN, J.R.; VAN DE VIJVER,

- B.; LANGE–BERTALOT, H. & KOPALOVÁ, K. (2014): *Humidophila* gen. nov., a new genus for a group of diatoms (Bacillariophyta) formerly within the genus *Diademsis*: species from Hawai'i, including one new species. – *Diatom Research* 29: 351–360. <https://doi.org/10.1080/0269249X.2014.889039>
- LYNGBYE, H.C. (1819): Tentamen hydrophytologiae danicae continens omnia hydrophyta cryptogama Daniae, Holsatiae, Faeroae, Islandiae, Groenlandiae hucusque cognita, systematice disposita, descripta et iconibus illustrata, adjectis simul speciebus norvegicis. – pp. [i]–xxxii, [1]–248, 70 pls. Hafniae [Copenhagen]: typis Schultzianis, in commissis Librariae Gyldendaliae. <https://doi.org/10.5962/bhl.title.6079>
- MAYER, A. (1937): Die Bacillariophyten–Gattungen *Fragilaria* und *Asterionella* in Bayern. – *Berichte der Bayerischen Botanischen Gesellschaft zur Erforschung der Heimischen Flora* 22: 50–84.
- MEISTER, F. (1912): Die Kieselalgen der Schweiz. – *Beiträge zur Kryptogamenflora der Schweiz*. K.J. Wyss, Bern 4: 254 pp., 48 pls.
- MICHALAK, I. & MESSYASZ, B. (2021): Concise review of *Cladophora* spp.: macroalgae of commercial interest. – *Journal of Applied Phycology* 33: 133–166. <https://doi.org/10.1007/s10811-020-02211-3>
- NOVAIS, M.H.; ALMEIDA, S.F.P.; BLANCO, S. & DELGADO, C. (2019): Morphology and ecology of *Fragilaria misarensis* sp. nov. (Bacillariophyta), a new diatom species from southwest of Europe. – *Phycologia* 58: 128–144. <https://doi.org/10.1080/00318884.2018.1524245>
- ØSTRUP, E. (1910): Danske Diatoméer med 5 tavler et Engelsk résumé. Udgivet paa Carlsbergfondets bekostning. – pp. [i]–xi, 1–323, pls 1–5. Kjøbenhavn [Copenhagen]: C.A. Reitzel Boghandel Bianco Lunos Bogtrykkeri.
- PATRICK, R.M. & REIMER, C.W. (1966): The diatoms of the United States. Exclusive of Alaska and Hawaii. Volume 1: Fragilariaceae, Eunotiaceae, Achnantheaceae, Naviculaceae. – *Monographs of the Academy of Natural Sciences of Philadelphia* 13: 1–688.
- PEETERS, V. & ECTOR, L. (2017): Atlas des diatomées des cours d'eau du territoire bourguignon. Volume 1: Centriques, Araphidées. – 309 pp., Direction Régionale de l'Environnement, de l'Aménagement et du Logement Bourgogne–Franche–Comté.
- ROSS, R.; COX, E.J.; KARAYEVA, N.I.; MANN, D.G.; PADDOCK, T.B.B.; SIMONSEN, R. & SIMS, P.A. (1979): An amended terminology for the siliceous components of the diatom cell. – *Nova Hedwigia, Beiheft* 64: 513–533.
- ROUND, F.E. (1979): The classification of the genus *Synedra*. – *Nova Hedwigia, Beiheft* 64: 135–146.
- SIMONSEN, R. (1987): Atlas and catalogue of the diatom types of Friedrich Hustedt. – Vol. 1, Catalogue, 525 pp.; Vol. 2, Atlas, pls 1–395, 597 pp.; Vol. 3, Atlas, pls 396–772, 619 pp., J. Cramer, Berlin–Stuttgart.
- SMITH, W. (1853): A synopsis of the British Diatomaceae; with remarks on their structure, function and distribution; and instructions for collecting and preserving specimens. The plates by Tuffen West. In two volumes. Vol. 1. – pp. [i]–xxxiii, 1–89, pls I–XXXI. London: John van Voorst, Paternoster Row.
- TUJI, A. (2004): Type examination of the ribbon–forming *Fragilaria capucina* complex described by Christian Gottfried Ehrenberg. – In: POULIN, M. (ed.), *Proceedings of the Seventeenth International Diatom Symposium*. Ottawa, Canada, 25th – 31st August 2002. Biopress Limited, Bristol, pp. 411–422.
- TUJI, A. (2007): Type examination of *Fragilaria gracilis* Østrup (Bacillariophyceae). – *Bulletin of the National Museum of Natural Sciences, Series B* 33: 9–12.
- TUJI, A. & WILLIAMS, D.M. (2006a): Examination of the type material of *Synedra rumpens* = *Fragilaria rumpens*, Bacillariophyceae. – *Phycological Research* 54: 99–103. <https://doi.org/10.1111/j.1440-1835.2006.00414.x>
- TUJI, A. & WILLIAMS, D.M. (2006b): Typification of *Conferva pectinalis* O. F. Müll. (Bacillariophyceae) and the identity of the type of an alleged synonym, *Fragilaria capucina* Desm. – *Taxon* 55: 193–199. <https://doi.org/10.2307/25065541>
- TUJI, A. & WILLIAMS, D.M. (2008a): Typification and type examination of *Synedra familiaris* Kütz. and related taxa. – *Diatom* 24: 25–29. https://doi.org/10.11464/diatom1985.24.0_25
- TUJI, A. & WILLIAMS, D.M. (2008b): Examination of type material of *Fragilaria mesolepta* Rabenhorst and two similar, but distinct, taxa. – *Diatom Research* 23: 503–510. <http://dx.doi.org/10.1080/0269249X.2008.9705772>
- TUJI, A. & WILLIAMS, D.M. (2008c): Examination of types in the *Fragilaria pectinalis*–*capitellata* species complex. – In: LIKHOSHWAY, Y. (ed.): *Proceedings of the Nineteenth International Diatom Symposium*. Listvyanka, Irkutsk, Russia, 28th August – 3rd September 2006. – pp. 125–139, Biopress Limited, Bristol.
- TUJI, A. & WILLIAMS, D.M. (2013): Examination of types in the *Fragilaria vaucheriae*–*intermedia* species complex. – *Bulletin of the National Museum of Natural Science, series B, Botany* 39: 1–9.
- TUJI, A. & WILLIAMS, D.M. (2017): *Fragilaria asterionelloides*, a new planktonic species of *Fragilaria* from Japanese reservoirs that forms star–shaped colonies. – *Bulletin of the National Museum of Natural Science, series B* 43: 45–50.
- TURLAND, N.J.; WIERSEMA, J.H.; BARRIE, F.R.; GREUTER, W.; HAWKSWORTH, D.L.; HERENDEEN, P.S.; KNAPP, S.; KUSBER, W.–H.; LI, D.–Z.; MARHOLD, K.; MAY, T.W.; MCNEILL, J.; MONRO, A.M.; PRADO, J.; PRICE, M.J. & SMITH, G.F., editors (2018): *International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017*. *Regnum Vegetabile*, Vol. 159. – pp. [i]–xxxviii, 1–253, Koeltz Botanical Books, Glashütten.
- VAN DE VIJVER, B. & ECTOR, L. (2020): Analysis of the type material of *Synedra perminuta* (Bacillariophyceae) with the description of two new *Fragilaria* species from Sweden. – *Phytotaxa* 468: 89–100. <https://doi.org/10.11646/phytotaxa.468.1.5>
- VAN DE VIJVER, B.; STRAUB, F.; WETZEL, C.E. & ECTOR, L. (2020a): Observations on and epitypification of *Synedra austriaca* Grunow (Fragilariaceae, Bacillariophyta). – *Notulae Algarum* 130: 1–5.
- VAN DE VIJVER, B.; ECTOR, L.; SCHUSTER, T.M. & WALTER, J. (2020b): Observations on and typification of *Synedra gloiophila* Grunow (Fragilariaceae, Bacillariophyta) and its transfer to the genus *Fragilaria* Lyngbye. – *Notulae Algarum* 145: 1–6.
- VAN DE VIJVER, B.; KUSBER, W.H.; ECTOR, L., SCHUSTER, T.M. & WALTER, J. (2020c): Original material of *Fragilaria gloiophila* (Grunow) Van de Vijver, Ector, T.M.Schuster & J.Walter (Fragilariaceae, Bacillariophyta) rediscovered in the Grunow collection. – *Notulae Algarum* 161: 1–3.

- VAN DE VIJVER, B.; MERTENS, A. & ECTOR, L. (2020d): Analysis of the type material of *Synedra deformis* W. Sm. and *Synedra vaucheriae* var. *deformis* Grunow (Fragilariaceae, Bacillariophyta). – *Cryptogamie Algologie* 41: 137–149. <https://doi.org/10.5252/cryptogamie-algologie2020v41a13>.
- VAN DE VIJVER, B.; TUSSET, E.; WILLIAMS, D.M. & ECTOR, L. (2020e): Analysis of the type of *Fragilaria alpestris* (Bacillariophyta) with the description of a new *Staurosira* species from the sub-Antarctic Region. – *Phytotaxa* 471: 1–15. <https://doi.org/10.11646/phytotaxa.471.1.1>
- VAN DE VIJVER, B.; LUNDHOLM, N.; LANGE, C.; WETZEL, C.E. & ECTOR, L. (2020f): Observations on the type material of *Synedra vaucheriae* var. *septentrionalis* Østrup (Fragilariaceae, Bacillariophyta) and its transfer to the genus *Fragilaria*. – *Notulae Algarum* 157: 1–4.
- VAN DE VIJVER, B.; ALEXSON, E.; REAVIE, E.; STRAUB, F.; JÓNSSON, G.S. & ECTOR, L. (2021a): Analysis of the type of *Synedra acus* var. *ostenfeldii* (Bacillariophyta) and its transfer to the genus *Fragilaria*. – *Botany Letters* 168: 85–95. <https://doi.org/10.1080/23818107.2020.1845973>
- VAN DE VIJVER, B.; WILLIAMS, D.M.; KELLY, M.; JARLMAN, A.; WETZEL, C.E. & ECTOR, L. (2021b): Analysis of some species resembling *Fragilaria capucina* (Fragilariaceae, Bacillariophyta). – *Fottea* 21: 128–151. <https://doi.org/10.5507/fot.2021.001>
- VAN DE VIJVER, B.; HÜRLIMANN, J.; WILLIAMS, D.M.; LEVKOV, Z.; WETZEL, C.E. & ECTOR, L. (2021c): *Fragilaria subrecaipitellata* (Fragilariaceae, Bacillariophyta), a new diatom species from Switzerland. – *Diatom Research* 36: 119–131. <https://doi.org/10.1080/0269249X.2021.1942221>
- VAN DE VIJVER, B.; WILLIAMS, D.M.; SCHUSTER, T.M.; KUSBER, W.H.; CANTONATI, M.; WETZEL, C.E. & ECTOR, L. (2022): Analysis of the *Fragilaria rumpens* complex (Fragilariaceae, Bacillariophyta) with the description of two new species. – *Fottea* 22: 93–121. DOI: <https://doi.org/10.5507/fot.2021.018>.
- VAN DER WERFF, A. (1955): A new method for cleaning and concentrating diatoms and other organisms. – *Internationale Vereinigung für Theoretische und Angewandte Limnologie: Verhandlungen* 12: 276–277. DOI: <https://doi.org/10.1080/03680770.1950.11895297>
- VAN HEURCK, H. (1881): *Synopsis des Diatomées de Belgique*. Atlas. – pls 31–77, Ducaju et Cie, Anvers.
- VANLANDINGHAM, S.L. (1971): *Catalogue of the fossil and recent genera and species of diatoms and their synonyms*. Part IV. *Fragilaria* through *Naunema*. 3301 Lehre, Verlag von J. Cramer 4: xi–xiv, 1757–2385.
- WETZEL, C.E. & ECTOR, L. (2015): Taxonomy and ecology of *Fragilaria microvaucheriae* sp. nov. and comparison with the type materials of *F. uliginosa* and *F. vaucheriae*. – *Cryptogamie Algologie* 36: 271–289. DOI: <https://doi.org/10.7872/crya/v36.iss3.2015.271>
- WILLIAMS, D.M. (1986): Comparative morphology of some species of *Synedra* Ehrenb. with a new definition of the genus. – *Diatom Research* 1: 131–152. DOI: <https://doi.org/10.1080/0269249X.1986.9704963>
- WILLIAMS, D.M. (2019): Spines and homologues in ‘araphid’ diatoms. – *Plant Ecology & Evolution* 152: 150–162. DOI: <https://doi.org/10.5091/plecevo.2019.1597>
- WILLIAMS, D.M. & KARTHICK, B. (2021): The correct use of the names *Synedra* Ehrenberg and *Catacombas* Williams & Round, a note on the name ‘*Hystrix* Bory 1822’, and some suggestions how to tackle the taxonomic relationships of *Synedra*. – *Diatom Research* 36: 107–118. DOI: <https://doi.org/10.1080/0269249X.2021.1880974>
- WILLIAMS, D.M. & ROUND, F.E. (1987): Revision of the genus *Fragilaria*. – *Diatom Research* 2: 267–288. DOI: <https://doi.org/10.1080/0269249X.1987.9705004>