

**This item is the archived peer-reviewed author-version of:**

Analysis of the type specimens of *Fragilaria alpestris* (Bacillariophyta) with description of two new 'araphid' species from the sub-Antarctic and Arctic Region

**Reference:**

Van de Vijver Bart, Tusset Eduardo, Williams David M., Ector Luc.- Analysis of the type specimens of *Fragilaria alpestris* (Bacillariophyta) with description of two new 'araphid' species from the sub-Antarctic and Arctic Region  
Phytotaxa - ISSN 1179-3155 - 471:1(2020), p. 1-15  
Full text (Publisher's DOI): <https://doi.org/10.11646/PHYTOTAXA.471.1.1>  
To cite this reference: <https://hdl.handle.net/10067/1744000151162165141>

**Analysis of the type specimens of *Fragilaria alpestris* (Bacillariophyta) with description of two new ‘araphid’ species from the sub-Antarctic and Arctic Region**

Bart Van de Vijver<sup>1,2</sup>, Eduardo Tusset<sup>3</sup>, David M. Williams<sup>4</sup> & Luc Ector<sup>5</sup>

<sup>1</sup>Meise Botanic Garden Meise, Research Department, Nieuwelaan 38, 1860 Meise, Belgium

<sup>2</sup>University of Antwerp, Department of Biology – ECOBE, Universiteitsplein 1, B-2610 Wilrijk, Belgium (correspondence: bart.vandevijver@plantentuinmeise.be)

<sup>3</sup>Universidade Federal do Paraná, Setor de Ciências Biológicas, Departamento de Botânica, Centro Politécnico, Curitiba, Paraná, Brasil

<sup>4</sup>The Natural History Museum, Department of Life Sciences, Cromwell Road, London, SW7 5BD, UK

<sup>5</sup>Luxembourg Institute of Science and Technology (LIST), Environmental Research & Innovation (ERIN) Department, 41 rue du Brill, L-4422 Belvaux, Luxembourg

## **Abstract**

During a survey of the sub-Antarctic diatom flora, several populations previously identified as *Fragilaria alpestris* were reanalysed and compared with type material of the latter species. The morphological ultrastructure of the type of *F. alpestris*, the sub-Antarctic populations and an additional population of *F. cf. alpestris* from Spitsbergen has been analysed using light and scanning electron microscopy observations. The analysis revealed that *Fragilaria alpestris* clearly belongs to the genus *Fragilaria* whereas the sub-Antarctic populations show all morphological features of the genus *Staurosira*. Comparison with similar taxa worldwide showed that these populations belonged to an unknown taxon that could not be identified using the currently available literature. A new species, *Staurosira vandenbusscheana* Van de Vijver sp. nov. is therefore described. The *F. cf. alpestris* population from Spitsbergen forms long, ribbon-like colonies, unlike the type of *F. alpestris* that never produces band-like colonies. Following the observation of additional morphological differences such as the presence of two rimoportulae and the shape of the linking spines, the Spitsbergen taxon is described as a new species: *Fragilaria confusa* sp. nov. The three taxa described herein share a number of morphological features. Their specific features are detailed below along with notes on their ecology. A literature survey and an analysis of the records for *F. alpestris* are given.

**Key-words:** *Fragilaria*, morphology, biogeography, new species

## Introduction

*Fragilaria alpestris* Krasske (in Hustedt 1931: 165) was based on samples collected in the Alps but no specific type locality was given ('*an überrieselten Felsen in den Zentralalpen, z.B. beim Hintersee in den Felber Tauern*', Hustedt 1931: 165). A possible more precise locality was mentioned in Krasske (1932: '*Im Juli 1927 im oberen Öztale. Untersucht wurden die Gräben und Bäche an der Straße von Längfeld nach Zwieselstein, Bäche und Sturzwasser zwischen diesem Orte und Vent und besonders Sturzwasser, Rinnsale, Schmelzwassertümpel der Höhen um Vent*'). The species was characterised by forming band-like colonies. The valves are linear with slightly concave margins and protracted, cuneate apices. The sternum is broad and linear. For valve dimensions, Hustedt (1931) reported 20–50  $\mu\text{m}$  for valve length and 2.5–3.0  $\mu\text{m}$  for valve width with stria density as 13–16 in 10  $\mu\text{m}$ .

Krammer & Lange-Bertalot (1991: 141) briefly discussed the taxonomic position of *F. alpestris* concluding that, due to insufficient data ('*zu wenig Populationen bekannt*', Krammer & Lange-Bertalot 1991, p. 141), it was not possible for them to make any definitive statement.

Problems of interpretation arose with the publication of specimens from a population of *F. alpestris* from the sub-Antarctic Iles Kerguelen in the southern Indian Ocean (Le Cohu 1988). Le Cohu (1988) provided an extensive morphological analysis that included many scanning electron microscopy observations. The observed specimens had a different suite of characters than were generally accepted for the genus *Fragilaria* as defined by Williams & Round (1987). Le Cohu (1999) reanalysed the morphology of the Kerguelen populations and, based on the structure of the striae and the areolae, transferred the species to the genus *Staurosirella* D.M. Williams & Round (1987: 274) as *Staurosirella alpestris* (Krasske in Hustedt 1931: 165) Le Cohu (1999: 826). Van de Vijver et al. (2002) subsequently found similar specimens in the neighbouring Iles

Crozet and transferred the species to the genus *Staurosira* Ehrenberg (1843a: 45) as *Staurosira alpestris* (Krasske in Hustedt 1931: 165) Van de Vijver (in Van de Vijver et al. 2002: 114) since the southern populations showed all the typical features of the genus *Staurosira*. Specimens of *Staurosirella alpestris* were further encountered on Heard Island (Van de Vijver et al. 2004, reported under the name *Staurosira alpestris*) and the Prince Edward Islands (Van de Vijver et al. 2008, reported under the name *Staurosira alpestris*) confirming its broad sub-Antarctic distribution in the southern Indian Ocean.

Krammer & Lange-Bertalot (1991) doubted the conspecificity of the sub-Antarctic populations with *Fragilaria alpestris* stating that the European populations presented all the characters for a typical *Fragilaria* sensu Williams & Round (1987). Unfortunately, a morphological analysis of the type population using scanning electron microscopy was never performed. Lange-Bertalot et al. (1996) designated sample B I 24 from the Krasske collection in Kassel (Germany) as lectotype for *F. alpestris*. Several other samples were listed in Lange-Bertalot et al. (1996), presumably those containing additional populations of *F. alpestris*, from both the Alps and Arctic Spitsbergen.

In this paper, lectotype material for *Fragilaria alpestris* has been studied using both light (LM) and scanning electron microscopy (SEM). In addition, several populations from the sub-Antarctic islands and the Arctic island of Spitsbergen were examined. Based on these results, the sub-Antarctic populations are described as a new species *Staurosira vandenbusscheana* Van de Vijver sp. nov., whereas the Spitsbergen population is described as *Fragilaria confusa* Van de Vijver, Tuset, D.M. Williams & Ector sp. nov. The three new species are compared with several others in *Fragilaria* and *Staurosira*. Notes on their ecology and, where possible, distributions are added.

## Material and methods

The lectotype for *F. alpestris*, sample B I 24 from the Krasske collection, is listed in the Krasske collection as sample n° 1471. It was collected on 9. VII 1927 (9<sup>th</sup> of July 1927) from Zwieselstein, Ötztal, Austria. Lange-Bertalot et al. (1996) indicated three additional samples from the Alps (B I 30, B I 31, B II 53) containing populations of *F. alpestris* and two samples from Spitsbergen (C II 215 & 216). For this study, all of the samples from the Alps were retrieved and prepared. The samples from Spitsbergen were not available. Raw material from one sample obtained from a diatom survey in Spitsbergen (Van de Vijver et al. 1999) was prepared for a detailed analysis of the *F. cf. alpestris* population. For the analysis of the sub-Antarctic populations, three samples with a high abundance of the taxon were selected for further analysis. Table 1 lists all samples used in this study.

Subsamples of all selected materials were prepared for light (LM) and scanning electron microscopy (SEM) observations following the method described in van der Werff (1955). Small volumes of the samples were cleaned by adding 37% H<sub>2</sub>O<sub>2</sub> and heating to 80°C for about 1 h. The reaction was completed by addition of saturated KMnO<sub>4</sub>. Following digestion and centrifugation (three times for 10 minutes at 3700 × rpm), the resulting cleaned material was diluted with distilled water to avoid excessive concentrations of diatom valves on the slides. Cleaned diatom material was mounted in Naphrax. The resulting slides were analysed using an Olympus BX53 microscope at 1000x magnification (N.A. 1.73), 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- $\mu\text{m}$  Isopore™ polycarbonate membrane filter (Merck Millipore). The stubs were sputter-coated with a gold-palladium layer reaching a thickness of 20 nm and studied using a ZEISS Ultra SEM microscope at 3 kV (Natural History Museum, London, UK). The Spitsbergen sample was sputter-coated with a platinum layer reaching a thickness of 20 nm and studied using a JEOL-JSM-7100F field emission scanning electron microscope at 2 kV. Slides and stubs 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, genus features for *Fragilaria*), Tuji & Williams (2006a, genus features for *Fragilaria*) and Round et al. (1990, genus features for *Staurosira*). For taxonomic comparisons, the following papers were consulted: Krammer & Lange-Bertalot (1991), Morales (2005), Cejudo-Figueiras et al. (2011) and Van de Vijver et al. (2014).

### **Taxonomic treatment**

***Fragilaria alpestris* Krasske in Hustedt 1931, p. 165, fig. 673 B (Krasske 1932, p. 98, pl. 2, fig. 1) (Figs 1—25)**

**TYPE:**—AUSTRIA, Zwieselstein, Ötztal (“Ötztal, feuchte Felsen links der Ache unterhalb Zwieselstein (coll. date 9 VII 1927)”), Krasske sample 1471 (B I 24), lectotype (designated in Lange-Bertalot et al. 1996, p. 82), kept in the Krasske Collection (Kassel, Germany).

### **Description (based on lectotype specimens)**

LM (Figs 1–20): Frustules in girdle view rectangular (Fig. 2). Band-like colonies not observed; often two cells observed linked together (Fig. 1). Valves linear with parallel margins, faintly constricted at centre, apices taper, distinctly protracted, rostrate to capitate. Valve dimensions (n=25): length 22–40  $\mu\text{m}$ , width 2.5–3.0  $\mu\text{m}$ . Sternum narrow (e.g., Figs 3, 4), sometimes wider (e.g., Figs 9–11), distinct, linear, with slight swelling near central area. Central area small, barely perceptible, extending to valve margins, never forming a distinct hyaline region but composed of several reduced striae, elliptical to apically elongated. Striae alternating, parallel becoming weakly radiate at the apices, 14–17 in 10  $\mu\text{m}$ . Areolae not discernible in LM.

SEM (Figs 21–25): Cingulum composed of three open copulae plus valvocopula (Fig. 21). Each band with small granules (Fig. 21) and a single row of poroids situated at pars media. Band tapers towards pole fitting around ligula of preceding band (Fig. 21, double arrow indicating ligula). Bands reducing in size, from valvocopula to final (4<sup>th</sup>) band. Mantle deep, with mantle striae restricted to first half of mantle; second half with large, irregularly shaped silica plaques (Fig. 21). Striae uniseriate, composed of large virgae relative to smaller vimines. Each stria composed of 4–5 round areolae, the latter externally covered by individual hymenes (Figs 22–24). Central striae clearly shortened, reduced to 1–3 areolae (Figs 22, 24). A continuous, dense series of small, conical spines present on valve face/mantle junction situated apex to apex, mostly associated with a virga (Figs 22–24). Spines, when broken, hollow, leaving a rounded, rimmed vestige (Figs 22, 23, arrows). One rimoportula present per valve, superimposed on the last stria at the apex. Apical pore field well developed, composed of several rows of small, round to squarish, rimmed pores (Fig. 23). Internally, rimoportula visible at the apex (Fig. 25, arrow).

**Ecology:**—Although ecological data are lacking for the original material, it is possible to derive some ecological preferences for *F. alpestris* from the dominant flora in the sample. A

community analysis of the lectotype slide for *F. alpestris* showed that the sample is dominated by *Tetracyclus rupestris* (Kützing 1849: 12) Grunow in Van Heurck (1881: pl. 52, figs 13, 14) and *Achnantheidium minutissimum* (Kützing 1833a: 578) Czarnecki (1994: 157). Subdominant taxa include *Gomphonema hebridense* W.Gregory (1854: 99), *Encyonopsis cesatii* (Rabenhorst 1853: 39) Krammer (1997: 156), *Eunotia diodon* Ehrenberg (1837: 45) and *Humidophila perpusilla* (Grunow 1860: 552) R.L.Lowe et al. (2014: 358). *Tetracyclus rupestris* is a typical species for wet rocks and moss habitats (Krammer & Lange-Bertalot 1991), mainly found in high altitude mountains of central Europe but absent in northern Europe. *Achnantheidium minutissimum* is known to prefer well oxygenated oligo- to mesotrophic habitats (Lange-Bertalot et al. 2017). The other taxa in the sample show a preference for oligotrophic, electrolyte-poor, circumneutral, often calcareous or calcium-bicarbonate lakes (and more rarely rivers) in higher altitudes (Lange-Bertalot et al. 2017). All taxa are indicators for good water quality. *Humidophila perpusilla* prefers wet bryophyte vegetation and moistened rocks, similar to *Tetracyclus rupestris* (Krammer & Lange-Bertalot 1991, Lange-Bertalot et al. 2017).

***Staurosira vandenbusscheana* Van de Vijver sp. nov.** (Figs 26–48)

**TYPE:**—INDIAN OCEAN, Heard Island, Northwest Cornice (sample Q293, coll. date 6 II 2001, leg. N.J.M. Gremmen, holotype BR!, slide no. 4626, isotype PLP! slide no. 381, University of Antwerp, Belgium).

LM (26–42): Frustules in girdle view rectangular, forming long band-like colonies. Solitary cells never observed. In valve face view, cells almost always connected to each other making a clear focus on the structure impossible. Valves linear with parallel margins, longer valves often with weakly constricted centre (e.g. Figs 27, 28). Apices distinctly protracted, rostrate to subcapitate.

Valve dimensions (n=30): length 15–32  $\mu\text{m}$ , width 3–4  $\mu\text{m}$ . Sternum moderately broad, linear. Lacking central area. Striae alternating, parallel throughout, becoming very weakly radiate near apices, 13–15 in 10  $\mu\text{m}$ . Areolae not discernible in LM.

SEM (Figs 43–48): Frustules in girdle view linked via solid spatulate, dendritic linking spines (Figs 43, 44). Cingulum composed of several plain, open copulae, reducing in size from valvocopula outwards, final bands sometimes fragmented (Fig. 43). Mantle plaques absent (Figs 43, 44). Mantle striae very short, composed of one or two areolae (Fig. 43). Valve face visible only when spines broken (Fig. 45). Striae uniseriate, composed of several, apically elongated, slit-like areolae gradually diminishing in size towards the sternum (Fig. 45). Rimoportulae absent (Figs 45, 48). Apical pore fields reduced to a few rows of very small, round pores, visible at both apices (Figs 45, 46, 48). Internally, areolae individually covered by irregularly shaped vela (Figs 47, 48). Virgae clearly raised between the sunken striae (Fig. 47). Apical pore fields located in a distinct depression (Fig. 47).

**Etymology:**—The species is named after my dear friend Mr. Walter Van den Bussche (Belgium) to honor him for his important efforts to study and conserve the native orchid flora of Belgium.

**Ecology:**—*Staurosira vandenbusscheana* has been observed on all sub-Antarctic islands in the southern Indian Ocean (Prince Edward Islands, Iles Crozet, Iles Kerguelen, Heard Island). The largest populations were observed on Heard Island and Iles Crozet where the species was found in circumneutral (pH 7.2–7.4, Heard Island) to very alkaline (pH 8.9–9.2, Iles Crozet) lakes and moss vegetation alongside rivers and lakes. Le Cohu (1999, reported as *Staurosirella alpestris*) observed the species in a few lakes on Ile Kerguelen. The species seems to prefer low to moderate conductivity values (>300  $\mu\text{S}/\text{cm}$ ) and low

phosphate and nitrogen concentrations (Van de Vijver & Beyens 1999). This is also confirmed by the accompanying diatom flora observed in most of the samples:

*Ctenophora pulchella* (Kützing 1844: 68) D.M. Williams & Round (1986: 330),  
*Fragilaria capucina* Desmazières (1830: No. 453), *Punctastriata jolinae* (Van de Vijver in Van de Vijver & Beyens 2002: 320) M.L. García, Maidana & Van de Vijver (in García et al. 2017: 113) and *Sellaphora tumida* Van de Vijver & Beyens (in Van de Vijver et al. 2002: 110).

***Fragilaria confusa* Van de Vijver, Tuset, D.M. Williams & Ector sp. nov.** (Figs 49–80)

**TYPE:**—ARCTIC OCEAN, Brøgger Peninsula, north-west Spitsbergen (sample SPITS1998-10, coll. date 19 VII 1997, leg. P. Ledeganck, holotype BR!, slide no. 4627, isotype PLP! slide no. 382, University of Antwerp, Belgium).

LM (Figs 49–69): Frustules in girdle view rectangular, forming long band-like colonies (Figs 49, 50), up to 25 linked cells. Valves linear with almost parallel margins, apices distinctly protracted, rostrate to capitate. Valve dimensions (n=30): length 30–70  $\mu\text{m}$ , width 2–3  $\mu\text{m}$ . Sternum narrow, linear, not wider at central area. Central area very small to absent, asymmetrical if present, formed by absence of reduced central striae. Striae alternate, parallel throughout, weakly radiate at the apices, 15–16 in 10  $\mu\text{m}$ . Areolae not discernible in LM.

SEM (Figs 70–80): Frustules connected by linking spines (Figs 70, 73, 74). Two spines types present: near the central area, spines spatulate, interlocking with adjacent spines (Fig. 74); closer to apices, spines acute, resembling shark teeth, never spatulate (Fig. 73). Mantle deep with mantle striae limited to the advalvar part of the mantle. Abvalvar mantle edge bearing large, irregularly shaped silica plaques (Fig. 70). Striae uniseriate, formed by pairs of large virgae and

series of relatively smaller vimines, enclosed forming small, round to apically elongated areolae (Fig. 71). Few central striae shortened (Fig. 71). Rimoportulae present, one located at each apex (Figs 71, 76, 77, arrows, 78), almost not separable from normal areolae. Apical pore field well developed composed of 4–5 rows of small, round to squarish pores (Figs 72, 76—80). Two apical spines extending out over pore field (Fig. 77). Small pseudosepta visible (Fig. 78). Cingulum composed of several open bands, perforated with a single row of poroids at pars media (Fig. 70).

**Etymology:**—The specific epithet ‘*confusa*’ (confusing) is proposed as its exact taxonomic position in the genus *Fragilaria* is rather confusing as there are several morphological features that are atypical for the genus *Fragilaria*.

**Ecology:**—*Fragilaria confusa* has been found in two alkaline brooklets with rather low conductivity values (< 200  $\mu\text{S}/\text{cm}$ ) in northwest Spitsbergen. Both samples were collected from submerged moss vegetation in these brooklets. Apart from a very large population of *F. confusa*, the sample was further dominated by *Meridion circulare* (Greville 1822: 213) C.Agardh (1831: 40), *Rossithidium petersenii* (Hustedt 1937: 179) Round & Bukhtiyarova (1996: 178) and *Cymbella arctica* (Lagerstedt 1873: 44) A.W.F.Schmidt (1875: pl. 10: fig. 12) with *Pinnularia streptoraphe* var. *parva* Krammer (1992: 168), *Geissleria paludosa* (Hustedt 1957: 286) Lange-Bertalot & Metzeltin (1996: 67) and *Caloneis backmanii* Cleve-Euler in Backman & Cleve-Euler (1922: 54) as common taxa. Most of these species are considered Arctic endemics with a very restricted distribution. *Meridion circulare* is known to prefer cold, fast-flowing brooks (Lange-Bertalot et al. 2017).

## **Discussion**

### ***Comparison of Fragilaria alpestris, F. confusa and Staurosira vandenbusscheana***

Morphological analysis of lectotype specimens of *F. alpestris*, the population from Spitsbergen and the sub-Antarctic populations, previously identified as *F. alpestris* (and subsequently *Staurosira alpestris* and *Staurosirella alpestris*) clearly showed that the three taxa are not conspecific requiring a formal description for the Spitsbergen population and the sub-Antarctic species. The type population of *F. alpestris* shows all the morphological characteristics of the genus *Fragilaria* (as described by Williams & Round 1987, Tuji & Williams 2006a) such as open, perforated girdle bands, one rimoportula per valve, mantle plaques, uniseriate striae externally occluded by individual hymenes and well-developed apical pore fields on both apices. The presence of the short spines forming a continuous row along the valve face/mantle junction is not unique within the genus *Fragilaria*, although conical spines as in *F. alpestris* are rarely seen. Apart from species forming colonies by means of linking spines, such as *F. mesolepta* Rabenhorst (1861: no. 1041) (Heudre et al. 2019), small acute spines could be observed in other species that never form colonies such as *Fragilaria vaucheriae* (Kützing 1833b: 24) J.B.Petersen (1938: 167) or *F. gloiophila* (Grunow in Van Heurck 1881: pl. 40, fig. 21) Van de Vijver et al. (2020: 2), although these species never presented uninterrupted rows of spines as typical for *F. alpestris*. Therefore, the taxonomic position of *F. alpestris* within the genus *Fragilaria* is justified.

Williams (2019) reviewed the presence of spines in araphid diatoms. He classified all *Fragilaria* taxa, for which the spine type was known, into 4 groups based on the presence/absence of spines and, when present, on the placement of the spines, either on the vimines or on the virgae. Based on this classification, *Fragilaria alpestris* would be placed in group 4, with spines on the virgae,

whereas *F. confusa*, having spines on the vimines, would be best placed in group 3 together with taxa such as *F. vaucheriae* and *F. capucina* (Williams 2019).

*Fragilaria confusa* shows a high morphological similarity with *F. alpestris* but differs significantly in forming, long, ribbon-like colonies. *Fragilaria alpestris*, on the other hand, does not form colonies, although both Hustedt (1931) and Krammer & Lange-Bertalot (1991) stated in their description that *F. alpestris* produced band-like colonies. Careful analysis of the type material, and of the three other samples from the Alps in which *F. alpestris* was present, revealed only a maximum of two cells connected to each other whereas colonies were always absent. This absence of colony-formation could be explained by the lack of linking spines. The weak link between frustules is then easily disrupted by sampling and preparation, or possibly even by simple movements in the water column.

Taxa such as *F. mesolepta*, *F. rumpens* (Kützing 1844: 69) G.W.F. Carlson (1913: 29) or *F. capucina* Desmazières (1830: No. 453), known for their very long chains up to often tens or hundreds of linked frustules (Tuji & Williams 2006b, 2008, Heudre et al. 2019, Van de Vijver et al. submitted), all produce typical, spatulate linking spines. The lack of colony-formation in *F. alpestris* and the observation of long, ribbon-like colonies, connected using linking spines in *F. confusa* is a crucial difference in separating both taxa. Based on its ultrastructure, *Fragilaria capucina* is quite similar to *F. confusa*. Both produce the same type of colonies with two different types of spines: spatulate linking spines near the central area and acute spines towards the apices (see Heudre et al. 2019, fig. 5D & E). The linking spines in *F. confusa* are broadly rounded whereas in *F. capucina*, the linking spines are more irregularly shaped. Both taxa also possess two rimoportulae, a feature that is rather uncommon in the genus *Fragilaria* (Rioual et al. 2017). There are, however, striking morphological differences separating *F. alpestris* from *F.*

*capucina*. The latter has broadly rounded and only weakly protracted apices whereas *F. confusa* has rostrate to often even capitate apices. *Fragilaria confusa* has a maximum valve width of 3  $\mu\text{m}$ , whereas the minimum valve width of *F. capucina* is 3.3 exceeding often 4.5  $\mu\text{m}$  (Tuji & Williams 2006a, Heudre et al. 2019). Additionally, *F. capucina* has a well-developed central area that is absent in *F. confusa*. *Fragilaria pararumpens* Lange-Bertalot et al. (in Hofmann et al. 2011: 269) also forms colonies using two types of spines, but the latter has a well-developed, inflated central area and possesses only one rimoportula per valve (Heudre et al. 2019, fig. 7). Other colony-forming *Fragilaria* taxa such as *F. subconstricta* Østrup (1910: 192) and *F. mesolepta* have different valve outlines (with clearly constricted central areas), uniform linking spines along the entire valve length and only one rimoportula.

*Staurosira vandenbusscheana* on the other hand lacks a lot of typical *Fragilaria* s.s. features (Williams & Round 1987, Round et al. 1990, Tuji & Williams 2006a). Rimoportulae are entirely lacking. At present, all known *Fragilaria* taxa possess at least one rimoportula per valve, which would make the placement of *S. vandenbusscheana* within the genus *Fragilaria* problematic.

The girdle bands in the sub-Antarctic populations are, in some case, fragmented, with the appearance of being broken, not unlike the quasifract bands seen in *Nanofrustulum* Round, Hallsteinsen & Paasche (1999, p. 345, see Morales et al. 2019) and lack perforations, which has not been observed in *Fragilaria* s.s. The areolae are covered in the valve interior contrary to the external hymenes in *Fragilaria* s.s. The apical pore fields in *S. vandenbusscheana* are composed of a series of irregular small pores, whereas in *Fragilaria* s.s., the apical pore fields always form distinct, well defined zones situated on the mantle. This combination of features however, is typical for the genus *Staurosira* (Williams & Round 1987) and therefore the species should be placed in this genus. Le Cohu (1999) placed the species in the genus *Staurosirella*. This seems

unlikely based on several observations: the vimines are short and slender, typical for *Staurosira*, whereas in *Staurosirella* the vimines are always much longer (Williams & Round 1987). The spines are typical for *Staurosira* as can be seen in taxa such as *S. construens* Ehrenberg (1843b: 424) (Round et al. 1990). The apical pore fields are also typical and located more on the valve mantle as can be seen in *S. construens* or *S. binodis* (Ehrenberg 1854: pl. 5/2: fig. 26) Lange-Bertalot in Hofmann et al. (2011: 260).

*Staurosira vandenbusscheana* shows some similarity to other small-celled fragilarioids such as *Staurosira pottiezii* Van de Vijver (in Van de Vijver et al. 2014: 257), *Pseudostaurosira alvarezii* Cejudo-Figueiras et al. (2011: 69), *P. subsalina* (Hustedt 1925: 106) E.Morales (2005: 115) and to a lesser extent *P. americana* E.Morales in Cejudo-Figueiras et al. (2011: 70), *Staurosira venter* (Ehrenberg 1854: 13) Cleve & J.D.Möller (1879: no. 242) and *S. binodis*.

The most similar taxa is *S. pottiezii*, recently described from the Maritime Antarctic Region. The latter is however slightly smaller (max. valve length 22 µm, max. valve width 3.5 µm) with a lower stria density (12–13 vs 13–15 in 10 µm), giving the new species a more elongated, slender outline. The virgae in *S. pottiezii* are broader and flattened whereas *S. vandenbusscheana* possesses clearly raised, narrow virgae. In girdle view, the frustules in *S. vandenbusscheana* are larger when compared to the illustrations in Van de Vijver et al. (2014, fig. 18) for *S. pottiezii* with Fig. 26 in the current paper for *S. vandenbusscheana*. The *Pseudostaurosira* species in this comparison differ mostly by the differences in genus morphology. The striae in

*Pseudostaurosira* are characterized in having a reduced number of areolae, often showing a complex inner structure involving branched volae (Williams & Round 1987, Cejudo-Figueiras et al. 2011). This areola structure has never been observed in the genus *Staurosira*. In *Staurosira*, spines are located on the virgae, contrary to *Pseudostaurosira* species where spines are usually

positioned on the vimines. This is certainly the case in the three species added to this comparison (see Cejudo-Figueiras et al. 2011, figs 97, 106 & 114). None of the three *Pseudostaurosira* species have a clear constriction in their valve outline, which is commonly observed in *S. vandenbusscheana*. Based on the generally accepted view of the morphology of *Staurosira venter*, the latter has a similar, never constricted valve outline and is usually smaller (Krammer & Lange-Bertalot 1991, pl. 132, figs 9–16). Unfortunately, the type material of *S. venter* has never been studied and therefore, our current understanding of the species has been subject to considerable species drift. Nevertheless, constricted valves are usually not observed under the name *S. venter*. Finally, *S. binodis* has clearly constricted valves with a constriction that is much more explicit as in *S. vandenbusscheana* (Krammer & Lange-Bertalot 1991, pl. 132, figs 23–27). Based on these differences, the separation of *S. vandenbusscheana* as an independent taxon is justified.

### ***Distribution of Fragilaria alpestris***

Most published accounts only record the name and have either a few or no illustrations. These records can only be verified if specimens are still available.

Since its first description in 1931 (in Hustedt 1931, Krasske 1932), *Fragilaria alpestris* has been sporadically recorded. Krasske (1938: 526) later found it to be widespread and common in Spitsbergen although given the current observations, it is possible that his specimens are *F. confusa*. Krammer & Lange-Bertalot (1991) discussed some historic observations of *F. alpestris* found in literature. Cleve-Euler (1953) illustrated two valves identified as *F. alpestris*. The drawings (Cleve-Euler 1953, fig. 354B) are similar to specimens from the lectotype of *F. alpestris* but her specimens were found in eutrophic lakes and rivers and, apparently, the

observed frustules formed long colonies, that are not observed in *F. alpestris*. Examination of the Cleve-Euler's specimens will be necessary to determine the taxonomic identity of the illustrated valves. Similarly, the specimen recorded as *F. alpestris* by Mölder & Tynni (1970: 129, pl. 1, fig. 1) requires examination, although the published figure shows a valve that is broad and linear, lacking a central constriction and a well-defined central area as has been observed in *F. alpestris*. It is possible that this valve also belongs to *F. confusa*. Unfortunately, the authors did not indicate whether the taxon made colonies.

Lange-Bertalot & Genkal (1999, pl. 2, figs 1 & 2), in their work on the diatoms from the Siberian Arctic, presented two valves with similar conical spines and areolae as *F. alpestris*, but with a unilateral, asymmetrical, central area, contrary to *F. alpestris* where based on all observations of the type material, the central area is usually bordered by shortened striae.

The observations in the sub-Antarctic region have already been discussed (Le Cohu 1988, 1999, Van de Vijver et al. 2002), which led to the description of *Staurosira vandenbusscheana*. In the Maritime Antarctic Region (southern Atlantic Ocean), a similar species was observed, identified as *F. alpestris* (Kawecka & Olech 1993, fig. 7) but based on the stria density and valve length, the illustrated valve should be identified as *S. pottiezii*, a species that is commonly observed in the Maritime Antarctic region (Van de Vijver et al. 2014).

According to Lange-Bertalot et al. (1996), *F. alpestris* was observed on the Arctic Svalbard archipelago (Spitsbergen). Unfortunately, the Spitsbergen slides from the Krasske collection were not available for examination.

During a survey of the diatom flora from the region around Ny Alesund (Spitsbergen), Van de Vijver et al. (1999) observed a population of a taxon they identified as *Fragilaria* cf.

*alpestris* in a small stream. Reanalysis of the sample (Van de Vijver, unpubl. res.) showed a population of an unknown *Fragilaria* s.s. taxon, forming band-like colonies using linking spines. The valves were unfortunately very eroded to allow a good morphological characterization of the taxon but the SEM observations and the formation of the colonies made clear that the population cannot be conspecific with *F. alpestris* (Van de Vijver, pers. obs.).

Most likely, the drawing in Oleksowicz & Luścińska (1992) of *F. alpestris* from Oscar II Land (Spitsbergen), despite being obscure, represents the same unknown taxon. Witon & Witkowski (2003, pl. 8, fig. 14) observed a *F. alpestris*-like population on the Faeroe Islands but the illustrated valves indicates that the species makes colonies and is larger and less elongated (lower length/width ratio) than *F. alpestris*.

Nardelli et al. (2014) shows one valve of a taxon from Brazil that might be identified as *F. alpestris*, although the central area seems to be slightly swollen, which is never the case in *F. alpestris*. Other illustrated records of *F. alpestris* are lacking in literature. Further research will be necessary to establish a more precise biogeographical range of *F. alpestris* and *F. confusa*. Based on our observations, it is possible that *F. confusa* is confined to a Nordic distribution, whereas *F. alpestris* has a very restricted distribution in the Alps.

## **Acknowledgements**

The authors sincerely thank Dr Peter Mansfeld (Krasske collection, Kassel, Germany) for helping us with retrieving the type material of *F. alpestris*. Mrs Sandra Wilfert and Ms Katharina Wilfert are acknowledged for deciphering the handwritten notes Krasske made for the samples. The late Dr N.J.M. Gremmen is thanked for providing the samples of Heard Island. Sampling on Iles Crozet was made possible with the logistic and financial support of the Institut Polaire

Français - Paul-Emile Victor (IPEV) in the frame of the Terrestrial Ecology program 136 (Dr Yves Frenot & Dr Marc Lebouvier). Sampling in Spitsbergen was done by Prof. Dr L. Beyens, Mr P. Ledeganck & Dr G. Potters. This study was further supported by the BELSPO MICROBIAN project to visit the Natural History Museum in London, UK. Dr Alex Ball and the staff of the IAC laboratory at the Natural History Museum are thanked for their help with the scanning electron microscopy observations.

## References

- Agardh, C.A. (1831) *Conspectus Criticus Diatomacearum*. Part 3. Litteris Berlingianis, Lund, pp. 33–48.
- Backman, A.L. & Cleve-Euler, A. (1922) Die fossile Diatomaceenflora in Österbotten. *Acta Forestalia Fennica* 22 (4): 1–73.
- Carlson, G.W.F. (1913) *Süsswasser-Algen aus der Antarktis, Süd-Georgien und den Falkland Inseln. Wissenschaftliche Ergebnisse der Schwedischen Südpolar-Expedition 1901–1903, unter leitung von Dr. Otto Nordenskjöld*. Band 4 (14). Lithographisches Institut des Generalstabs, Stockholm, pp. 1–94.
- Cejudo-Figueiras, C., Morales, E.A., Wetzel, C.E., Blanco, S., Hoffmann, L. & Ector, L. (2011) Analysis of the type of *Fragilaria construens* var. *subsalina* (Bacillariophyceae) and description of two morphologically related taxa from Europe and the United States. *Phycologia* 50 (1): 67–77.  
<https://doi.org/10.2216/09-40.1>
- Cleve, P.T. & Möller, J.D. (1879) *Diatoms. Part IV, No. 217–276*. Esatas Edquists Boktryckeri, Uppsala, pp. 169–216.

- Cleve-Euler, A. (1953) Die Diatomeen von Schweden und Finnland. Teil III. Monoraphideae, Biraphideae 1. *Kongliga Svenska-Vetenskaps Akademiens Handlingar, series 4, 5*: 1–255.
- Cox, E.J. & Ross, R. (1981) The striae of pennate diatoms. In: R. Ross, ed., *Proceedings of the Sixth Symposium on Recent and Fossil Diatoms*. Budapest, September 1-5, 1980. Taxonomy · Morphology · Ecology · Biology. Otto Koeltz, Koenigstein. pp. 267–278.
- Czarnecki, D.B. (1994) The freshwater diatom culture collection at Loras College, Dubuque, Iowa. In: Kociolek, J.P. (Ed.) *Proceedings of the 11th International Diatom Symposium, San Francisco, California, 12–17 August 1990*. *Memoirs of the California Academy of Sciences*, Number 17, pp. 155–173.
- Desmazières, J.B.H.T. (1830) *Plantes cryptogames du nord de la France*. Ed. 1. nos 451–500. Lille.
- Ehrenberg, C.G. (1837) Über ein aus fossilen Infusorien bestehendes, 1832 zu Brod verbacknes Bergmehl von den Grenzen Lapplands in Schweden. *Bericht über die zur Bekanntmachung geeigneten Verhandlungen der Königl. Preuß. Akademie der Wissenschaften zu Berlin 1837*: 43–45.  
<https://doi.org/10.1002/andp.18371160116>
- Ehrenberg, C.G. (1843a) Mittheilungen über 2 neue asiatische Lager fossiler Infusorien-Erden aus dem russischen Trans-Kaukasien (Grusien) und Sibirien. *Bericht über die zur Bekanntmachung geeigneten Verhandlungen der Königlich-Preussischen Akademie der Wissenschaften zu Berlin 1843*: 43–49.
- Ehrenberg, C.G. (1843b) Verbreitung und Einfluss des mikroskopischen Lebens in Süd- und Nord-Amerika. *Abhandlungen der Königlichen Akademie der Wissenschaften zu Berlin 1841 (Erster Teil)*: 291–445.

- Ehrenberg, C.G. (1854) *Mikrogeologie. Einundvierzig Tafeln mit über viertausend grossentheils colorirten Figuren, Gezeichnet vom Verfasser*. Leopold Voss, Leipzig, 40 pls.
- García, M.L., Maidana, N.I., Ector, L. & Morales, E.A. (2017) *Staurosira patagonica* sp. nov., a new diatom (Bacillariophyta) from southern Argentina, with a discussion on the genus *Staurosira* Ehrenberg. *Nova Hedwigia, Beiheft* 146: 103–123.  
<https://doi.org/10.1127/1438-9134/2017/123>
- Gregory, W. (1854) Notice of the new forms and varieties of known forms occurring in the diatomaceous earth of Mull; with remarks on the classification of the Diatomaceae. *Quarterly Journal of Microscopical Science* 2: 90–100.
- Greville, R.K. (1822) A description of two new plants of the order Algae, found in Scotland. *Memoirs of the Wernerian Natural History Society* 4 (Part 1): 213–217, pl. 8.
- Grunow, A. (1860) Über neue oder ungenügend gekannte Algen. Erste Folge, Diatomeen, Familie Naviculaceen. *Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien* 10: 503–582.
- 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 (2): 327–339.  
<https://doi.org/10.5091/plecevo.2019.1619>
- Hofmann, G., Werum, M. & Lange-Bertalot, H. (2011) *Diatomeen im Süßwasser-Benthos von Mitteleuropa. Bestimmungsflora Kieselalgen für die ökologische Praxis. Über 700 der häufigsten Arten und ihre Ökologie*. pp. [1]–908, 133 pls. Königstein: Koeltz Scientific Books.

- Hustedt, F. (1925) Bacillariales aus den Salzgewässern bei Oldesloe in Holstein. *Mitteilungen der geographischen Gesellschaft und der Naturhistorischen Museums in Lübeck*, Zweite Reihe, 30: 84–121.
- Hustedt, F. (1931) Die Kieselalgen Deutschlands, Österreichs und der Schweiz unter Berücksichtigung der übrigen Länder Europas sowie der angrenzenden Meeresgebiete. In: Rabenhorst, L. (ed.) *Kryptogamen Flora von Deutschland, Österreich und der Schweiz*. Bd. 7 (Teil 2, Lief. 1). Akademische Verlagsgesellschaft Geest & Portig K.-G., Leipzig, pp. 1–176, figs 543–682.
- Hustedt, F. (1937) Süßwasserdiatomeen von Island, Spitzbergen und den Färöer-Inseln. *Botanisches Archiv* 38: 152–207.
- Hustedt, F. (1957) Die Diatomeenflora des Flußsystems der Weser im Gebiet der Hansestadt Bremen. Denkschrift über den heutigen ökologischen Zustand der Wasserstraßen im bremischen Staatsgebiet auf Grund der Kieselalgen-Flora mit Beziehung auf die Abwasserverhältnisse. *Abhandlungen der Naturwissenschaftlichen Verein zu Bremen* 34 (3): 181–440.
- Kawecka, B. & Olech, M. (1993) Diatom communities in the Vanishing and Ornithologist Creek, King George Island, South Shetlands, Antarctica. *Hydrobiologia* 269–270: 327–333.  
<https://doi-org.proxy.bnl.lu/10.1007/BF00028031>
- Krammer, K. (1992) *Pinnularia* eine Monographie der europäischen Taxa. *Bibliotheca Diatomologica* 26: 1–353.
- Krammer, K. (1997) Die cymbelloiden Diatomeen. Eine Monographie der weltweit bekannten Taxa. Teil 2. *Encyonema* part., *Encyonopsis* and *Cymbellopsis*. *Bibliotheca Diatomologica* 37: 1–469.

- Krammer, K. & Lange-Bertalot, H. (1991) Bacillariophyceae 4. Teil: Achnantheaceae. Kritische Ergänzungen zu *Navicula* (Lineolatae) und *Gomphonema*. Gesamtliteraturverzeichnis Teil 1–4. In: Ettl, H., Gärtner, G., Gerloff, J., Heynig, H. & Mollenhauer, D. (eds.) *Süßwasserflora von Mitteleuropa*. Gustav Fischer Verlag, Stuttgart, Jena, 437 pp.
- Krasske, G. (1932) Beiträge zur Kenntnis der Diatomeenflora der Alpen. *Hedwigia* 72 (3): 92–134.
- Krasske, G. (1938) Beiträge zur Kenntnis der Diatomeen-Vegetation von Island und Spitzbergen. *Archiv für Hydrobiologie* 33: 503–533.
- Kützing, F.T. (1833a) Synopsis diatomearum oder Versuch einer systematischen Zusammenstellung der Diatomeen. *Linnaea* 8 (5): 529–620, pls XIII–XIX.
- Kützing, F.T. (1833b) Algarum aquae dulcis Germanicarum. Decas I. pp. [1–80]. Collegit Fridericus Traugott Kützing, Societ. Bot. Ratisbon. Sodalis. Halis Saxonum [Halle], in commissis C.A. Schwetschkii et fil.
- Kützing, F.T. (1844) *Die Kieselschaligen Bacillarien oder Diatomeen*. W. Köhne, Nordhausen, 152 pp.  
<http://dx.doi.org/10.5962/bhl.title.64360>
- Kützing, F.T. (1849) *Species Algarum*. F.A. Brockhaus, Leipzig, 922 pp.
- Lagerstedt, N.G.W. (1873) Sötvattens-Diatomaceer från Spetsbergen och Beeren Eiland. *Bihang till Kongliga Svenska Vetenskaps-Akademiens Handlingar* 1 (14): 1–52.
- Lange-Bertalot, H. & Genkal, S.I. (1999) Diatoms from Siberia I. Islands in the Arctic Ocean (Yugorsky-Shar Strait). Diatomeen aus Siberien I. Insel im Arktischen Ozean (Yugorsky-Shar Strait). *Iconographia Diatomologica* 6: 1–271.

- Lange-Bertalot, H. & Metzeltin, D. (1996) Oligotrophie-Indikatoren. 800 Taxa repräsentativ für drei diverse Seen-Typen. Kalkreich - Oligodystroph - Schwach gepuffertes Weichwasser [Indicators of oligotrophy. 800 taxa representative of three ecologically distinct lake types. Carbonate buffered – Oligodystrophic - Weakly buffered soft water]. *Iconographia Diatomologica* 2: 1–390.
- Lange-Bertalot, H., Külbs, K., Lauser, T., Nörpel-Schempp, M. & Willmann, M. (1996) Dokumentation und Revision der von Georg Krasske beschriebenen Diatomeen-Taxa [Diatom taxa introduced by Georg Krasske. Documentation and revision]. *Iconographia Diatomologica* 3: 1–358.
- Lange-Bertalot, H., Hofmann, G., Werum, M. & Cantonati, M. (2017) *Freshwater benthic diatoms of Central Europe: over 800 common species used in ecological assessment. English edition with updated taxonomy and added species*. Koeltz Botanical Books, Schmitten-Oberreifenberg, 942 pp.
- Le CoHU, R. (1988) *Fragilaria alpestris*, *Opephora naveana* nov. sp. et le complexe *Synedra ulna* (Bacillariophycées, Araphidinées) ; morphologie et ultrastructure. *Cryptogamie Algologie* 9 (2): 101–116.
- Le CoHU, R. (1999) Révision des principales espèces de Fragilariales (Bacillariophyta) des îles Kerguelen. *Canadian Journal of Botany* 77 (6): 821–834.  
<https://doi.org/10.1139/b99-035>
- 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 (4): 351–360.

<https://dx.doi.org/10.1080/0269249X.2014.889039>

Mölder, K. & Tynni, R. (1970) Über Finnlands rezente und subfossile Diatomeen IV. *Bulletin of the Geological Society of Finland* 42: 129–150.

Morales, E.A. (2005) Observations of the morphology of some known and new fragilarioid diatoms (Bacillariophyceae) from rivers in the USA. *Phycological Research* 53 (2): 113–133.

<https://doi.org/10.1111/j.1440-183.2005.00378.x>

Morales, E.A., Wetzel, C.E., Novais, M.H., Buczkó, K., Morais, M.M. & Ector, L. (2019) Morphological reconsideration of the araphid genus *Pseudostaurosira* (Bacillariophyceae), a revision of *Gedaniella*, *Popovskayella* and *Serratifera*, and a description of a new *Nanofrustulum* species. *Plant Ecology and Evolution* 152 (2): 262–284.

<https://doi.org/10.5091/plecevo.2019.1604>

Nardelli, M.S., Bueno, N.C., Ludwig, T.A.V., Tremarin, P.I. & Bartozek, E.C.R. (2014) Coscinodiscophyceae and Fragilariophyceae (Diatomeae) in the Iguazu River, Paraná, Brazil. *Acta Botanica Brasílica* 28 (1): 127–140.

<https://doi.org/10.1590/S0102-33062014000100013>

Oleksowicz, A.S. & Luścińska, M. (1992) Occurrence of algae on tundra soils in Oscar II Land, Spitsbergen. *Polish Polar Research* 13 (2): 131–147.

Østrup, E. (1910) *Danske Diatoméer*. C.A. Reitzels Boghandel, Kjøbenhavn, 323 pp., 5 pls.

<https://doi.org/10.5962/bhl.title.1044>

Petersen, J.B. (1938) *Fragilaria intermedia* – *Synedra Vaucheriae*? *Botaniska Notiser* 1938 (1–3): 164–170, fig. 1.

- Rabenhorst, L. (1853) *Die Süßwasser-Diatomaceen (Bacillarien) für Freunde der Mikroskopie*.  
Eduard Kummer, Leipzig, 72 pp., 10 pls.  
<https://doi.org/10.5962/bhl.title.8348>
- Rabenhorst, L. (1861) *Algen Europa's, Fortsetzung der Algen Sachsens, Resp. Mittel-Europas*.  
*Dec. 5–6. Nos 1041–1060*. Dresden.
- Rioual, P., Flower, R.J., Chu, G., Lu, Y., Zhang, Z., Zhu, B. & Yang, X. (2017) Observations on  
a fragilarioid diatom found in inter-dune lakes of the Badain Jaran Desert (Inner Mongolia,  
China), with a discussion on the newly erected genus *Williamsella* Graeff, Kociolek &  
Rushforth. *Phytotaxa* 239 (1): 28–50.  
<https://doi.org/10.11646/phytotaxa.329.1.2>
- 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. & Bukhtiyarova, L. (1996) Four new genera based on *Achnanthes* (*Achnanthidium*)  
together with a re-definition of *Achnanthidium*. *Diatom Research* 11 (2): 345–361.  
<http://dx.doi.org/10.1080/0269249x.1996.9705389>
- Round, F.E., Crawford, R.M. & Mann, D.G. (1990) *The diatoms: biology & morphology of the  
genera*. Cambridge University Press, Cambridge, 747 pp.
- Round, F.E., Hallsteinsen, H. & Paasche, E. (1999) On a previously controversial “fragilarioid”  
diatom now placed in a new genus *Nanofrustulum*. *Diatom Research* 14 (2): 343–356.  
<https://doi.org/10.1080/0269249X.1999.9705476>
- Schmidt, A. [W.F.] (1875) *Atlas der Diatomaceen-kunde. Series I (Heft 3)*. Commisions-Verlag  
Von Ludwig Siever's Buchandlung, Aschersleben, pls 9–12.

- Tuji, A. & Williams, D.M. (2006a) Typification of *Conferva pectinalis* O. F. Müll. (*Bacillariophyceae*) and the identity of the type of an alleged synonym, *Fragilaria capucina* Desm. *Taxon* 55 (1): 193–199.  
<http://dx.doi.org/10.2307/25065541>
- Tuji, A. & Williams, D.M. (2006b). Examination of the type material of *Synedra rumpens* = *Fragilaria rumpens*, Bacillariophyceae. *Phycological Research* 54 (2): 99–103.  
<https://doi.org/10.1111/j.1440-1835.2006.00414.x>
- Tuji, A. & Williams, D.M. (2008). Examination of type material of *Fragilaria mesolepta* Rabenhorst and two similar, but distinct, taxa. *Diatom Research* 23 (2): 503–510.  
<https://doi.org/10.1080/0269249X.2008.9705772>
- van der Werff, A. (1955) A new method of concentrating and cleaning diatoms and other organisms. *Verhandlungen der internationalen Vereinigung für theoretische und Angewandte Limnologie* 12: 276–277.  
<https://doi.org/10.1080/03680770.1950.11895297>
- Van de Vijver, B. & Beyens L. (1999) Freshwater diatoms from Ile de la Possession (Crozet Archipelago, Subantarctica): an ecological assessment. *Polar Biology* 22: 178–188.  
<https://doi.org/10.1007/s003000050408>
- Van de Vijver, B. & Beyens, L. (2002) *Staurosira jolinae* sp. nov. and *Staurosira circula* sp. nov. (Bacillariophyceae), two new fragilarioid diatoms from Subantarctica. *Nova Hedwigia* 75 (3–4): 319–331.  
<https://doi.org/10.1127/0029-5035/2002/0075-0319>

- Van de Vijver, B., Ledeganck, P., Potters, G. & Beyens, L. (1999) Diatom communities from alkaline environments of the Brøgger peninsula, north-west Spitsbergen. *Nova Hedwigia* 68 (1–2): 93–115.  
<https://doi.org/10.1127/nova.hedwigia/68/1999/93>
- Van de Vijver, B., Frenot, Y. & Beyens, L. (2002) Freshwater diatoms from Ile de la Possession (Crozet Archipelago, Subantarctica). *Bibliotheca Diatomologica* 46: 1–412.
- Van de Vijver, B., Beyens, L., Vincke, S. & Gremmen, N.J. M. (2004) Moss-inhabiting diatom communities from Heard Island, sub-Antarctic. *Polar Biology* 27: 532–543.  
<https://doi.org/10.1007/s00300-004-0629-x>
- Van de Vijver, B., Gremmen, N. & Smith, V. (2008) Diatom communities from the sub-Antarctic Prince Edward Islands: diversity and distribution patterns. *Polar Biology* 31 (7): 795–808.  
<https://doi.org/10.1007/s00300-008-0418-z>
- Van de Vijver, B., Morales, E.A. & Kopalová, K. (2014) Three new araphid diatoms (Bacillariophyta) from the Maritime Antarctic Region. *Phytotaxa* 167 (3): 256–266.  
<https://dx.doi.org/10.11646/phytotaxa.167.3.4>
- Van de Vijver, B., Ector, L., Schuster, T.M. & Walter, J. (2020) 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., Williams, D.M., Kelly, M., Jarlman, A., Wetzel, C.E. & Ector, L. (submitted) Analysis of some species resembling *Fragilaria capucina* (*Fragilariaceae*, *Bacillariophyta*). *Fottea*.

Van Heurck, H. (1881) *Synopsis des Diatomées de Belgique*. Atlas. pls XXXI–LXXVII [31–77].

Anvers: Ducaju et Cie.

Williams, D.M. & Round, F.E. (1986) Revision of the genus *Synedra* Ehrenb. *Diatom Research* 1 (2): 313–339.

<https://doi.org/10.1080/0269249X.1986.9704976>

Williams, D.M. & Round, F.E. (1987) Revision of the genus *Fragilaria*. *Diatom Research* 2 (2): 267–288.

<https://doi.org/10.1080/0269249X.1987.9705004>

Williams, D.M. (2019) Spines and homologues in ‘araphid’ diatoms. *Plant Ecology and Evolution* 152 (2): 150–162.

<https://doi.org/10.5091/plecevo.2019.1597>

Witon, E. & Witkowski, A. (2003) Diatom (Bacillariophyceae) flora of early Holocene freshwater sediments from Skalafjord, Faeroe Islands. *Journal of Micropalaeontology* 22 (2): 183–208.

<https://doi.org/10.1144/jm.22.2.183>

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

Sample	Locality	Date (D-M-Y)	collector
Sample 901 (B I 30)	Höllentalklamm bei Garmisch, feuchte Felsen	12 VII 1925	Krasske collection
Sample 902 (B I 31)	Höllentalklamm bei Garmisch, feuchte Felsen	12 VII 1925	Krasske collection
Sample 1422 (B II 53)	An Moos auf feuchten Felsen südl. von Hintersee, Felber Tal	13 VIII 1926	Krasske collection
Sample 1471 lectotype (B I 24)	Ötztal, feuchte Felsen links der Ache unterhalb Zwieselstein	9 VII 1927	Krasske collection
SPITS1998-10	Brøgger Peninsula, north-west Spitsbergen, small brooklet flowing out of moss vegetation (pH 7.7, cond. 170 $\mu$ S/cm)	19 VIII 1997	P. Ledeganck
BW277	Jardin Japonais, Ile de la Possession, Iles Crozet, sample taken from algal mats on the bottom of a large lake (pH 9.2, cond. 272 $\mu$ S/cm)	5 I 1998	B. Van de Vijver
Q181/2	Skua Beach West, Heard Island, sample taken from moss and algal mats on very wet peat deposits with downslope running water) (pH 7.2, cond. 20 $\mu$ S/cm)	28 I 2001	N.J.M. Gremmen
Q293 holotype	Northwest Cornice, Heard Island, sample taken from a moss vegetation along a riverbank in a spring and flush area (pH 6.3, cond. 9 $\mu$ S/cm)	6 II 2001	N.J.M. Gremmen

## Figure captions

**FIGURES 1–25.** *Fragilaria alpestris*. LM (1–20) and SEM (21–25) views. Lectotype population from the Ötztal (sample Krasske 1471). 1–2. Frustules in girdle view, solitary or two frustules together. 3–20. Valve views showing the broad range of valve dimensions. 21. SEM external view of an obliquely positioned solitary valve. The double arrow indicates the ligula. 22. SEM external view of an entire valve. The arrows indicate the rimmed pores. 23. SEM external detail of a valve apex with the rimoportula, apical pore field and extra rimmed pore (arrow). 24. SEM external detail of the central area. Note the shortened spines, the external hymenes and the conical spines. 25. SEM internal view of an entire valve. Scale bars = 10  $\mu\text{m}$  except for Figs 23 & 24 where scale bar = 1  $\mu\text{m}$ .

**FIGURES 26–48.** *Staurosira vandenbusscheana* LM (26–42) and SEM (43–48) views. Holotype population from Heard Island (sample Q293). 26. Frustules in girdle view, linked together to form a ribbon-like colony. 27–42. Valve views showing the broad range of valve dimensions. 43. SEM external view of several frustules linked with linking spines. 44. SEM external detail of the linking spines and the copulae. 45. SEM external view of an entire valve. The external view is partly obscured by the remains of a second, connected valve. 46. SEM external detail of a valve apex with the apical pore field. 47. SEM internal view of part of the valve showing areola occlusions. 48. SEM internal view of an entire valve. Scale bars = 10  $\mu\text{m}$  except for Fig. 46 where scale bar = 1  $\mu\text{m}$ .

**FIGURES 49–70.** *Fragilaria confusa* LM (49–69) and SEM(70) views. Holotype population from Spitsbergen (sample SPITS1998-10). 49–50. Frustules in girdle view, linked together to

form ribbon-like colonies showing the size range. 50–69. Valve views showing the broad range of valve dimensions. 70. SEM external view of several frustules linked with linking spines. Scale bars = 10  $\mu\text{m}$ .

**FIGURES 71–80.** *Fragilaria confusa* SEM views. 71. external view of an entire valve showing 2 rimoportulae and linking spines. 72. external detail the valve apex with the structure of the apical pore field, the mantle plaques and the two apical spines. 73. external detail of the valve apices in girdle view showing the acute spines. 74. external detail of the central area in girdle view showing the spatulate linking spines. 75. external detail of the spatulate linking spines. 76–77. external detail of both apices showing each a rimoportula, an apical pore field and two apical spines. 78. internal view of an entire valve. 79–80. internal detail of both apices showing each a rimoportula. Scale bars = 1  $\mu\text{m}$  except Figs 71 & 78 where scale bar = 10  $\mu\text{m}$ .







