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Revision of the genus *Stauroforma* (Staurosiraceae, Bacillariophyceae) based on varieties of *Fragilaria virescens* described by Albert Grunow

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Abstract

A revision of the genus *Stauroforma* is proposed based on the analysis of several historic slides prepared by Grunow to describe *Fragilaria virescens* var. *exigua*. The original materials are analysed using both light and scanning electron microscopy together with a critical examination of the original drawings and notes Grunow made on his new taxa. Based on this, the genus description of *Stauroforma* is emended and the morphological descriptions of *S. exiguiformis* and *S. inermis* are updated. Grunow's variety *subsalina* is raised to species level as *Stauroforma subsalina*. A new species, *Stauroforma subcassubica* is described splitting it from *S. cassubica,* the latter having larger valves. The results of this revision will enable a more exact identification of the different *Stauroforma* species observed in freshwater and brackish water bodies in Europe.

Keywords

Historical Material; Morphology; New Combinations; New Species; Revision; *Stauroforma*

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Introduction

The genus *Stauroforma* Flower, V.J.Jones *et* Round was originally described to accommodate 'araphid' diatom taxa bearing the following morphological features: formation of linear colonies, lanceolate to elliptic–lanceolate valves with almost parallel margins, a very reduced to absent sternum, opposite striae, often continuing without interruption over the sternum, absence of rimoportulae and a large, not curved valvocopula (Flower *et al.,* 1996). Spines are not always present and an apical porefield may be present at one or both apices, although some species lacking an apical porefield have been included in this genus (Flower *et al.,* 1996; Talgatti *et al.,* 2014). The genus was based on *Fragilaria exiguiformis* Lange–Bertalot as *typus generis*, a new name Lange–Bertalot (1993) introduced when he raised the taxon *Fragilaria virescens* var. *exigua* Grunow to species level. A new name in the genus *Fragilaria* was necessary to avoid homonymy with *Fragilaria exigua* (W.Smith) Lemmermann, a species introduced by Lemmermann for *Triceratium exiguum* W.Smith (Smith, 1856, p. 87 in Lemmermann, 1908, p. 409). *Fragilaria exiguiformis* was the first valid and legitimate name for *Fragilaria virescens* var. *exigua* Grunow at the rank of species and thus is available as the basionym for *Stauroforma exiguiformis*. There were initially doubts about the validity of the new name as the replaced synonym was not correctly cited (the original date of 1881 was missing). Since the same publication as the original replaced synonym was correctly cited on the same page for a different species, it can be assumed that the replaced synonym in Lange–Bertalot (1993, p. 45) should read as "*Fragilaria virescens* var.? *exigua* Grunow in Van Heurck, Syn. [Belg.] pl. 44: figs 2, 3. 1881 [– *Fragilaria* (*virescens* var.) *exigua* Grunow in Cleve & Möller no. 144. 1878b, nom. inval.]" making the new name validly published. Without this valid publication,

the genus *Stauroforma* would have been invalid since it was based on an invalid *typus generis*. According to AlgaeBase, at present, only six species are included in *Stauroforma* (Guiry & Guiry, 2025).

Flower *et al.* (1996) discussed the nomenclatural history of *Fragilaria virescens* var. *exigua* and *F. exiguiformis*. For *Fragilaria virescens* var. *exigua*, they note that its first mention was in Cleve & Möller's *Diatoms* where the name appears in the species list for three slides in this set. The first occurrence was in Part II (Cleve & Möller, 1878a, p. [2], n°59), a slide made from a sample collected in Aberdeen by Dr Dickie ('Aberdeen – Coll. By Mr. Dickie, authentic') with the slide labelled simply as '*Orthosira dickiei* W.Smith Aberdeen'. In the accompanying text, *Fragilaria virescens* var. *exigua* appears as '*Fragilaria* (*virescens* v.) *exigua* Grunow' (Cleve & Möller, 1878a, p. [2]). The second occurrence was in Part III (Cleve & Möller, 1878b, p. 4, n°144), a slide made from a sample from Kobbe Bay, Spitsbergen, collected by A. van Goës ('Spitsbergen, Kobbe Bay – Coll. by A. v Goës') with the slide labelled simply as '*Navicula hilseana* Janisch'. In the text, *Fragilaria virescens* var. *exigua* also appears as 'Fragilaria (virescens v.) exigua Grunow' but with the added comment 'conf. N:o 59' in brackets (Cleve & Möller, 1878b, p. 4). The implication is that Grunow considered both sets of specimens to be the same taxon but was unsure as to whether they were best considered a variety of *Fragilaria virescens* or as the species *Fragilaria exigua*. The third occurrence is much later in Part VI (Cleve & Möller, 1882, p. 6, n° 324, the final slide of the series), a slide made from a sample from Greenland, Atanek, collected by Dr Holst ('Greenland, Atanek. Coll. by Dr. N.O. Holst') with the slide not labelled for any species just the locality: 'Greenland Atanek'. In the text, *Fragilaria virescens* var. *exigua* appears as '*Fragilaria* (*virescens* var.?) *exigua* Grunow *et* var. *eunotiaeformis* Grunow' (Cleve & Möller, 1882, p. 6). The first two occurrences lacked a description and illustration and should be considered *nomina nuda*. The third has no nomenclatural significance as it follows on from Van Heurck (1881, plate XLIV, figs 2–3, see below) and one presumes Grunow meant it to be the same as the two previous occurrences.

As the names mentioned lacked both a description and illustration, these first records are *nomina nuda*. Later, Grunow in Van Heurck (1881, plate XLIV, figs 2–3) illustrated several valves and colonies under the name *Fragilaria virescens* var.? *exigua* Grunow, validating the varietal name (Flower, *et al.* 1996, p. 42). As type material, Flower *et al.* (1996, pp. 43, 54) indicated two slides from two different localities: Aberdeen and Spitsbergen, i.e. the original localities mentioned in Cleve & Möller (1878a, b). They stated also that the origin of the drawings in Van Heurck (1881, plate XLIV, figs 2–3) should be analysed to determine where the illustrated specimens came from. Lange–Bertalot (in Krammer & Lange–Bertalot, 1991, p. 137, 2000, p. 137 and a further comment on p. 582) cited only the slide from Spitsbergen to represent the type ('Der Typus ist in der Legende zu Cleve & Möller no. 144 von Spitzbergen as *Fragilaria (virescens* var.) *exigua* bezeichnet') – they do not illustrate any type specimens from that slide. The Herbarium of the Natural History Museum in Vienna (W, Austria) holds Grunow's collection including all of his drawings and a copy of Van Heurck's *Atlas du Synopsis des diatomées de Belgique* (Van Heurck, 1880–1885) annotated by Grunow. Grunow marked most of the drawings in the *Atlas* indicating the origin of the specimen either by adding his sample number and/or the type locality. Figure 1 shows the annotated drawings for *Fragilaria virescens* var. *exigua*. The first pair of drawings (Van Heurck, 1881, plate XLIV, fig. 2) was based on Grunow sample 2631 collected from 'Tom a Char' (= Tom–a–Char, near Logie Coldstone, Aberdeenshire, Scotland, UK) whereas the two drawings of Van Heurck (1881, plate XLIV, fig. 3) were taken from Cleve & Möller's *Diatoms* slide no. 59 from Aberdeen. Therefore, these samples should preferentially be taken into consideration when choosing a lectotype for this name.

Grunow in Van Heurck (1881) illustrated several other small–celled varieties of *Fragilaria virescens*: *F. virescens* var.? *subsalina* Grunow, *F. virescens* var.? *oblongella* Grunow and *F. virescens* [var. *oblongella*] f. *clavata* Grunow. The drawings for these three infraspecific taxa were all based on Grunow 2661, a brackish sample collected on the Scottish island of Arran near Corriegills (written in Van Heurck, 1881 as *Carrieghills*). Although original material for these three taxa has not been studied, they all have interesting, and often incorrect, taxonomic histories, not in the least due to the absence of knowledge of their morphology.

The present paper presents a revision of the taxonomic history of *Fragilaria virescens* var. *exigua* and several related varieties based on Grunow's original material. One new combination is proposed: *Stauroforma subsalina* (Grunow) Van de Vijver, T.M.Schust., D.M.Williams *et* Kusber *comb. nov.*, *stat. nov*. In the analysed material, one new species was observed: *Stauroforma subcassubica* Van de Vijver, T.M.Schust., D.M.Williams *et* Kusber *sp. nov*. In addition, the morphology of the Antarctic species *Stauroforma inermis* Flower *et al.* is re–described with further illustration, and discussed and compared with the historic Grunow taxa.

Material and Methods

For this study, several historic samples have been used from the Van Heurck collection, although we were unable to use the original material Grunow had in his possession, since it is missing or now not usable.

Sample 2631 (Tom–a–Char near Logie Coldstone, Aberdeenshire, Scotland, UK): only a slide is available in the Grunow collection at W; a similar slide is also present in the Van Heurck collection in BR. These slides were made by Eugene Weissflog and distributed among his colleagues. Van Heurck (1896, p. 113)

wrote the following about the Weissflog collection that is now conserved in the Van Heurck diatom collection in BR: "*The celebrated collection of our excellent friend, prepared by him between 1867 and 1892, which has formed part of our collection since 1892. The Weissflog Collection comprises about 2,500 preparations of rare diatoms, mostly selected, and all prepared with the greatest care. These preparations have been used for the works of Deby, Cleve, Grunow, Rattray, Witt, Ad. Schmidt, etc.".*

Sample 2661 (Carrighills, brackish; probably Isle of Arran, Corriegill, Scotland, UK): the original slide is missing from the Grunow collection. Some of the original material was sacrificed to make a new slide, which was conserved in Vienna, but following analysis of this new slide, no diatoms could be found. According to Grunow's accession books, sample 2661 was based on original material from sample WA 129 in the Walker Arnott collection, which is now largely conserved in the Van Heurck collection. Sample WA 129 was collected on '18 viii 1854' from a brackish pool at Corriegills, Arran according to his handwritten collection catalogue.

Cleve & Möller slide 59: This slide, which is based on material collected in Aberdeen by Dr Dickie, most likely originates from the same locality as sample WA 37 in the Walker Arnott collection (= BM 24051 'Aberdeen, Dr Dickie'). WA 37 was, however, collected in 1853 by Dr Redfern from a cave, located south of Cove near Aberdeen, Scotland (UK). Comparison of the diatom composition b*et*ween both slides revealed them to be almost identical making WA 37 an excellent addition for the observations of Cleve & Möller slide 59. Smith (1856, p. 60) declared that the material Dr Dickie and Dr Redfern collected, was taken from the same locality but probably in a different year (Dr Dickie = 1851, Dr Redfern = 1853). A survey of all *F. virescens* slides in BM, done a while ago, revealed several slides from Cove near Aberdeen (Williams, pers. comm.): BM 11191 ('Cave at Cove, nr Aberdeen, 37'); BM 22657 ('Cave at Cove, near Aberdeen, S. 409'); BM 24605 ('Cave at Cove, near Aberdeen, S. 409'); BM 25420 ('Cove nr Aberdeen, 38'); BM 25425 ('Cave at Cove nr. Aberdeen, S. 411); BM 31422 ('Cave at Cove, nr Aberdeen, 37). They are all based on the Walker Arnott material from the Cave at Cove near Aberdeen.

Cleve & Möller slide 144: this slide was made based on a sample collected by A. van Goës near Kobbe Bay on the Arctic island of Spitsbergen. No original material was left for analysis. Additionally, the type slide of *Stauroforma inermis* Flower *et al.* was examined and the specimens imaged. The slide was based on a sample collected from a sediment core taken in Moss Lake, Signy Island, South Orkney Islands, Maritime Antarctic Region (BM 82390). Only a slide was available. Therefore, to highlight the ultrastructure of *S. inermis*, sample VH4, collected during the austral summer of 2003–2004 by Louise Cromer from the Vestfold Hills, Antarctic Continent was also used.

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_2O_2 and heating to 80 °C for about 1 h. The reaction was completed by addition of saturated $KMnO_4$. Following digestion and centrifugation (three times for 10 minutes at 3700× rpm), the resulting cleaned material was diluted with distilled water to avoid excessive concentrations of diatom valves on the slides. Cleaned diatom material was mounted in Naphrax. The resulting slides were analysed using an Olympus BX53 microscope at 1000× magnification (UPlan FL N 100× oil objective, N.A. 1.30), equipped with Differential Interference Contrast (Nomarski) optics and the Olympus UC30 Imaging System connected to the Cell Sense Standard program. For each taxon, the number of specimens, measured at random on the type slide, is indicated (n=X). Although it proved not always possible to measure 50 valves or more, which might be more reliable to estimate the range in valve dimensions, it proved often to be very difficult to find sufficient measurable specimens in the material. Therefore, we consider a minimum of 20 specimens sufficient to estimate the species variability. For each population, at least 25, but often many more, valves are illustrated using LM to determine its morphological variability. An ecological characterisation based on the accompanying diatom flora, is added.

To complete the morphological analysis, the ultrastructure of each population is assessed using SEM. For that purpose, part of the suspension was filtered through polycarbonate membrane filters with a pore diameter of 5 µm, pieces of which were affixed on aluminum stubs after air–drying. Stubs were sputter–coated with a gold–palladium layer reaching a thickness of 15 nm. Observations and photomicrography were performed at the Natural History Museum in London (UK) using a Zeiss® Ultra plus scanning electron microscope at 3 kV. Slides and stubs are stored at the BR–collection. Plates were prepared using Photoshop CS5.

Terminology used in the description of the various structures of the siliceous cell wall is based on Ross *et al.* (1979, areola structure), Cox & Ross (1981, stria structure), Flower *et al.* (1996, genus features for *Stauroforma*), and Williams (2019, spines). The term 'sternum' is used for the axial area (Round, 1979). For taxonomic comparisons and/or ecological characterisation, the following papers were consulted: Brockmann (1950), Flower *et al.* (1996), Krammer & Lange–Bertalot (1991, 2000), Snoeijs *et al.* (1991), Witkowski & Lange–Bertalot (1993), Witkowski *et al.* (2000), and Talgatti *et al.* (2014).

For the typification of new species, we chose to use the entire slide as the holotype following the usual interpretation of article 8.2 of the International Code for Nomenclature for algae, fungi, and plants (Turland *et al.*, 2025) by diatomists. Although the taxon is illustrated by all other figures, that in a strict sense are also specimens of the original material, we chose an appropriate image that is linked to the designated holotype specimen by stating "The holotype is illustrated by Fig. X". In doing so, the identity of the species can be fixed to a valve that is not exclusively showing the typified name, but may be most characteristic for the taxon. All novelties are registered proactively according to Art. 42.4 (Turland *et al.*, 2025).

Results

In the present paper, five different taxa were identified in the analysed samples. The original materials of *Fragilaria virescens* var. *exigua* were compared and the observations showed that all investigated populations belong to the same species (Figs 6–84) named *Stauroforma exiguiformis* (Lange–Bertalot) Flower *et al.* We designate Cleve & Möller slide 59 from Aberdeen as the lectotype for the species as this was never formally done. As an aside, Flower *et al.* cited Cleve & Möller no. 59 in their discussion (Flower *et al.*, 1996, pp. 42, 43), but later, in their section on 'Type material', cited Cleve & Möller no. 56, an obvious typo (Flower *et al.*, 1996, p. 54). Walker Arnott sample 37, most likely prepared from the same

sample as the one used to make Cleve & Möller slide 59, is designated as epitype to the above lectotype as it proves to be very important to document the ultrastructure of the taxon, illustrating and discussing features not discernible on Cleve & Möller slide 59.

The other varieties described by Grunow can be grouped under two names. *Fragilaria virescens* [var. *oblongella*] f. *clavata* Grunow was described at species level as *Fragilaria schulzii* C.Brockmann (Brockmann, 1950, p. 13). Brockmann (1950) added that he did not doubt for it to be the same as *Fragilaria virescens* [var. *oblongella*] f. *clavata*, a taxon he knew from Schulz (1926), who observed and illustrated it in a sample from the Gulf of Gdansk. As Brockmann (1950) strongly doubted a relation with *F. virescens*, he described the taxon as a new species, naming it in honor of Paul Schulz. In 2014 the species was transferred to the genus *Stauroforma* by Gogorev & Lange (2014, p. 71) as *S. schulzii* (C.Brockmann) Gogorev. During the analysis of this heteropolar species, a second, much smaller heteropolar species of *Stauroforma* was observed, although Grunow did not mention it in Van Heurck (1881). A literature search showed that this taxon has some similarity with a small *Fragilaria* species described as *Fragilaria cassubica* Witkowski *et* Lange–Bertalot (Witkowski & Lange–Bertalot, 1993), but that it markedly differed in valve dimensions and stria density, justifying the description of a new species.

A fourth species is represented by two taxa: *Fragilaria virescens* var. *subsalina* Grunow and *Fragilaria virescens* var. *oblongella* Grunow. Comparison with similar taxa and a thorough revision of its taxonomic history showed that both varieties most likely represent the same taxon and that they should be separated as an independent species in the genus *Stauroforma*. Therefore, the new combination *Stauroforma subsalina* (Grunow) Van de Vijver, T.M.Schust., D.M.Williams *et* Kusber *comb. nov.*, *stat. nov.* is proposed.

Finally, *Stauroforma inermis* is better characterised based on the original type slide from Signy Island and SEM analysis of an Antarctic Continent population. This species has been observed occasionally in western European rivers and lakes but most likely these northern hemisphere observations of *S. inermis* likely represent *S. subsalina*.

Every species is separately documented and discussed below.

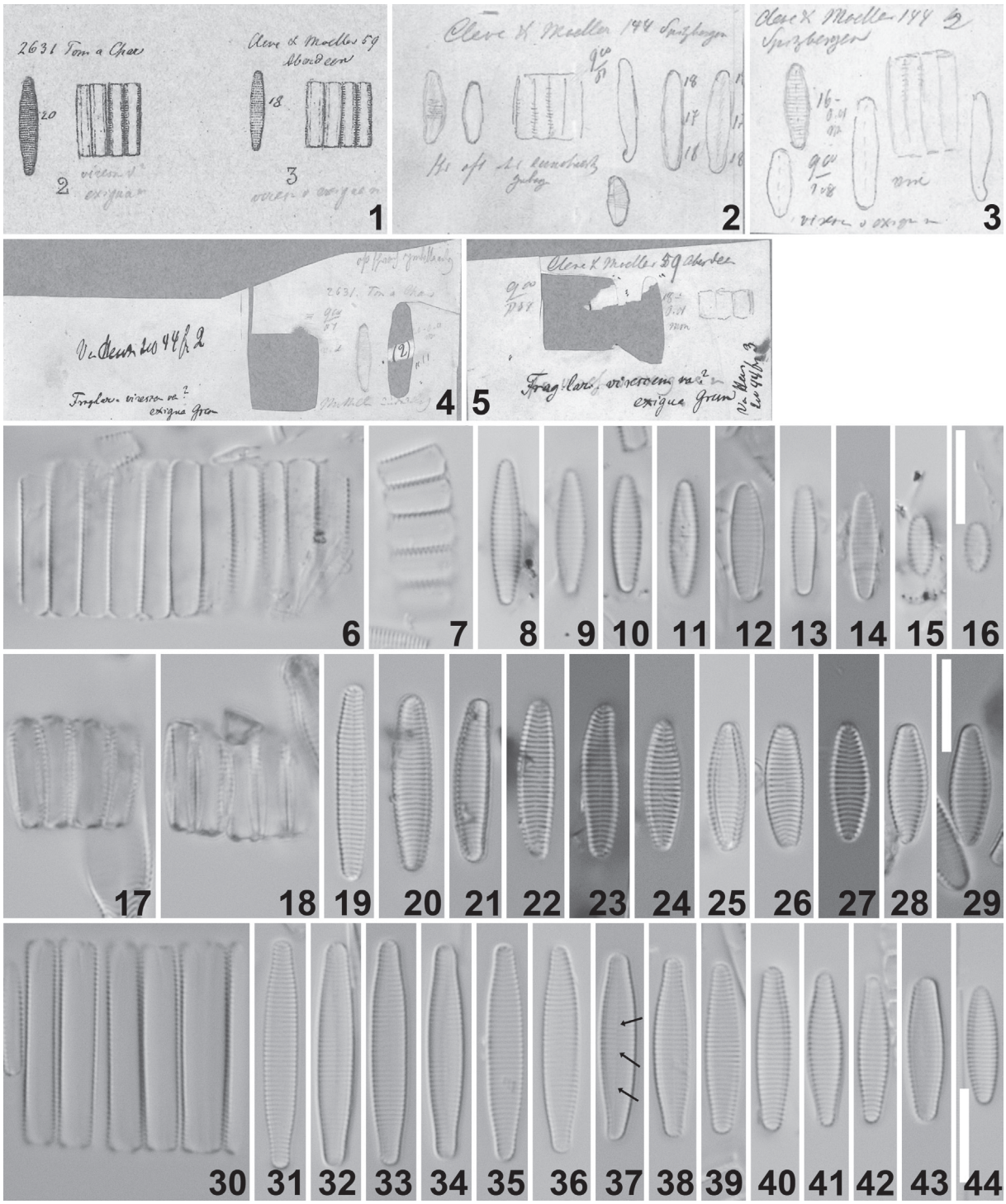
Stauroforma exiguiformis (Lange–Bertalot) Flower, V.J.Jones *et* Round (Figs 1–84)

Basionym: *Fragilaria exiguiformis* Lange–Bertalot in Lange–Bertalot (1993), *Bibliotheca Diatomologica* 27, p. 45.
≡ *Fragilaria virescens* var. *exigua* Grunow (Van Heurck, 1881, pl. XLIV: figs 2, 3).
≡ *Fragilariforma virescens* var. *exigua* (Grunow) M.Poulin in Hamilton *et al.* (1992, p. 30, table 4).
– *Fragilaria virescens* var. *exigua* Grunow (Cleve & Möller, 1878b, n°144) nom. inval.
non *Fragilaria exigua* (W.Smith) Lemmermann (Lemmermann, 1908) = *Staurosira exigua* (W.Smith) Van de Vijver *et* Guiry (Van de Vijver & Guiry 2022, p. 2).

LM (Figs 1–78): Frustules rectangular in girdle view, forming long ribbon–like colonies (Figs 6, 7, 17, 18, 30, 45–47). Valves isopolar, linear to linear–lanceolate in longer specimens, more lanceolate to elliptic–lanceolate in shorter valves. Margins weakly convex. Apices variable, slightly protracted, rostrate (Figs 33, 52) to almost not protracted, broadly rounded (Figs 26, 43, 57). Valve dimensions (n = 60): length 5–25 µm, width 3.0–4.5 µm. Sternum almost indiscernible in LM, very narrow, faint (Figs 19, 37, 53, 67, 68), visible as thin line extending from apex to apex (Fig. 37, arrows). Striae parallel, equidistant, straight extending from margin to margin, 17–19 in 10 µm; striae curved at apices.
SEM (Figs 79–84): frustules connected by marginal, bifurcated, broad linking spines, extending along the entire valve edge (Figs 79–81). Spines located on virgae at valve face edge (Figs 81, 82). Cingulum composed of 5–6 plain, non–perforated broad copulae. Occasionally, extra layer of silica forming reticulate pattern on girdle bands (Figs 79, 80). Mantle deep, at valve face/mantle junction with 1–2 areolae continuing from valve face striae onto mantle; remaining mantle hyaline, plain. Series of small but distinct mantle plaques present at mantle edge, larger near apices (Figs 79, 80). Valve face flat. Striae slightly sunken between weakly raised virgae (Fig. 81). Striae uniseriate, composed of small, rounded areolae. Areola density: ca 40–45 in 10 µm. Rimoportulae and apical porefields absent. Internally, striae sunken between clearly raised virgae (Fig. 83). Areolae individually covered by volae (Fig. 84).

Lectotype (here designated): BR II–3–B11! (Cleve & Möller slide n°59, 'Aberdeen'; figure 8 illustrates the lectotype specimen). The lectotype was seleced from the gathering Grunow used for the validating illustration.
Isolectotypes (here designated): BM 31422 ('Cave at Cove, nr Aberdeen, [Walker Arnott] 37), BM 11191 ('Cave at Cove, nr Aberdeen, [Walker Arnott] 37'), W0164969 (Cleve & Möller slide n°59, 'Aberdeen')
Epitype (here designated for the above selected lectotype for *S. exiguiformis*): BR–4902! (Cave south of Cove near Aberdeen, Scotland, UK, Walker Arnott sample 37, leg. Dr Redfern; Figure 80 illustrates the features of the epitype specimen).
Registration: http://phycobank.org/105384
Type locality: Aberdeen, Scotland, leg. Dr Dickie (George Dickie)

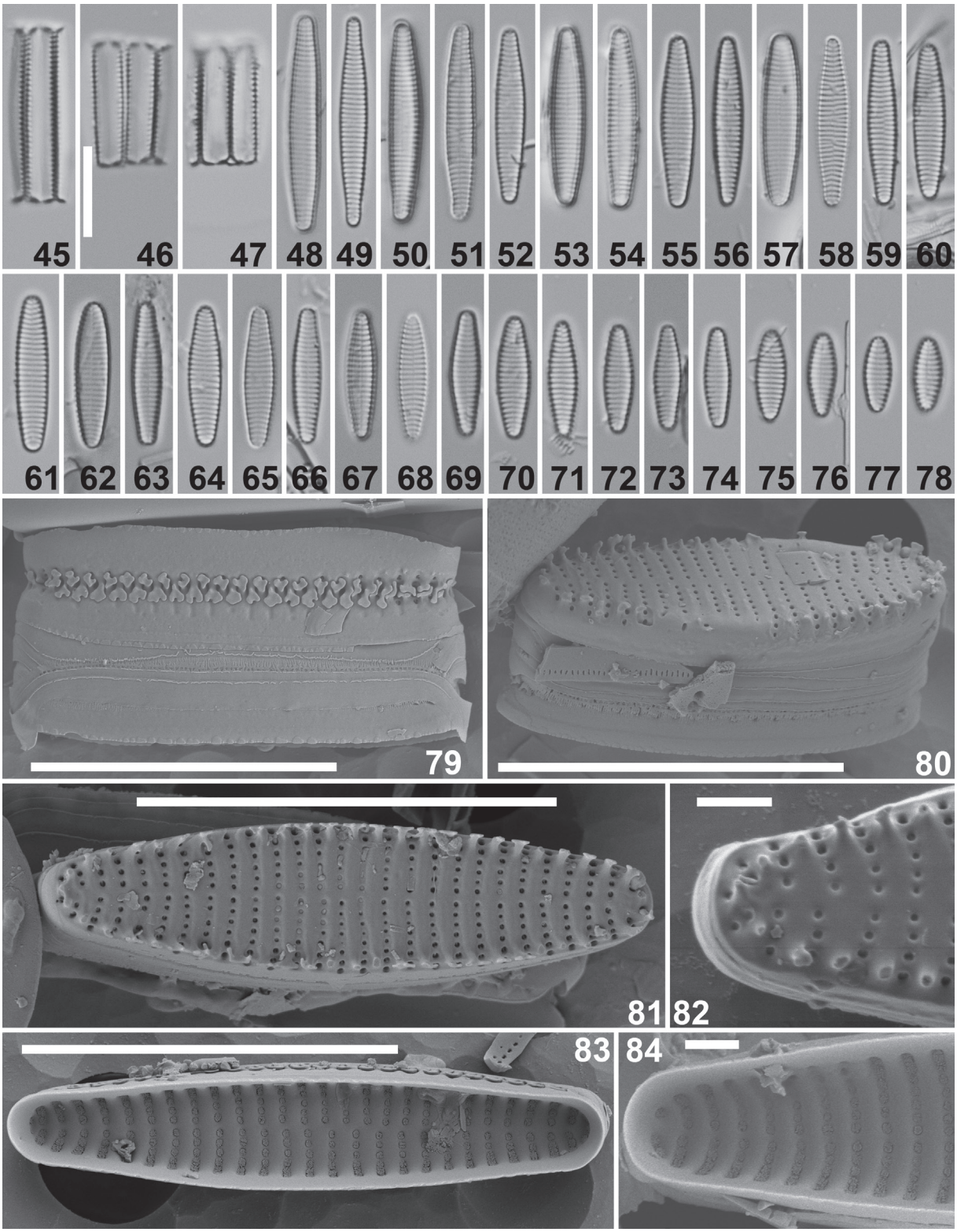
Analysed populations: Scotland, Tom–a–Char, Logie Coldstone, Aberdeenshire (BR IX–20–B6!; W0164968 (slide Grunow sample 2631!); Cave south of Cove near Aberdeen (BR–4902 = Walker Arnott sample 37; BM 11191 ('Cave at Cove, nr Aberdeen, 37'); BM 22657 ('Cave at Cove, near Aberdeen, S. 409'); BM 24605 ('Cave at Cove, near Aberdeen, S. 409'); BM 25420 ('Cove nr Aberdeen, 38'); BM 25425 ('Cave at Cove nr. Aberdeen, S. 411); BM 31422 ('Cave at Cove, nr Aberdeen, 37); Norway, Spitzbergen, Kobbe Bay [= Kobbefjorddalen],



Figs 1–44. *Stauroforma exiguiformis* (Lange–Bertalot) Flower *et al.* Original drawings and Light microscope images of historic populations. **(1)** Annotated drawing in Van Heurck (1881, plate XLIV, figs 2, 3). **(2–3)** Original Grunow drawings of Cleve & Möller slide n°144 from Spitsbergen. **(4)** Original Grunow drawing of the population in his sample 2631 Tom a´Char. **(5)** Original Grunow drawing of the population in Cleve & Möller slide n°59 from Aberdeen. **(6–16)** Lectotype population from Cleve & Möller slide n°59 from Aberdeen. Fig. 6. shows a ribbon–like colony. **(17–29)** Additional population from Cleve & Möller slide n°144 from Spitsbergen. Images taken from air–mounted slide. Figs 17 and 18 show ribbon–like colonies. **(30–44)** Additional population from Tom a´Char (slide IX–20–B6 in BR). Fig. 30 shows a ribbon–like colony. The scale bars 10 µm.

Axel van Goës (BR II–6–A6!, BM 116763!, W0164970 = Cleve & Möller slide n°144, ‘Spitsbergen’).

Associated diatom flora: WA 37 and Cleve & Möller n° 59 are from the same material collected near Aberdeen. The sample is dominated by *Brachysira microcephala* (Grunow) Compère, *Angusticopula dickiei* (Thwaites) Houk, Klee *et* H.Tanaka, *Cavinula variostriata* (Krasske) D.G.Mann *et* Stickle, *Nitzschia palustris* Hust. and *Stauroforma exiguiformis*. Other, less frequent taxa



Figs 45–84. *Stauroforma exiguiformis* (Lange–Bertalot) Flower *et al.* LM and SEM images taken from the epitype material (BR–4902, Cave near Aberdeen, Scotland, Walker Arnott sample 37). **(45–78)** LM views of population arranged in decreasing length. Figs 45–47 represent frustules linked into ribbon–like colonies. **(79–80)** SEM views of several connected frustules in girdle view showing the cingulum and the linking spines. **(81)** SEM external view of an entire valve. Note the absence of apical porefields. **(82)** SEM external detail of the valve apex with linking spines. **(83)** SEM internal view of an entire valve showing the sternum and virgae. **(84)** SEM internal detail of the valve apex indicating the lack of an apical porefield. Scale bars 10 µm (45–81, 83) and 1 µm (82, 84).

include several species of *Eunotia*, such as *E. botuliformis* F.Wild, Nörpel *et* Lange–Bertalot, *Adlafia* sp., *Fallacia vitrea* (Østrup) D.G.Mann, *Fragilaria* cf. *acidoclinata* Lange–Bertalot, *Humidophila perpusilla* (Grunow) R.L.Lowe *et al.* and *H. gallica* (W.Sm.) R.L.Lowe *et al.* According to Lange–Bertalot *et al.* (2017) most of these species are typical for nutrient–poor, usually acidic, electrolyte poor aerophilic habitats on siliceous substrates.

Stauroforma schulzii (C.Brockmann) Gogorev (Figs 85–105)

Basionym: *Fragilaria schulzii* C.Brockmann in Brockmann (1950), Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft 478, p.13, pl. 3: fig. 12; pl. 4: fig. 14.
Holotype: FR Senckenberg Museum B 5909. Holotype specimen indicated as Kreuztisch (Zeiss, linksseitig) 13·5/81·2.
Type locality: Weser River at Bremerhaven (Germany).
Analysed populations: Scotland, Corriegills [= Carrieghills], Arran Island [W0164964, W0164965 Grunow sample 2661 = Walker Arnott sample 129 (=BM 31814)]
≡ *Opephora schulzii* (C.Brockmann) Simonsen (Simonsen, 1962)
≡ *Martyana schulzii* (C.Brockmann) Snoeijs (Snoeijs *et al.*, 1991)
= *Fragilaria virescens* [var. *oblongella*] f. *clavata* Grunow (Van Heurck, 1881, pl. XLIV: fig. 4).

LM (85–99): Frustules solitary, rectangular to weakly trapezoid. Valves distinctly heteropolar, ovoid in outline with broadly rounded head pole and acutely rounded foot pole. Valve dimensions (n = 20): length 8–25 µm, width 4–5 µm. Sternum not to almost indiscernible in LM very narrow, almost non–existing, visible as a very thin, hyaline line running from apex to apex. Striae parallel, straight, equidistant, at apices clearly curved, 15–17 in 10 µm.
SEM (100–105): Spines absent (Figs 100–102). Cingulum composed of at least 8 open, non–perforated copulae decreasing in width with valvocopula being largest. Abvalvar edges with very thin siliceous ridge (Fig. 100). Mantle deep (Fig. 100). Striae continuing from valve face/mantle junction to halfway of mantle, composed of 5 rounded areolae, decreasing in size towards mantle edge (Figs 100, 101). Half of mantle hyaline, plain. Mantle plaques only present at the apices (Fig. 100). Valve face flat. Virgae raised relative to the vimines forming fairly large, rounded to square areolae (Figs 101, 102). Areola density: ca 33 in 10 µm. Rimoportula absent. Apical porefield present at both apices (Fig. 102), surrounded by an irregular pattern of small ridges and granules (Figs 103, 104). Porefield at foot pole largest, covering apex almost entirely, composed of dense network of small, rimmed porelli each located in small depression (Figs 102, 103). At head pole, porefield smaller, composed of small network of sunken porelli (Fig. 104). Internally, striae located in grooves spanning entire valve width (Fig. 105). Apical porefield distinct. Areolae covered by individual volae (Fig. 105).

Associated diatom flora: *Stauroforma schulzii* is generally known to be a brackish species (Brockmann, 1950; Simonsen, 1962; Snoeijs, *et al.* 1991; Witkowski & Lange–Bertalot, 1993; Witkowski *et al.*, 2000). *Fragilaria virescens* f. *clavata* was present in Grunow sample 2661 which was made from material of sample WA 129 in the Walker Arnott collection conserved in the Van Heurck collection in BR. Analysis of the species flora in that sample showed that it was dominated by *Opephora mutabilis* Sabbe *et* Vyverman *nom. inval.*, *Staurosirella martyi* (Héribaud) E.Morales *et* Manoylov and *Stauroforma subsalina* (Grunow) Van de Vijver *et al.* Other less frequent taxa include several *Navicula* species such as *N. digitoradiata* (W.Gregory) Ralfs, *N. gregaria* Donkin, *N. rhynchotella* Lange–Bert. and *N. vaneei* Lange–Bertalot, *Amphora copulata* (Kützing) Schoeman *et* R.E.M.Archibald, *Hippodonta linearis* (Østrup) Lange–Bertalot *et al.*, *Planothidium delicatulum* (Kützing) Round *et* Bukhtiyarova, *Pseudostaurosira subsalina* (Husted) E.Morales, and *Tabularia fasciculata* (C.Agardh) D.M.Williams *et* Round. This species composition reflects brackish conditions, either at the coast or in inland electrolyte–rich waters, consistent with the succinct notes in the Walker Arnott collection stating that the sample was collected in a brackish pool but with notable freshwater influence. This freshwater influence was visible in the (relatively rare) presence of *Meridion circulare* (Greville) C.Agardh.

Taxonomic remarks: The classification of *Stauroforma schulzii* has differed several times during the past few decades. Originally placed in the (at that time) catch–all genus *Fragilaria*, subsequently placed in *Opephora* as *O. schulzii* (C.Brockmann) Simonsen (Simonsen, 1962, p. 33), because of the valves' heteropolar, clavate outline. Snoeijs *et al.* (1991) later placed it in *Martyana* together with *Fragilaria atomus* Hust. The reasons given by Snoeijs *et al.* (1991, p. 170) for placing the two species in *Martyana* were the absence of a rimoportula, its valve cell outline, the "step" at the head pole, a large apical porefield on the foot pole, conspicuously curved copulae, and the absence of marginal linking spines. Since 2006, *Martyana* has been considered a synonym of *Staurosirella* (Morales & Manoylov, 2006) and the morphological features of *S. schulzii* do not correspond with the genus description of *Staurosirella*. It should also be noted that *S. schulzii* lacks the step Snoeijs *et al.* (1991) mentioned, but has a gently sloping head pole instead.

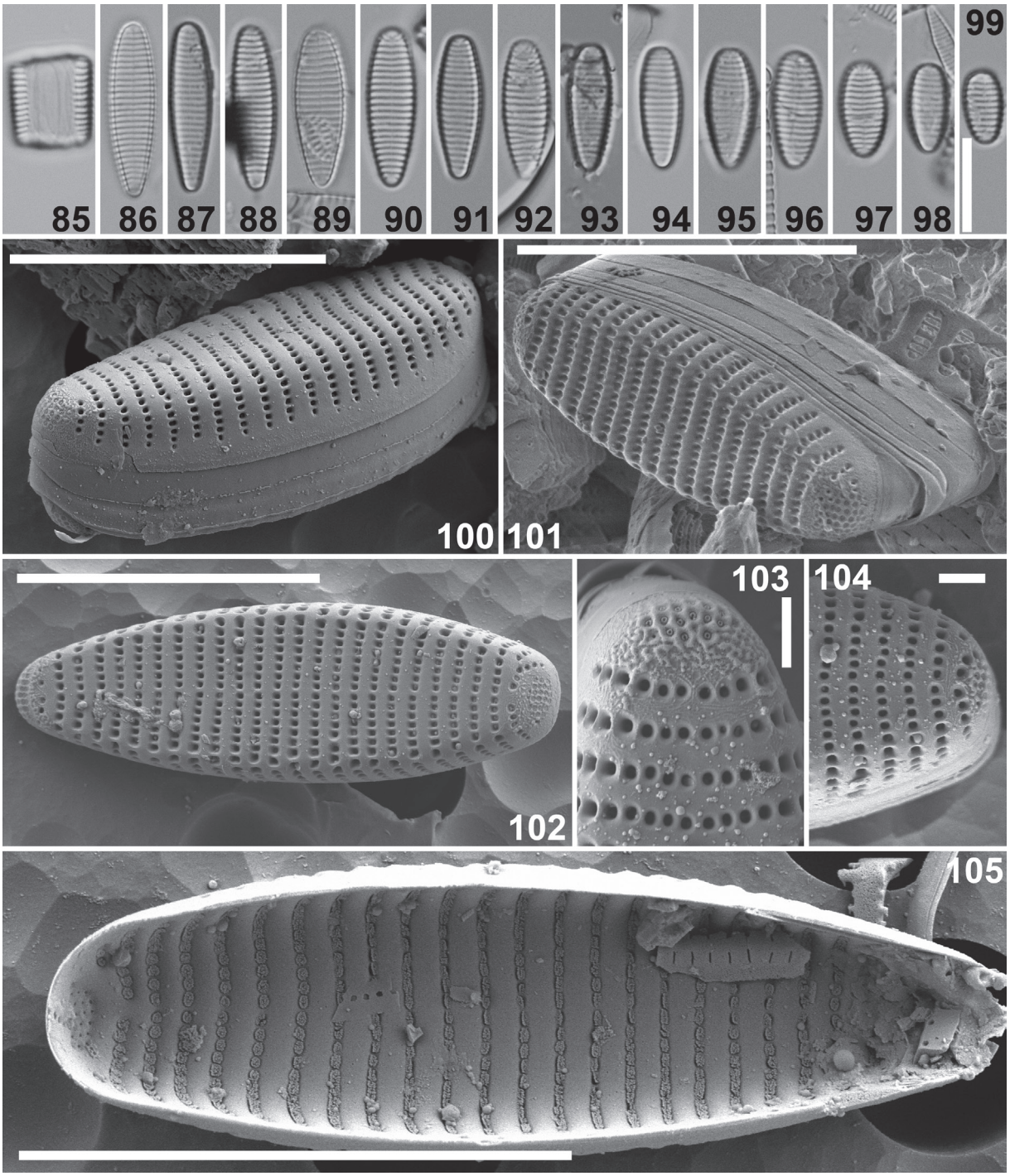
Witkowski & Lange–Bertalot (1993, p. 127) reported larger valve dimensions for *S. schulzii* with a valve length up to 50 µm and a valve width up to 7 µm.

Stauroforma subcassubica Van de Vijver, T.M.Schust., D.M.Williams *et* Kusber *sp. nov.* (Figs 106–130)

Description
SEM (127–130): Spines absent (Figs 127–129). Cingulum composed of several (3–5?) narrow, open, non–perforated copulae. Abvalvar edges of copulae often with very thin siliceous ridge (Fig. 127). Mantle moderately deep with striae shortly continuing from valve face/mantle junction onto mantle composed of 1–4 rounded areolae (Fig. 127). Half of mantle hyaline, plain with a thin layer of

small mantle plaques at the edge (Fig. 128). Valve face flat except at head pole. Virgae weakly raised, broader than striae. Striae sunken between virgae, uniseriate, composed of fairly large, rounded to square areolae (Figs 128, 129). Rimoportula absent. Very reduced apical porefield present at foot pole, composed of only a few very small porelli (Figs 127, 128). At head pole, striation irregular, forming a denser network of small areolae in a slightly depressed area (Fig. 127). Internally, striae located in deep grooves between distinctly raised virgae, spanning entire valve width (Fig. 130).

Holotype: BR–4903 (Meise Botanic Garden, Belgium) Figure 109 illustrates the holotype specimen.

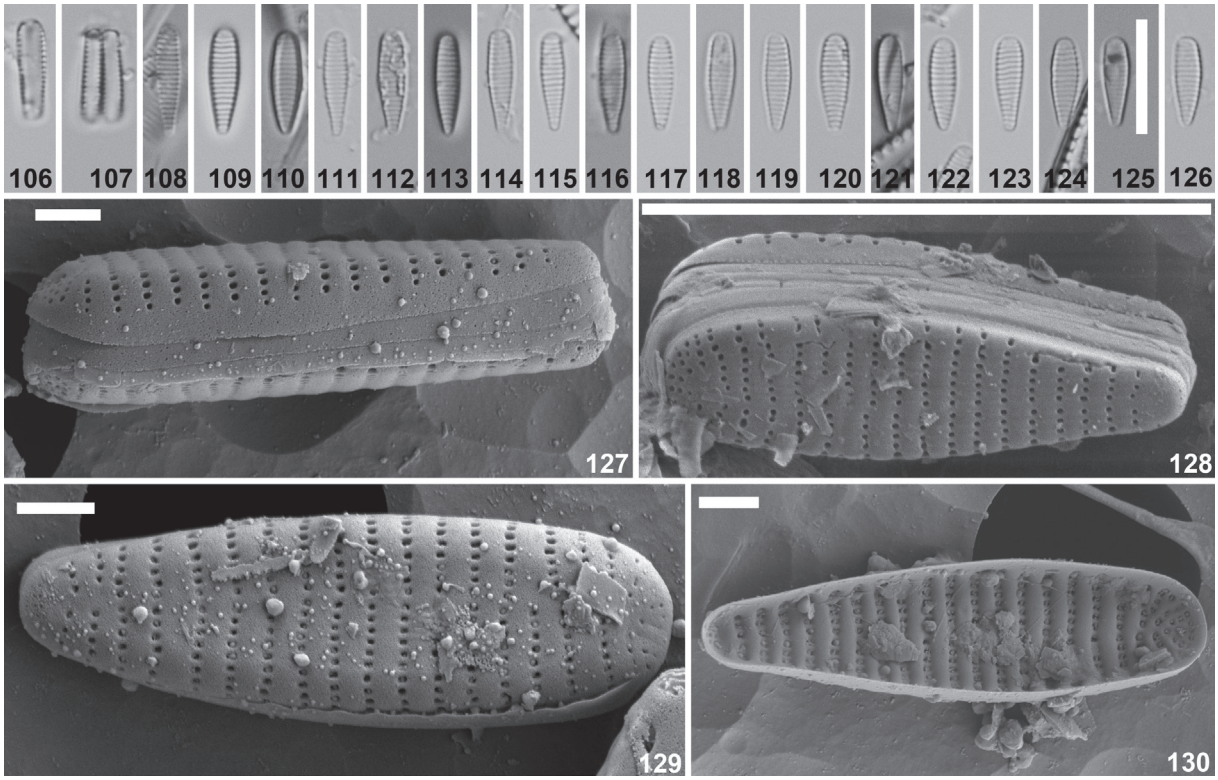


Figs 85–105. *Stauroforma schulzii* (C.Brockmann) Gogorev. LM and SEM images taken from Walker Arnott sample 129 (BR–4903, Scotland, Corriegills [= Carrieghills], Arran Island = Grunow sample 2661). **(85–99)** LM views of population arranged in decreasing length. Fig. 85 represents a frustule in girdle view. **(100–101)** SEM views of several frustules in girdle view showing the cingulum, the absence of spines, and the apical porefields. **(102)** SEM external view of an entire valve. Note the heteropolarity and the apical porefields. **(103)** SEM external detail of the foot pole and the large apical porefield. **(104)** SEM external detail of the head pole with the apical porefield. **(105)** SEM internal view of an entire valve showing the sternum and virgae. Scale bars 10 μm (85–102, 105) and 1 μm (103, 104).

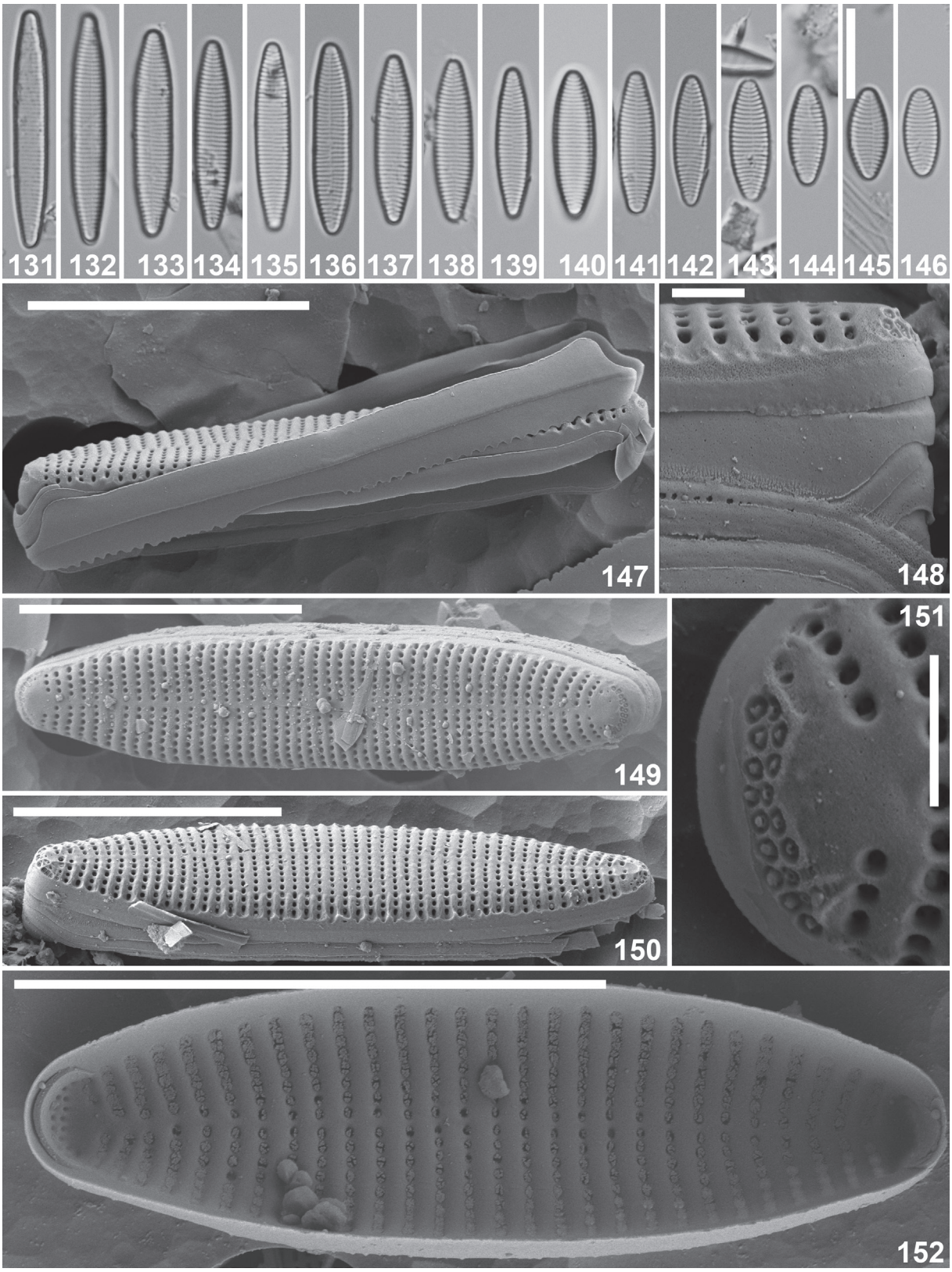
Isotype: Slide 456 (University of Antwerp, Belgium), BM 31814 (Natural History Museum, London, UK), W0164964, W0164965 (Natural History Museum, Vienna, Austria)
Type locality: Scotland, Corriegills [= Carrieghills], Arran Island, Walker Arnott sample 129 (= Grunow sample 2661)
Registration: http://phycobank.org/105479
LM (106–126): Frustules solitary, rectangular to weakly clavate. Valves distinctly heteropolar, narrowly ovoid in outline with broadly rounded head pole and acutely rounded, elongated foot pole. Valve dimensions (n=20): length 8–10 µm, width 2.0–2.5 µm. Sternum absent. Striae parallel, straight, equidistant throughout entire valve, 22–24 in 10 µm.

Associated diatom flora: A very small population of *Stauroforma subcassubica* was found in Walker Arnott sample 129 (= Grunow sample 2661). The sample was collected from a brackish pool but with notable freshwater influence, visible in the (relatively rare) presence of *Meridion circulare*. The sample was dominated by *Opephora mutabilis*, *Staurosirella martyi* and *Stauroforma subsalina* (Grunow) Van de Vijver *et al.* Other less frequent taxa include several *Navicula* species such as *N. digitoradiata*, *N. gregaria*, *N. rhynchotella* and *N. vaneei*, *Amphora copulata*, *Hippodonta linearis*, *Planothidium delicatulum*, *Pseudostaurosira subsalina*, and *Tabularia fasciculata*, reflecting brackish conditions, either at the coast or in inland electrolyte–rich waters (Lange–Bertalot, *et al.* 2017; Witkowski, *et al.* 2000).

Taxonomic remarks: *Stauroforma subcassubica* may be conspecific with *Fragilaria cassubica*, a species described by Witkowski & Lange–Bertalot (1993, p. 67), who observed small aggregates in the shape of small, ribbon–like colonies. Type material should be checked to verify this observation, but the material is not available. Therefore, we have to base our comparison on our observations and the published pictures in Witkowski & Lange–Bertalot (1993, fig. 4i–n). In the Walker Arnott sample WA 129, *S. subcassubica* seems to show only solitary frustules or frustules connected in pairs. Both species differ in valve outline with *S. subcassubica* having a less protracted foot pole, and clearly in valve dimensions. All observed valves of *S. subcassubica* never exceeded 10 µm, whereas this is the minimum length reported by Witkowski & Lange–Bertalot (1993, p. 67) for *F. cassubica* that is almost double in length (9–20 µm). It is, however, always possible that the Walker Arnott population represented the smallest valves of *F. cassubica*. But clear differences were also noted in valve width (2–2.5 µm in *subcassubica*



Figs 106–130. *Stauroforma subcassubica* Van de Vijver, T.M.Schust., D.M.Williams *et* Kusber *sp. nov.* LM and SEM images taken from the holotype material (BR–4903, Walker Arnott sample 129, Scotland, Corriegills [= Carrieghills], Arran Island = Grunow sample 2661). **(106–126)** LM views of population arranged in decreasing length. Figs 106 and 107 represent frustules in girdle view, solitary or in connected in pairs. **(127)** SEM view of a frustule in girdle view showing the cingulum, the absence of spines, and the depressed step at the head pole. **(128)** SEM external view of an entire valve in oblique view. Note the heteropolarity and the apical porefield at the foot pole. **(129)** SEM external view of an entire valve. **(130)** SEM internal view of an entire valve showing the sternum and virgae. Scale bars represent 10 µm (106–126, 128) and 1 µm (127, 129, 130).



Figs 131–152. *Stauroforma subsalina* (Grunow) Van de Vijver, T.M.Schust., D.M.Williams *et* Kusber *comb. nov.* LM and SEM images taken from Walker Arnott sample 129 (BR–4903, Scotland, Corriegills [= Carrieghills], Arran Island = Grunow sample 2661). **(131–146)** LM views of population arranged in decreasing length. **(147)** SEM views of a frustule in girdle view showing the detached valvocopula, the absence of spines, and the apical porefield. **(148)** SEM external detail of the valve apex with the position of the apical porefield and the girdle structure. **(149–150)** SEM external view of two entire valves. **(151)** SEM external detail of an apex with a large apical porefield. **(152)** SEM internal view of an entire valve showing the sternum and virgae. Scale bars 10 μm (131–147, 149, 150) and 1 μm (148, 151).

versus 3–4 in *F. cassubica*) and stria density (22–24 in 10 µm for *S. subcassubica* versus 15–18 in 10 µm in *F. cassubica*). According to Witkowski & Lange–Bertalot (1993, p. 67), specimens with spines should be present in the population. Their fig. 4l indeed may show a frustule that presents blunt, broad spines, although it is not clearly discernible whether these are really spines. The population in the Walker Arnott sample did not contain valves with spines. Based on these differences, the split of the Walker Arnott population as a separate species is justified. *Fragilaria cassubica* presents similar morphological features as *S. subcassubica* and therefore, the former should also be transferred to the genus *Stauroforma*. However, as long as the original type material of *F. cassubica* has not been revised, a transfer should not be made, to avoid potentially incorrect conclusions.

Lange–Bertalot in Krammer & Lange–Bertalot (1991, plate 127, figs 9–14) identified several valves that actually represent *F. cassubica* as *Fragilaria subsalina* (Grunow) Lange–Bertalot At the time, the combination was invalid due to the lacking a basionym and the *comb. nov., stat. nov.* declaration. Later, Lange–Bertalot (1993, p. 49) made the new combination after changing the identification to the newly described *F. cassubica* in Witkowski & Lange–Bertalot (1993) (note, that the illustrations in Krammer & Lange–Bertalot (1991) were still referred to as *F. subsalina*). The illustrated valves are clearly larger than *S. subcassubica* and hence most likely represent *F. cassubica*.

Stauroforma rinceana Méléder *et al.* was described in 2018 from the Baie de Bourgneuf, Lyarne (France) (Li *et al.*, 2018, p. 88), showing some resemblance to *S. subcassubica*, based on valve dimensions (although *S. rinceana* is wider with 2–3.5 µm). The valve outline, as shown by the LM observations in Li *et al.* (2018, figs 179–183), is less clavate in *S. rinceana*, although the SEM observations (Li *et al.*, 2018, figs 465–471) show more elongated, clavate valves with cuneate, not broadly rounded head poles. It is unclear wh*et*her these SEM observations of *S. rinceana* belong to one, or two different taxa. *Stauroforma subcassubica* has more broadly rounded head poles, narrower valves and an always completely absent sternum, contrary to *S. rinceana* showing a broader sternum (based on the shown SEM images in Li *et al.*, 2018).

Stauroforma subsalina (Grunow) Van de Vijver, T.M.Schust., D.M.Williams *et* Kusber *comb. nov., stat. nov.* (Figs 131–152)

Basionym: *Fragilaria virescens* var. *subsalina* Grunow in Van Heurck (1881), Synopsis des Diatomées de Belgique, Atlas, plate XLIV, fig. 5.

LM (131–146): Frustules solitary, rectangular. Valves isopolar, linear to linear–lanceolate in larger specimens becoming strictly lanceolate to elliptic–lanceolate in shorter valves. Margins straight to convex. Apices shortly protracted, cuneately rounded. Valve dimensions (n = 50): length 10–35 µm, width 4–5 µm. Sternum only very weakly discernible in LM, very narrow, almost non–existing, visible as a very thin, hyaline line extending from apex to apex (Figs 136, 141). Striae parallel, straight, equidistant, at apices clearly curved, 20–22 in 10 µm.

SEM (147–152): Spines absent (Figs 147, 149, 150). Narrow, irregular siliceous ridge extending around valve edge. Cingulum composed of several (probably 3–4) open, non–perforated copulae decreasing in width with valvocopula being the largest. Abvalvar edges with very thin siliceous ridge (Figs 147, 148). Advalvar edge dentate, fitting under mantle (Fig. 147). Mantle rather shallow. Striae not continuing from valve face/mantle junction onto mantle (Figs 148, 150). Mantle hyaline, plain with a thin layer of small mantle plaques at edge (Fig. 150). Valve face flat (Figs 149, 150). Virgae clearly raised, broader than striae with small ridges present at valve margin on virgae (Fig. 150). Striae sunken between virgae, uniseriate, composed of small rounded areolae (Figs 149–151). Rimoportula absent. Apical porefield present at both apices (Figs 149–150), almost equal in size and shape (Figs 149–150). Porefields composed of 1–2 series of very small, rimmed porelli, sunken within individual depressions (Figs 149–151). Internally, striae located in grooves spanning entire valve width, crossed by a clear sternum (Fig. 152). Striae bordered by raised virgae (Fig. 152). Areolae covered by individual irregular volae.

Lectotype (here designated): W0164965 (slide Grunow sample 2661, conserved at the Natural History Museum, Vienna, Austria).

Isolectotype (here designated): BR–4903 (Walker Arnott sample 129, Figure 138 illustrates the isolectotype specimen); BM 31814 (Walker Arnott sample 129); W0164964 (slide Grunow sample 2661). Lecto– and isolectotype were designated from material Grunow had used for the validating illustration.

Registration (of the new combination): http://phycobank.org/105386.

Registration (of the lectotype): http://phycobank.org/105387.

Analysed populations: Scotland, Corriegills [= Carrieghills], Arran Island [W0164964, W0164965 Grunow sample 2661 = Walker Arnott sample 129 (=BM 31814)]

≡ *Fragilaria subsalina* (Grunow) Lange–Bertalot *sensu* Lange–Bertalot (1993) *non sensu* Krammer & Lange–Bertalot (1991)

= *Fragilaria virescens* var. *oblongella* Grunow in Van Heurck (1881, pl. XLIV: fig. 6)

Associated diatom flora: Stabell (1981) considered *S. subsalina* to be a brackish taxon and this is also reflected in the associated diatom flora in Grunow sample 2661 (WA 129). See therefore the discussion under *S. schulzii*.

Taxonomic remarks: Grunow in Van Heurck (1881) described two taxa from this sample that could only be distinguished based on their stria density. *Fragilaria*

virescens var. *subsalina* was characterised as having 20 striae in 10 µm whereas *F. virescens* var. *oblongella* had only 15 striae. Although more than 50 valves were measured and identified in the lectotype sample, valves with a stria density lower than 20 could not be found. During the survey, a handful of valves of *Pseudostaurosira subsalina* were found, showing a vague resemblance to *Stauroforma subsalina*, although *Pseudostaurosira subsalina* possesses a wider sternum and more punctate striae with a stria density of 15 in 10 µm. It is possible that Grunow identified these valves as *F. virescens* var. *oblongella*. Hustedt (1959, p. 164) separated both varieties on ecological grounds with the var. *oblongella* being a freshwater taxon and the var. *subsalina* preferring more brackish conditions, although both were described from the same (brackish) material. At present, both varieties are considered synonyms and since the var. *subsalina* is the most reported name, preference is given to this variety name.

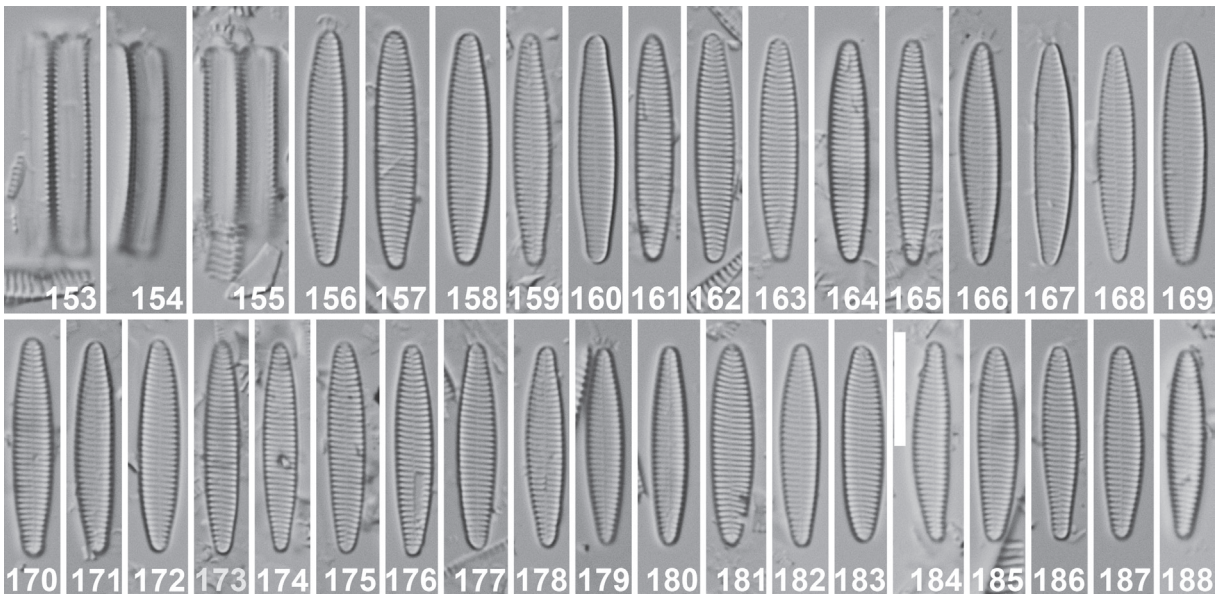
Stabell (1981) examined specimens identified as *F. virescens* var. *subsalina* but some of the observed valves have a continuous series of marginal linking spines, lack apical porefields and seem to form colonies, features so far only found in *S. exiguiformis* but not in the type material of *S. subsalina*. This raises doubt about the identification and discussed morphology in Stabell (1981).

Lange–Bertalot initially connected the name *Fragilaria subsalina* (initially noted by Krammer & Lange–Bertalot, 1991, p. 138 [2000, p. 138], but invalidly published) with valves identified as *F cassubica* (see above) (Krammer & Lange–Bertalot, 1991, plate 127, figs 9–15). Later he changed his opinion and provided the valid combination *Fragilaria subsalina* (Grunow) Lange–Bertalot but did not illustrate its morphology (Lange–Bertalot, 1993, p. 49). The identity of *F. subsalina* (basionym: *F. virescens* var. *subsalina* Grunow) remained unclear until now. Lange–Bertalot (1993, p. 49) stated this "*solange bis das Typenmaterial Grunows überprüft werden konnte*" (until the type material can be analysed).

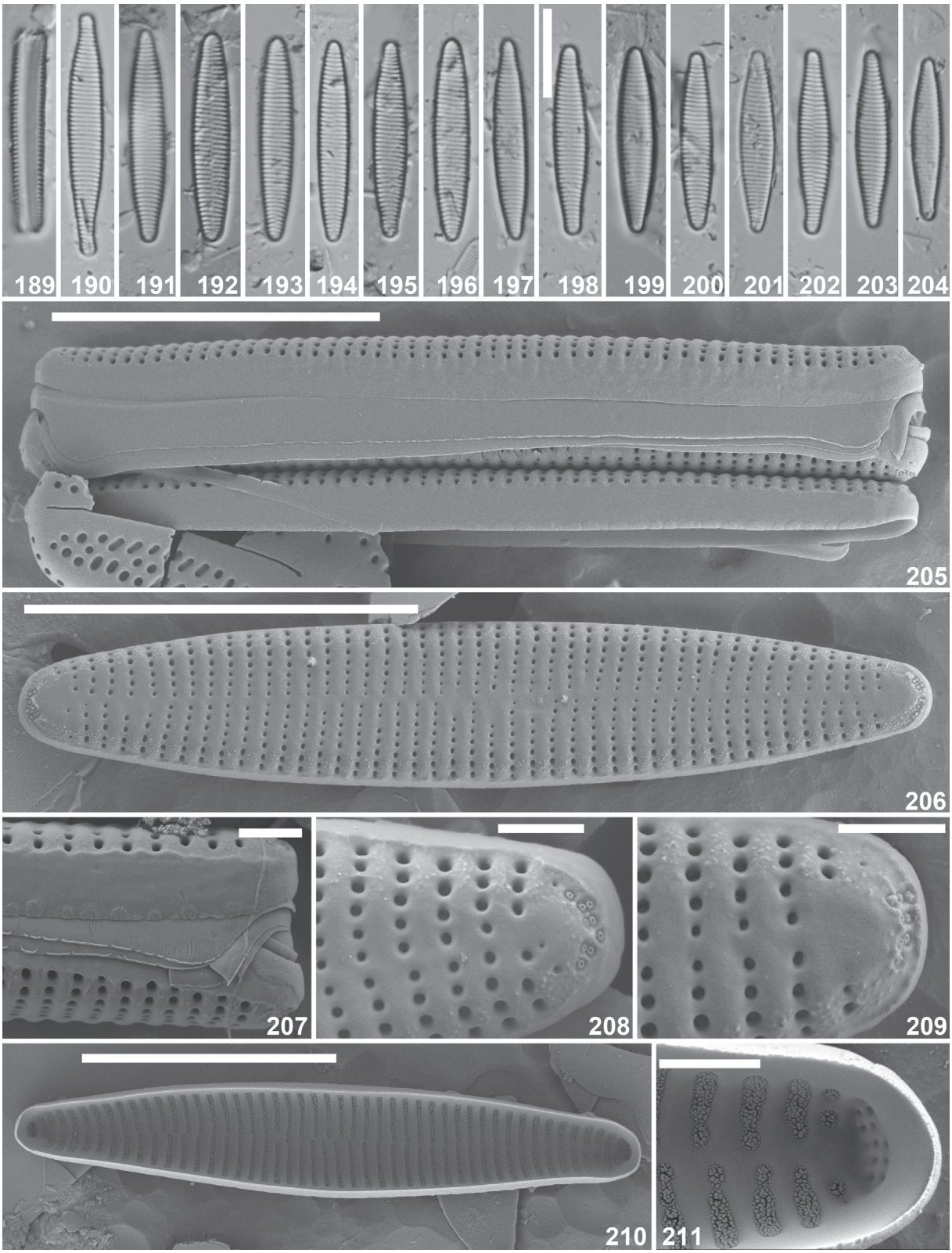
***Stauroforma inermis* Flower, V.J.Jones *et* Round (Figs 153–211)**

LM (153–204): Frustules solitary or in pairs, rectangular. Longer colonies at present not observed. Valves isopolar, linear to linear–lanceolate with straight to slightly convex margins. Apices either non–protracted, cuneately rounded, to protracted, rostrate (Figs 162, 184, 190, 202). Valve dimensions (n = 60): length 17–28 µm, width 3.5–4 µm. Sternum almost not discernible in LM, very narrow, almost non–existing, visible as a very thin, hyaline line running from apex to apex (Figs 158, 177, 178). Striae weakly radiate, not parallel, straight, equidistant, becoming more radiate at the apices, 20–21 in 10 µm.

SEM (205–211): Spines absent (Figs 205, 206). Irregular pattern of siliceous papillae and ridges visible at valve margin. Cingulum composed of three open, non–perforated copulae decreasing in width with valvocopula being the largest. Abvalvar edges with very thin siliceous ridge (Figs 205, 207). Mantle rather deep. Striae not continuing from valve face/mantle junction onto mantle (Fig. 205). Mantle hyaline, plain with well–developed mantle plaques at edge (Fig. 205). Valve face flat with clearly raised virgae, broader than striae. Striae sunken between virgae, uniseriate, composed of small, rounded areolae (Figs 206–209). At valve margin, irregular pattern of small siliceous granules visible (Fig. 205). Rimoportula absent. Apical porefield present at both apices (Fig. 206),



Figs 153–188. *Stauroforma inermis* Flower *et al.* LM images taken from the holotype slide (BM 82390, Moss Lake, Signy Island, Antarctica, Lake site SG4, South Orkney Islands, Maritime Antarctic Region). **(153–188)** LM views of population arranged in decreasing length. Figs 153–155 represent frustules in girdle view, solitary or in pairs. Scale bar represents 10 µm.



Figs 189–211. Stauroforma inermis Flower *et al*. LM and SEM images taken from Vestfold Hills, Antarctic Continent (sample VH 4, leg. J. Gibson). **(189–204)** LM views of population arranged in decreasing length. Fig. 189 shows a frustule in girdle view. **(205)** SEM views of a frustule in girdle view showing the valvocopula, the absence of spines, and the hyaline mantle. **(206)** SEM external view of an entire valve. **(207)** SEM external detail of the apex in girdle view with the position of the apical porefield. **(208–209)** SEM external detail of both apices of one valve with the small apical porefield. **(210)** SEM internal view of an entire valve showing the sternum and virgae. **(211)** SEM internal detail of the areolae covered with volae and the apical porefield. Scale bars 10 µm (189–206, 210) and 1 µm (207–209, 211).

almost equal in size and shape, located on a thin, step–like depression. Porefields composed an irregular pattern of 6–10 very small rimmed porelli, sunken within a thickened irregular pattern of ridges (Figs 207–209). Small hyaline area separating apical porefields from the last striae at apices. Internally, striae located in grooves spanning entire valve width, bordered by raised virgae (Fig. 210). Areolae covered by continuous series of irregular volae (Fig. 211).
Holotype: BM 82390
Type locality: Moss Lake, Signy Island, Antarctica, Lake site SG4, South Orkney Islands, Maritime Antarctic Region
Analysed population: Antarctic Continent, Vestfold Hills (sample VH 4, leg. J. Gibson)

Associated diatom flora: The type slide of *S. inermis* is dominated by the latter with several Antarctic endemic freshwater taxa being less frequent: *Psammothidium abundans* (Manguin) Bukht. *et* Round, *Pinnularia australomicrostauron* Zidarova, Kopalová *et* Van de Vijver, *Navicula bicephaloides* Van de Vijver *et* Zidarova, *Caloneis australis* Zidarova, Kopalová *et* Van de Vijver, *Sellaphora* cf. *elorantana* (Lange–Bertalot) C.E.Wetzel, *Stauroneis latistauros* Van de Vijver *et* Lange–Bertalot and *Gomphonema maritimo–antarcticum* Van de Vijver, Kopalová, Zidarova *et* Kociolek.

Taxonomic remarks: Flower *et al.* (1996, p. 55) reported small morphological differences b*et*ween the Antarctic type population of *Stauroforma inermis* and the European populations. The valves in the Antarctic populations are more lanceolate in outline and the apical porefields seem different in size. Nevertheless, they considered them to be conspecific as they found it impossible to evaluate the significance of these differences. Currently, *S. inermis* seems to be regularly reported in European waters (e.g. Heudre *et al.*, 2018). The observation of the type of *F. virescens* var. *subsalina* raises doubts about these European records of *S. inermis*. When comparing their morphology, several, small differences can be seen. *Stauroforma subsalina* has straight, parallel striae compared to *S. inermis* that has more radiate striae, although no difference in stria density (20–22 in 10 µm) could be observed. *Stauroforma inermis* is slightly narrower (3.5–4 µm) compared to *S. subsalina* (4–5 µm). The virgae in *S. subsalina* bear low siliceous ridges, not observed in *S. inermis*. Additionally, the apical porefields in *S. subsalina* are larger with more than 10 porelli, contrary to the smaller porefields in *S. inermis*. Although subtle, we propose that the combination of all these differences is sufficient to separate them into two species. Especially, since *S. inermis* so far has only been confirmed from the Antarctic Continent and the Maritime Antarctic Region (Zidarova *et al.*, 2016) with certainty, but seems to be absent from the rest of the world, except for some (doubtful) records in western Europe.

Discussion

Almost all known species of *Stauroforma* are typically found in more brackish waters (coastal areas) or environments with higher electrolyte contents. The only exception seems to be the colony–forming *S. exiguiformis* that was described from an acidic, oligotrophic, even aerophilic environment (cave near Aberdeen), although the species was also observed in aquatic environments on Spitsbergen and in Scotland, but always dominated by acidophilic species.

The original description of the genus *Stauroforma* included the formation of linear colonies, the absence of rimoportulae, a large valvocopula, presence or absence of spines and a reduced or even absent sternum (Flower *et al.*, 1996, p. 53). Originally, the genus was based on 2 species, of which only one fitted the genus description. *Stauroforma inermis* does not produce colonies, lacks spines and possesses an apical porefield, three features that not only do not seem to fit into the genus description of *Stauroforma*, but also differ markedly from the generitype *S. exiguiformis*. All species transferred or described so far into the genus *Stauroforma*, including the new combinations in this contribution, share more morphological features with *S. inermis* than with *S. exiguiformis*. Most of these taxa lack spines, do not form colonies, and they all have an apical porefield on one (foot pole) or both apices. A variable feature seems to be the absence/presence of areolae on the mantle with *S. schulzii* clearly having a long series of areolae on the mantle running down from the valve face whereas *S. inermis* and *S. subsalina* lack this feature. *Stauroforma reimeri* (E.Morales, Manoylov *et* Bahls) E.Morales, described from North America, has rudimentary marginal spines that cannot function as linking spines (Morales *et al.*, 2010, fig. 37) and also presents long series of areolae on the mantle. We therefore propose that the genus definition of *Stauroforma* needs to be emended to include characters for all currently known species.

***Stauroforma* Flower, V.J.Jones *et* Round, *emend.* Van de Vijver, T.M.Schust., D.M.Williams *et* Kusber**
Frustules solitary or connected via linking spines to form long, ribbon–like colonies. Valves isopolar or heteropolar, clearly clavate to linear and linear–lanceolate. Mantle deep, usually plain, occasionally with long striae running down from valve face to halfway the mantle. Mantle plaques present. Sternum present or absent. Apical porefields usually present at one or both poles. Colony–forming species lacking porefields. Internally, areolae covered by volae. Girdle composed of 4–6 broad, open plain copulae, the valvocopulae being the largest.

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