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RESEARCH ARTICLE

Revision of the *Staurosirella leptostauron* complex (Staurosiraceae, Bacillariophyta) in Europe with the description of three new species

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Abstract

Background and aims – Small-celled araphid diatoms form an important part of the diatom flora in our rivers and lakes. Although several of these species are frequently reported, their correct taxonomic identity is often obscured due to a lack of good knowledge of the original (type) material.
Material and methods – Several historical (nineteenth century) original samples were retrieved from different European and North American diatom collections. The samples have been analysed using light (LM) and scanning electron microscopy (SEM).
Key results – *Staurosirella crux* comb. nov., based on Ehrenberg's *Navicula crux*, proved to be the oldest valid name for *Staurosirella harrisonii*, the latter now being considered a younger synonym. A new European species, *S. neorhomboides* sp. nov., is described to replace the name *S. rhomboides*, now considered a younger synonym of *S. leptostauron*. The North American populations of *S. rhomboides* and *S. martyi* differ sufficiently from the type populations and are described as new species: *S. moralesii* sp. nov. and *S. manoyloviana* sp. nov. The new combination *Staurosirella informis* comb. nov. is proposed for a taxon described in 1856 from the French Pyrenees as *Odontidium informe*. *Staurosirella leptostauron* turns out to be insufficiently described and is now documented for further use.
Conclusion – The analysis of the original (type) material corrected several taxonomic errors and better characterised the morphology of several commonly observed *Staurosirella* species.

Keywords

araphid diatoms, Bacillariophyceae, new species, *Staurosirella*, type material

INTRODUCTION

The diatom genus *Staurosirella* D.M.Williams & Round (Staurosiraceae, Bacillariophyta) was described in 1987 by Williams and Round, split from the catch-all genus *Fragilaria* Lyngb. (Williams and Round 1988). The genus *Staurosirella* is characterised by isopolar or heteropolar valves, broad uniseriate striae composed of slit-like, linear areolae, internally occluded by finely branched volae, and relatively narrow vimines. Morales and Manoylov (2006a) further refined the description of the genus. When spines are present, they can be linking, or may simply be

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rudimentary, acute, granulate, or short. Rimoportulae are always absent. Most species possess apical pore fields, usually on both apices, but they can vary in size and shape, ranging from a very large pore field, extending onto the valve face and the mantle, to a very reduced aggregate of small, rounded pores. The cingulum is composed of several (usually > 5) open (rarely closed), plain copulae. The valvocopula is larger than the copulae and mostly bears well-developed, robust fimbriae (Williams and Round 1988; Morales and Manoylov 2006a).

At present, *Staurosirella* includes more than 50 published names (Guiry and Guiry 2023). Recently, a large number of new species has been described from all continents (Morales and Manoylov 2006b; Van de Vijver et al. 2014; Almeida et al. 2015; Seeligmann et al. 2018; Guerrero et al. 2019; Osório et al. 2021; Van de Vijver 2022, 2023). In addition, several commonly reported species, such as *Staurosirella pinnata* (Ehrenb.) D.M.Williams & Round, have been the focus of renewed taxonomic analyses resulting in a more refined characterisation of some of these species (Morales et al. 2015, 2019).

During the past two years, intensive taxonomic research based on the analysis of historical samples from several European diatom collections, such as the Van Heurck collection (BR, Belgium), the Ehrenberg collection (BHUPM, Germany), the Kützing collection (BM, United Kingdom), and the Grunow collection (W, Austria), revealed major inconsistencies in the identification of common European *Staurosirella* taxa, clearly demonstrating the need for a more detailed revision of historical type material as it was successfully done in the past for other diatom genera such as *Pinnularia*, *Brachysira*, *Ulnaria*, and *Eunotia* (e.g. Pinseel et al. 2021; Van de Vijver et al. 2021a, 2021b; Williams and Van de Vijver 2021; Van de Vijver and Lange-Bertalot 2022).

One of the most iconic and characteristic *Staurosirella* species in Europa, mainly due to its typical cruciform valve outline, is *Staurosirella leptostauron* (Ehrenb.) D.M.Williams & Round. In 1854, Christian Gottfried Ehrenberg (1795–1876) originally published it as *Biblarium leptostauron* Ehrenb. from a sample named 'Silbergrauer Polierschiefer von Cassel', a city in central Germany, and illustrated this new species with two small line drawings (Ehrenberg 1854: plate XII, figs 35–36). Two years later, the Reverend William Smith (1808–1857) described a second cruciform *Staurosirella* as *Odontidium harrisonii* W.Sm. (transferred to the genus *Staurosirella* as *S. harrisonii* (W.Sm.) E.Morales & C.E.Wetzel (Morales et al. 2015)) from a sample collected near Hull (United Kingdom). Furthermore, Smith described a variety β being 'a smaller form with more acute angles' (Smith 1856: 18, plate LX, figs 373–374). The latter was properly described as *Fragilaria harrisonii* var. *rhomboides* Grunow from a sample taken in Moosach (a village near Munich, Germany) (Grunow 1862: 368).

In 2006, Morales and Manoylov analysed a large number of *Staurosirella* populations from several North American rivers (Morales and Manoylov 2006b). Based on their investigations, but without analysing the original European type material from the nineteenth and early twentieth centuries, they transferred three former species of *Fragilaria* and *Opephora* to the genus *Staurosirella*: *S. martyi* (Hérib.) E.Morales & Manoylov, *S. dubia* (Grunow) E.Morales & Manoylov, and *S. rhomboides* (Grunow) E.Morales & Manoylov. Although these three species are regularly observed in European waters and at least two of them (*S. dubia* and *S. martyi*) were included in the newest edition of the Freshwater Diatom Flora for Central Europe (Lange-Bertalot et al. 2017), their correct taxonomic identity has been obscured by a lack of proper analysis of their type material. Additional complications arose by including many populations from different parts of the world under these names, resulting in a drift in species concepts, and amending the original description to fit a broad array of population. For instance, Witkowski et al. (1996) discussed the morphology of *Staurosirella martyi* (as *Fragilaria martyi* (Hérib.) Lange-Bert.), but it is clear from the illustrated populations that at least five different taxa are grouped under the name *martyi*, and that most of them likely represent distinct species.

In this paper, we analyse the original (type) material of several *Staurosirella* species commonly reported in Europe. The material included the original Ehrenberg material for *Navicula crux* Ehrenb. and *Biblarium leptostauron*, and samples kept in BR from the collections of William Smith and the Scottish botanist George A. Walker Arnott (1799–1868) for *Odontidium harrisonii* and its var. β, as well as *Odontidium informe* W.Sm. Additionally, type material from the Grunow collection in Vienna (W) for *Fragilaria harrisonii* var. *dubia* and var. *rhomboides*, and fossil material collected by Héribaud from the Auvergne for *Opephora cantalense* Hérib. and *O. martyi* Hérib. kept in BM were also investigated. In addition, the original slide and material used to illustrate *S. rhomboides* and *S. martyi* in Morales and Manoylov (2006b) were analysed to illustrate their interpretation of both species. Based on these results, several new species are described here: *Staurosirella neorhomboides* Van de Vijver, Kusber & Jüttner sp. nov., *S. manoyloviana* Van de Vijver, Jüttner & D.M.Williams sp. nov., and *S. moralesii* Van de Vijver, Jüttner & D.M.Williams sp. nov. Two new combinations are proposed: *Staurosirella crux* (Ehrenb.) Van de Vijver & Kusber comb. nov. and *S. informis* (W.Sm.) Van de Vijver comb. nov. All discussed taxa are illustrated using light (LM) and scanning electron microscopy (SEM) observations. The ecological preferences of the different species are derived from so-called ecological profiling: the assessment of the associated diatom flora in the different samples, followed by an analysis of the ecological preferences of these associated species.

MATERIAL AND METHODS

In this study, a large number of historical samples from various European diatom collections was brought

together to clarify the taxonomic identity of the *S. leptostauron* complex. Table 1 lists all samples used in this study together with all information available about these samples. In total, 15 samples (and slides) were investigated.

A subsample of each of the selected materials was prepared for LM and SEM observations following the method described in van der Werff (1955). Small volumes of subsamples were cleaned by adding 37% H_2O_2 and subsequently heated to 80°C for about 1–2 h. The reaction was completed by addition of saturated $KMnO_4$. Following digestion and rinsing by centrifugation (three times 10 minutes at 4500 × rpm), the resulting cleaned diatom material was diluted with distilled water to avoid excessive concentrations of diatom valves and an aliquot was placed on a slide and mounted in Naphrax®. Slides were analysed using an Olympus BX53 microscope at ×1000 magnification (UPLanFL N 100× objective, N.A. 1.30), equipped with Differential Interference Contrast (Nomarski) optics and the Olympus UC30 Imaging System. For each taxon, the number of specimens, measured at random on the type slide, is indicated (n = X). To assess the associated diatom flora in each sample, at least 200 valves were enumerated and identified on random transects.

For SEM analysis, parts of the oxidised suspensions were filtered through a 5 µm Isopore™ polycarbonate membrane filter (Merck Millipore). Filters were air-dried and pieces were affixed to aluminium stubs. The stubs were sputter-coated with a platinum layer of 10 nm and studied using a ZEISS Ultra scanning electron microscope at 3 kV and 6 mm working distance (Natural History Museum, United Kingdom). Additional observations were preformed using a JEOL-JSM-7100F field emission scanning electron microscope, operated at 2 kV and 4 mm working distance (Meise Botanic Garden, Belgium). Slides, samples and stubs analysed in this study are stored at the BR collection (Meise Botanic Garden, Belgium). Figures were prepared using Photoshop CS5.

Terminology used for the description of the various structures of the siliceous cell wall is based on Ross et al. (1979, areola structure), Cox and Ross (1981, stria structure), Morales (2005, girdle structure), Williams and Round (1988, *Staurosirella* genus features), and Morales and Manoylov (2006a, *Staurosirella* genus features). For the taxonomic treatment, the following papers were consulted: Krammer and Lange-Bertalot (1991), Witkowski et al. (1996), Morales (2005), Morales and Manoylov (2006a, 2006b), Morales et al. (2010a, 2010b, 2015, 2019), Guerrero et al. (2019), Osório et al. (2021), and Van de Vijver (2022, 2023).

For typification of the new species, we chose to use the entire sample as the holotype following Article 8.2 of the International Code of Nomenclature for algae, fungi, and plants (Turland et al. 2018). The type specimen is illustrated by an image, irrespective of the fact that the slide comprises many specimens of the described taxon, by stating "Figure X illustrates the holo/lectotype", ensuring that the identity of the species can be fixed.

RESULTS AND DISCUSSION

Based on the morphological analysis of the selected (historical and recent) populations, we propose important taxonomic changes in the genus *Staurosirella*, which alter the generally accepted ideas of some taxa considerably and may therefore not meet with universal approval. Commonly used names such as *Staurosirella harrisonii, S. dubia*, and *S. rhomboides* should no longer be used, as they represent more recent synonyms of other taxa. Others, such as *S. martyi*, represent different taxa. Based on their valve outline, two groups can be recognized: a first group with (almost) isopolar cruciform/rhomboid valves and a second with heteropolar, ovoid to clavate valve outlines.

Species of *Staurosirella* with cruciform and/or rhomboid valve outline

Ehrenberg originally described *Navicula crux* (Ehrenberg 1838: 184) in the raphid genus *Navicula*, because he observed a '*sutura media interruptis* [interrupted by a median groove]' mistaking the broader, thickened sternum for a raphe structure. On his original drawings (Fig. 1A), however, he did not indicate a raphe structure, and in the original material only a valve lacking a raphe could be found (Fig. 1B–H). Although the largest valves in the Ehrenberg material seem to be somewhat more robust, most of the observed valves show a high similarity with the population in the type material of *Staurosirella harrisonii* (W.Sm.) E.Morales & C.E.Wetzel from Hull (United Kingdom) (Fig. 2). In addition, the populations observed in the Grunow and Kützing material collected in Moosach (Germany) (Supplementary materials 1–3) show that *Navicula crux* and *Staurosirella harrisonii* are conspecific. As *Navicula crux* is the oldest name in the same rank that was validly published, it has priority over *S. harrisonii* (Turland et al. 2018: Art. 11.4). Based on the observed morphological features, the latter species is transferred to the genus *Staurosirella* as *Staurosirella crux* (Ehrenb.) Van de Vijver & Kusber comb. nov.

Staurosirella crux (under the name *Fragilaria harrisonii* or *Staurosirella harrisonii*) has been considered by some authors as a synonym of the more commonly known *Staurosirella leptostauron* (Ehrenb.) D.M.Williams & Round (Hustedt 1931; Patrick and Reimer 1966; Krammer and Lange-Bertalot 1991). *Staurosirella leptostauron* was first published within the genus *Biblarium* Ehrenb. that was proposed for rejection by Williams (1986) in favour of the more commonly used genus *Tetracyclus* Ralfs (Wiersema et al. 2018). However, the name *Biblarium leptostauron* was introduced by Ehrenberg (1854: 8, plate XII, figs 35–36) who provided a name and an illustration for his new taxon. As he treated Bacillariophyta as animals ("Infusionstierchen"), the International Code

Table 1. List of all samples used in this paper (s.n. = sine numero).

Sample	Locality	Investigated taxon	Collection date	Collector	Collection	Collection number
Ehrenberg sample 2726	Polirschiefer bei Cassel, Germany	*Navicula crux, Biblarium leptostauron*	?	C.G. Ehrenberg	BHUPM	BHUPM s.n.
Smith s.n.	Hull, United Kingdom	*Odontidium harrisonii*	15 Jan. 1854	R. Harrison	BR	BR-4685
Grunow s.n.	Moosach near Munich, Germany	*Fragilaria harrisonii* var. *rhomboides*	?	A. Grunow	BR, W	BR-4819, W0164841
Kützing 921	Moosach near Munich, Germany	*Fragilaria harrisonii* var. *rhomboides*	?	?	BR	BR-4820
Smith s.n.	Cauterets, Gave de Lizez, France	*Odontidium informe*	Jul. 1856	W. Smith	BR	BR-4821
Smith s.n.	Gave de la Reine, France	*Odontidium informe*	Jul. 1856	W. Smith	BR	BR-4822
Walker Arnott S445	Redesdale, Hermits Well, United Kingdom	*Odontidium informe*	Aug. 1856	R.K. Greville	BR	BR-4823
Smith s.n.	Burnham, Norfolk, United Kingdom	*Odontidium harrisonii* var. β	1 Jan. 1854	Mr. Brookes	BR	BR-4824
Smith s.n.	Lough Derg, County Clare, Ireland	*Odontidium harrisonii* var. β	24 Jul. 1854	W. Smith	BR	BR-4825
Morales s.n.	Willow Creek, Waushara, Wisconsin, United States	*Staurosirella moralesii*, *S. manoyloviana*	1993	?	ANSP, BR	ANSP G.C 100049b, BR-4826
Jüttner s.n.	Killen Burn, Highland, Scotland, United Kingdom	*Staurosirella neorhomboides*	?	I. Jüttner	BR	BR-4827, slide 435
Grunow 552	Stienitz See, Berlin, Germany	*Fragilaria harrisonii* var. *dubia*	?	Amic. Reinhardt	BR, W	BR-4828, W0164812, W0164813
Héribaud s.n.	Dépôt de Neussargues, Cantal, France	*Opephora martyi*	1901?	P. Marty	BR	BR-4829
Héribaud s.n.	Dépôt de Joursac, Cantal, France	*Opephora cantalense*	1903?	M.J. Pagès-Allary?	BM	BM 68398
Smith s.n.	Ormesby, Norfolk, United Kingdom	*Staurosirella martyi*	10 Apr. 1853	M. Bridgeman	BR	BR-4830

for Zoological Nomenclature (ICZN) must be followed before treating a taxon name under the International Code for Botanical Nomenclature (ICN). The name was introduced as a species group name (ICZN 1999: Art. 11) without description or diagnosis (ICZN 1999: Art. 12.1) but with an indication because the name was assigned to an image of the taxon (ICZN 1999: Art. 12.2.7). Thus, the name is treated as valid under the ICN (Turland et al. 2018: Art. 38.7).

The search for *S. leptostauron* in Ehrenberg's sample 2726 was not successful (contrary to *S. crux*). Due to the usage of Canada balm by Ehrenberg, the marked parts of the deposited mica were obscured and Ehrenberg's specimens of this species could not be identified. Ehrenberg's drawings, based on his own observations, show two different valves, one without striae and one with striae (Fig. 4A). According to Ehrenberg's original drawings and measurements, *Biblarium leptostauron* might be 30–35 µm long with a width/length ratio between 0.52 and 0.55 (vs 0.67–0.78 in *Biblarium crux* as Ehrenberg called the latter taxon in 1845). The illustrated valve is more heteropolar than in *B. crux* and near the apices nearly parallel and much narrower than in *B. crux* (width-near-the-apex/width 0.23–0.30 vs 0.37–0.43 in *B. crux*). *Biblarium leptostauron* shares the main character (the "leptostauron") with *B. crux* that was drawn with a raphe-like transapical structure and a central node due to misinterpretations by Ehrenberg of lengthwise broken valves. The striae of one valve (6/10 µm) of *B. leptostauron* are in the range of *B. crux* but drawn not as broad as in *B. crux*, the other valve lacks striae. It is questionable that both *B. leptostauron* valves are conspecific. It should be mentioned that Ehrenberg interpreted his Cassel material in different ways and his treatment in the Mikrogeologie (Ehrenberg 1854) was probably merely based on his old drawings instead of on new observations. It is also possible that the valve lacking striae is simply a representation of a girdle band. Thus, *B. leptostauron* as Ehrenberg conceived it, remains doubtful and in contrast to *B. crux* insufficiently described.

When Hustedt (1931) transferred *Biblarium leptostauron* to the genus *Fragilaria* as *F. leptostauron* (Ehrenb.) Hust., he listed many synonyms including *Odontidium informe* W.Sm. (Smith 1857: 10) and *Staurosirella harrisonii* (as *Odontidium* or *Fragilaria*). As these names are no longer considered to be synonyms of

S. leptostauron (see the results in this paper), Hustedt's transfer of *Biblarium leptostauron* to the genus *Fragilaria* in his treatment is not helpful to identify what should be comprised under that name.

Grunow (1862) mentioned on page 368 *Biblarium leptostauron* as a synonym of *Fragilaria harrisonii* (W.Sm.) Grunow, clearly being unaware of *Navicula/Biblarium crux*. He also described at the same time two varieties: *F. harrisonii* var. *rhomboides* Grunow and *F. harrisonii* var. *dubia* Grunow. Analysis of the type material of *F. harrisonii* var. *rhomboides* showed that its morphology corresponds to that of Ehrenberg's drawings (Ehrenberg 1854: plate XII, figs 35–36) (Fig. 4A) for *Biblarium leptostauron*, suggesting a likely conspecificity. However, Grunow (1862) linked *B. leptostauron* with *F. harrisonii* var. *genuina*, his name for what he considered the nominate variety of *F. harrisonii*, whereas for *F. harrisonii* var. *rhomboides* Grunow listed *Odontidium harrisonii* var. β and *Staurosira pinnata* Ehrenb. as synonyms. Unpublished data show that *Staurosira pinnata* in fact represents an entirely different species, often confused with *Staurosira construens* (Bart Van de Vijver unpubl. data).

Odontidium harrisonii var. β was first mentioned in Roper (1854: 77) as *Odontidium tabellaria* W.Sm., when Roper presented the observations he made on a handful of samples collected a few years earlier from the River Thames. Roper's specimens were identified as *Odontidium tabellaria* by William Smith who "from a drawing, thought might be referred to his *Odontidium tabellaria* […]" (Roper 1854: 77; Roper's published illustrations are labelled *Odontidium harrisonii* ?, Roper 1854: pl. VI, fig. 6a, b). To complicate matters, *Odontidium tabellaria* was not formally described until two years later by William Smith (1856: 17) and represents actually *Staurosira tabellaria* (W.Sm.) Leud.-Fortm. Roper's illustrations (Roper 1854: plate VI, figs 6a, b) do indeed look similar to that of Smith (1856: 18, plate LX, fig. 374), who associated it with his newly described *O. harrisonii* W.Sm. But as the valves were smaller with more acute angles, Smith (1856) described it as *O. harrisonii* var. β (Supplementary materials 5–6; Gregory had noted this taxon earlier in Gregory 1854: 100, pl. IV, fig. 22, but the drawings are suggestive of something different altogether). In his comments, Smith (1856: 18–19) noted that this variety β resembled *O. harrisonii* so closely that he had no doubt as to include it as one of its varieties, although Smith never validly described it at the variety rank, despite the fact that he stated that *O. harrisonii* var. β was a widespread diatom taxon. *Fragilaria harrisonii* var. *rhomboides* was described six years later by Grunow (1862: 368) from Moosach (near Munich, Germany) (Fig. 4) without an illustration. The drawing in Smith (1856: plate LX, fig. 374) (Supplementary material 5A), shows a valve with a more rhombic, only weakly cruciform valve outline, very similar to *Biblarium leptostauron*. *Fragilaria harrisonii* var. *rhomboides* from Moosach should therefore be considered as a synonym for *Biblarium leptostauron*, and the material from the Grunow population offers a good opportunity to characterise the morphology of the latter.

Morales and Manoylov (2006b: 352, figs 26–33, 96–101) discussed the morphology of *Fragilaria harrisonii* var. *rhomboides* and this taxon was raised to species level in the genus *Staurosirella* as *Staurosirella rhomboides* (Grunow) E.Morales & Manoylov (Morales et al. 2010a: 43), however, basing their account on a North American population. Unfortunately, they did not study the original (type) material from Moosach, nor any other specimens mentioned in Smith (1856). However, after taking all these materials into account, there are clear differences between the North American population identified as *S. rhomboides*, and the original Moosach population considered to be the type. In Kützing's sample from Moosach, a similar population was found (Supplementary material 2K–Z; also BM 18680, 18070, "Moosach") compared to Grunow's sample from the same locality. All valves in the Moosach population have a clear cruciform valve outline that is retained even in the smallest specimens (see Fig. 5L and Supplementary material 2Z), whereas the North American population has a more lanceolate to rhombic-lanceolate shape (Fig. 5). Additional differences in the structure of the apical pore field, the presence of short, parallel ridges on the virgae in line with the vimines (absent in the North American population) and the structure and more complex shape of the marginal striae, in our opinion exclude conspecificity (compare to Morales and Manoylov 2006b: figs 96–101). A comparison of the morphology of both populations made clear that the North American population represents a new species that will be described as *Staurosirella moralesii* Van de Vijver, Jüttner & D.M.Williams sp. nov.

In their analysis of the *Odontidium* species described by Smith (1856), Morales et al. (2015) discussed *Odontidium harrisonii* and its variety β based on material from Burnham, Norfolk, United Kingdom, stating that this could be the type material for *O. harrisonii*. Most likely this is not the case, as the largest and most typical population of *O. harrisonii* is in the Hull material (see above), as also indicated by Smith (1856: 18). Morales et al. (2015: 458) wrote "We searched for the var. β in the same material we analysed for the nominate variety but could not find any organism resembling the drawing presented by Smith (1856: supplementary plate 60, fig. 374)." Our analysis showed that a small population of the variety β is indeed present in the Burnham sample (Supplementary material 5A–J). Moreover, in the Walker Arnott diatom collection (part of the Van Heurck collection in BR), several populations from the British Isles (Supplementary material 7) listed in Walker Arnott's hand-written catalogue as *O. harrisonii* var. β, have a similar morphology compared to that in the Moosach population, confirming their conspecificity. Since Grunow used the Moosach population as material for the species description, we formally designate this material as lectotype for *S. rhomboides*.

In Europe, several populations were identified as *Staurosirella rhomboides* based on Morales and Manoylov (2006b) or *Staurosira mutabilis* (W.Sm.) Grunow as Werum and Lange-Bertalot (2004: plate 1) erroneously identified this taxon in 2004. Based on their morphological characteristics (valve outline, valve dimensions), the description of a new species, *Staurosirella neorhomboides* Van de Vijver, Kusber & Jüttner sp. nov. (Fig. 7), can be justified. Only a handful of published illustrations of these European populations could be found. Werum and Lange-Bertalot (2004) erroneously identified valves from Bavaria (Germany) as *Staurosira mutabilis*, discussing the rationale for using *Staurosira* instead of *Staurosirella* in the figure legend, an opinion now abandoned. In Morales et al. (2015), the type material of *Staurosirella mutabilis* (W.Sm.) E.Morales & Van de Vijver is illustrated, clearly contradicting the identification of the valves as *S. mutabilis* in Werum and Lange-Bertalot (2004). Peeters and Ector (2017: 267) reported this species from Burgundy (France) as *Staurosirella* sp4, illustrating a large population using LM and SEM. On the website 'Diatom Flora of Britain & Ireland', a population from Killen Burn (Scotland, United Kingdom) is shown as *S. rhomboides* (Jüttner et al. 2022). The newly described species *S. neorhomboides*, based on the Killen Burn population, differs from *S. rhomboides* (= *S. leptostauron*) in lacking the typical cruciform valve outline, and the largest valves have a more rhomboid outline instead (compare Figs 4 and 6). The smallest valves, however, have a more elliptic-lanceolate outline. The North American population, identified by Morales and Manoylov (2006b) as *S. rhomboides*, now described here as *S. moralesii* (Figs 5–6), is usually broader (valve width 5.5–9 µm vs 4–7 µm in *S. neorhomboides*), has a lower stria density (7–9 vs 10–11 in 10 µm) and a more elongated valve outline reaching almost 40 µm as maximum length (compared to maximum 18 µm in *S. neorhomboides*). Further differences are found in the ultrastructural details, such as spine shape (broad, singular in *S. moralesii* vs multiple, granulate in *S. neorhomboides*), the structure of the apical porefield (multiple rows of small pores in *S. moralesii* vs multiple slit-like rows in *S. neorhomboides*), the width of the striae (broader than the virgae in *S. moralesii* vs narrower in *S. neorhomboides*), and the depressed headpole in *S. moralesii*, a feature absent in *S. neorhomboides*. Therefore, both new species (Figs 5, 7) should be separated as different species. They also clearly differ from *Staurosirella crux* (Fig. 1), *S. leptostauron* (Fig. 4), and *S. informis* (Fig. 3).

Analysis of the type material of *Odontidium informe* (Fig. 3) showed that there are several morphological differences (more rhomboid instead of cruciform valve outline, less protracted apices) compared to the other species warranting its transfer to the genus *Staurosirella* as a separate species: *Staurosirella informis* (W.Sm.) Van de Vijver comb. nov. (Fig. 3). After it was validly described in 1857, this species has been rarely reported since, except in non-published collection catalogues and sample collections of the nineteenth century (Bart Van de Vijver pers. obs.). Another example of such a 'forgotten taxon' is *Synedra fontinalis* W.Sm., now *Fragilaria fontinalis* (W.Sm.) Van de Vijver et al., described from the same floristic excursion William Smith made to the Pyrenees in 1856, and recently restudied based on the type material at Edinburg Botanical Garden (Smith 1857; Van de Vijver et al. 2021c). The Scottish botanist George A. Walker Arnott (1799–1868) listed several samples in his collection from the British Isles as containing *S. informis* (as *O. informe*), one of which was also analysed in the current study to establish conspecificity (Supplementary material 4) with the original Pyrenees material.

It is possible that *Fragilaria leptostauron* var. *woerthensis* A.Mayer (Mayer 1937: 73) might also represent *S. informis*, but analysis of Mayer's type material from Bavaria (Germany), which was not available for this study, will be necessary to confirm this hypothesis. It is unclear whether Mayer's material still exists (Rolf Klee pers. comm.). The original drawings in Mayer (1937: plate IV, figs 14–16) show a lanceolate-rhomboid, isopolar valve, most likely identical to *S. informis,* but more detailed morphological observations are necessary to confirm this. Bey and Ector (2013: 268) illustrate a taxon provisionally named '*Staurosirella chavauxii* nom. nud.', which, according to Bey and Ector (2013) "will be described by E. Morales", but that has never been done (Guiry and Guiry 2023). It appears as '*S. chavauxii* Morales et al. in prep.' in a study on the biodiversity of calcareous springs in Poland (Okoń et al. 2020: 656). The absence of published records of *S. informis* in the twentieth century is most likely a consequence of the fact that the species has been confused with or has been considered a synonym of *S. rhomboides* or *S. leptostauron*. The results of the present study contradict now this presumed synonymy and reinstall the taxon as an independent species.

Heteropolar *Staurosirella* species with ovoid to clavate valve outline

One taxon, often considered morphologically closely related to *S. leptostauron*, but with a heteropolar, ovoid valve outline, is *Staurosirella dubia*, first described as *Fragilaria harrisonii* var. γ *dubia* Grunow (1862: 368, plate IV(7), fig. 8a–d) from the Stienitzsee (Lake Stienitz) near Berlin (Germany). The original material of the latter, catalogued by Grunow as his sample 552, shows a rather large, robust, solitary species of *Staurosirella*. This is in contrast to the population indicated by Morales and Manoylov (2006b: figs 13–25) showing isopolar, linear to linear-lanceolate valves with weakly protracted (in longer specimens), acutely rounded apices. The original (unpublished) drawings Grunow made of the Stienitzsee population (Fig. 10A) confirm the heteropolarity of the species, although these drawings clearly differ from some of the valves used to illustrate *Fragilaria harrisonii* var. γ *dubia* in Grunow (1862: plate IV(7), fig. 8a–d), the basionym for *S. dubia*, showing mostly isopolar valves with rostrate apices. The origin of the latter drawings

could not be determined as no sample number was written next to these original Grunow drawings in the Grunow drawing collection held at W.

Heteropolar valves similar to *S. dubia* are often reported as *Staurosirella martyi* in the literature. For instance, LM images in Lange-Bertalot et al. (2017: plate 11, figs 47–51), identified as *S. leptostauron* var. *dubia* (Grunow) Edlund, a synonym of *S. dubia*, present less similarity with the type of *S. dubia* in the Grunow material, than the valves illustrated on the same plate as *S. martyi* (Lange-Bertalot et al. 2017: plate 11, figs 52–56). It is therefore very likely that valves identified as *S. martyi* in fact represent *S. dubia*. Conspecificity of the type of *S. dubia* and the presumed *S. dubia* population in Morales and Manoylov (2006b) has to be excluded, not only due to the type specimens of *S. dubia* being heteropolar and its valve dimensions, but also based on the absence of spines (and spine vestiges) in the type population, which is contrary to the North American population where all valves possess double marginal spines on the virgae between striae (see Morales and Manoylov 2006b: figs 90–92, 95). The confusion probably occurred because the type material of both the original material of *Fragilaria harrisonii* var. *dubia* and *Opephora martyi* Hérib., the latter being the basionym for *S. martyi,* was never studied before. Witkowski et al. (1996) discussed the biogeography and morphology of *S. martyi* (as *Fragilaria martyi* (Hérib.) Lange-Bert.). However, none of the illustrated valves were taken from the original material from Neussargues (France). The valves from Joursac (France) (Witkowski et al. 1996: figs 1–6) in fact represent *Opephora cantalense* Hérib., a species also described in 1903 by Héribaud and now considered a synonym of *S. martyi* (Krammer and Lange-Bertalot 1991; Witkowski et al. 1996). The other valves illustrated in Witkowski et al. (1996: figs 7–52) originate from various populations worldwide (e.g. Austria, Chile, Germany, Iceland). Based on our analysis of the *S. martyi* type material, it is clear that most likely these valves do not belong to *S. martyi* and represent several (probably new) taxa.

Our analyses of the type material of both *S. dubia* and *S. martyi* revealed, however, that both species share a large number of common morphological features, such as the absence of marginal spines, a heteropolar valve shape, the shape of the apical pore field, and an apical depression at the headpole. Larger valves in the fossil type material of *Staurosirella martyi* (Figs 8–9) from Neussargues (France) have a typical clavate outline with a clear constriction between the valve centre and the headpole, a feature often lacking in the populations of *S. dubia* (Fig. 10). Valves in the type population of *S. martyi* tend to be longer with a length of up to 40 µm whereas *S. dubia* valves in the type material never exceeded 25 µm. However, in another (historical) population, found in a sample collected near Ormesby (Norfolk, United Kingdom) and present in the William Smith collection in BR (Supplementary material 8), longer valves were observed (up to 35 µm). The only difference between the type of *S. dubia* and the type of *S. martyi* seems to be the stria density with a slightly lower stria density in *S. martyi* (6–7 in 10 µm) compared to 7–8 in 10 µm in *S. dubia*, but this difference seems so minor that conspecificity between the two species is very likely. Although Grunow described *Fragilaria harrisonii* var. γ *dubia* in 1862 and *Opephora martyi* was described 40 years later, the latter will still have priority in the species rank following ICN Article 11.2 (Turland et al. 2018).

We also investigated the type population of *Opephora cantalense* (Fig. 11) from nearby Joursac (France), but could not find any morphological differences between these taxa. The main difference Héribaud (1903) indicated was the broader sternum in *O. cantalense* compared to *S. martyi* ("Se distingue de l'*Opephora martyi* par la forme de l'aréa, par le nombre et la disposition des côtes, ainsi que par la striation de la face connective."), and a different stria number in 10 µm (6 for *S. martyi*, 5.5–6 for *O. cantalense*). These differences are insufficient to separate these taxa. Héribaud also described several varieties in either taxon as var. *capitata*, but analysis of the original material showed that they simply belong to the normal cell diminution series, and therefore should not be considered as separate taxa. Héribaud (1908: 10) also described the heteropolar *Opephora glangeaudi* Hérib., illustrated by two line drawings (Héribaud 1908: plate XIV, figs 17–18), which is possibly another species of *Staurosirella*. Unfortunately, the original material from the Dépôt de la Garde (Cantal, France) could not be accessed. Based on the two small drawings of Héribaud, it is impossible to accept or reject conspecificity with either species of *Staurosirella*.

Round proposed the new genus *Martyana* Round for *Opephora martyi*, based on the absence of an apical pore field at the headpole, the presence of a step at the headpole, the absence of spines, and the structure of the areolae and striae (Round et al. 1990: 673). Morales and Manoylov (2006b) already discussed the genus *Martyana* in detail and concluded that there were insufficient morphological characters to erect a new genus and included *Opephora martyi* in *Staurosirella*, making the genus *Martyana* a younger synonym of the genus *Staurosirella*.

An analysis of the type material of *S. martyi* (and the populations identified as *S. dubia*) also indicated that the populations used to illustrate these species in Morales and Manoylov (2006b) do not belong to either, but represent new species. The population of *S. martyi* from Willow Creek (USA) was re-investigated here (Figs 12–13). The observed population shows some similarity with the type of *S. martyi*, but all valves are much wider (7–10 µm with only 5–7.5 µm width for *S. martyi*) and larger with a length in several specimens reaching 70 µm, given the valves a more robust outlook. Moreover, the areolae in the Willow Creek sample are usually clearly visible in LM contrary to *S. dubia* where the areolae are almost never or very difficult discernible. We therefore exclude conspecificity and following a comparison with all previously discussed taxa, the population is described as a new species: *Staurosirella manoyloviana* Van de

Table 2. Comparison table of all *Staurosirella* species discussed in this paper. Figures: figures in this paper; Suppl. materials: supplementary materials related to this paper.

	Staurosirella crux	*Staurosirella informis*	*Staurosirella leptostauron*	*Staurosirella moralesii*	*Staurosirella neorhomboides*	*Staurosirella martyi*	*Staurosirella manoyloviana*
Figures	1, 2	3	4	5, 6	7	8–11	12–13
Suppl. materials	1, 2A–J, 3A–B	4	2K–Z, 3C–F, 5–7	8		9	
Length (µm)	10–36	15–22	15–23	10–40	5–20	9–38	15–70
Width (µm)	7–24	7–9	10–16	5–9	3.5–7.0	5–10	8–10
Valve outline	cruciform in larger valves becoming subovoid to rhomboid in smaller specimens	isopolar, rhombic-lanceolate in larger valves, more strictly lanceolate in smaller specimens	distinctly cruciform throughout its entire cell cycle	almost isopolar, with a slightly larger footpole, rhombic throughout the entire cell diminution series	weakly heteropolar, slightly broader headpole, more acute footpole, rhombic-lanceolate to strictly lanceolate and elliptical	heteropolar, larger valves with clear constriction between valve middle and headpole, smaller valves ovoid in shape	distinctly heteropolar, ovoid in shape throughout the entire cell diminution series
Sternum	rather wide, linear to weakly lanceolate	moderately broad, lanceolate, slightly widened near the centre	broad, distinctly lanceolate, widened near the valve centre, often showing irregular markings	variable, moderately broad, mostly lanceolate, to narrow and linear in some valves	variable, moderately broad, lanceolate, slightly widened near the centre to very narrow, linear	narrow to moderately broad, linear to lanceolate	narrow, linear, very rarely lanceolate
Spines	irregular, rudimentary, grouped as verrucae-like structures	irregularly shaped on the virgae	flattened, irregularly shaped, blunt, on the virgae	large, flattened marginal, on the virgae	single or double, irregular, on the virgea	absent	absent
Apical pore field	very large, equal in size on both apices, composed of a large number of parallel rows of very small, slit-like pores	present on both apices, equal in size and shape, composed of at least 7 long rows of small, rounded pores, covered occasionally by small silica plates	present on both apices, clearly different in size and shape, giving the valves an heteropolar appearance	present on both apices, larger at the footpole, composed of at least 7 long rows of small, rounded pores, covering the entire foot pole, smaller on the headpole	present on both apices, larger at the footpole, composed of at least 7 long rows of small, rounded pores, covered by distinct, silica plates	at footpole very large, composed of > 8 long rows of small, rounded to squarish pores, much smaller at headpole, restricted to a few small pores	present on both apices, much larger on the footpole, composed of 5– 7 long rows of small, rounded pores
Striae in 10 µm	5–6	6–7	ca 9	7–8	9–10	6–7	5–6
Striation pattern	alternating, radiate to weakly curved	weakly radiate	parallel to weakly radiate at the centre, becoming more radiate towards the apices	parallel in the middle, becoming weakly radiate at the apices	weakly radiate throughout the entire valve	parallel in the middle becoming gradually weakly radiate towards the apices	alternating, parallel throughout to weakly radiate towards the apices
Lineolae in LM	clearly discernible	occasionally weakly discernible	only very rarely discernible	not discernible	not discernible	often discernible	clearly discernible

Vijver, Jüttner & D.M.Williams sp. nov. (Fig. 11). Another morphological closely related species, *Staurosirella subrobusta* E.Morales & Manoylov, has comparably large valves but has an almost isopolar valve outline, a broader sternum, and a dense series of granulate spines on the valve margins (Morales and Manoylov 2006b), the latter absent in *S. manoyloviana*.

The results of our study highlight the importance and even necessity of including historical material in taxonomic studies of diatoms. Although phycologists in the nineteenth century, such as Ehrenberg and Grunow, usually made very accurate drawings, comparison between these drawings and LM observations is not always easy and misinterpretations can occur, leading to incorrect identifications, taxonomic drift, and/or shoehorning new populations into historical names. It is therefore crucial that taxonomic analyses, especially those involving taxonomic changes (new combinations, transfers, and synonymies), include the revision of original material, when it is available. A better analysis and documentation of historical material is the basis for avoiding making incorrect or incomplete taxonomic interpretations. Historical diatom collections, such as the Grunow collection in Vienna (W), have become more accessible, facilitating the search for these materials (Schuster et al. 2023).

TAXONOMIC TREATMENT

Table 2 presents an overview of all morphological discriminating features of the seven discussed species. An additional Fig. 14 represents the largest and smallest valve of each species.

Staurosirella crux (Ehrenb.) Van de Vijver & Kusber, **comb. nov.**

Figs 1, 2, Supplementary materials 1, 2A–J, 3A–B

Navicula crux Ehrenb. (**basionym**), Die Infusionsthierchen als vollkommene Organismen. Ein Blick in das tiefere organische Leben der Natur: 184. 1838. (Ehrenberg 1838)

Biblarium crux (Ehrenb.) Ehrenb. (Ehrenberg 1845: 74)

Odontidium harrisonii W.Sm. (Smith 1856: 18)

Dimeregramma harrisonii (W.Sm.) Ralfs (Pritchard 1861: 790)

Fragilaria harrisonii (W.Sm.) Grunow (Grunow 1862: 368)

Diatoma harrisonii (W.Sm.) Cleve (Cleve 1868: 219)

Rhaphoneis harrisonii (W.Sm.) O'Meara (O'Meara 1875: 296)

Staurosira harrisonii (W.Sm.) Grunow (Cleve and Möller 1877: No. 25)

Nematoplata harrisonii (W.Sm.) Kuntze (Kuntze 1898: 416)

Staurosirella lata Levkov et al. (Levkov and Williams 2011: 5)

Staurosirella harrisonii (W.Sm.) E.Morales & C.E.Wetzel (Morales et al. 2015: 468)

Type locality. Germany, Polierschiefer bei Cassel, Ehrenberg BHUPM drawing sheet 2348, BHUPM sample 2726.

Lectotype. BHUPM 420310 ε w 'Cassel' (Kasten = case 42, Buch = folder 3, mica strip 10 ε white ring) **(designated here)**, specimen illustrated as our Fig. 1D.

Isolectotype. BHUPM s.n., specimen illustrated as our Fig. 1G **(designated here)**.

Registration for the new combination. http://phycobank.org/103338

Registration for the typification. http://phycobank.org/103841

Analysed material. GERMANY • Polierschiefer bei Cassel; Ehrenberg sample 2726, Ehrenberg [icon!] drawing sheet 2348; BHUPM • Moosach near München; Grunow sample s.n., Moosach W0164841 [filed as *Staurosira harrisonii* under *Odonti*[*di*]*um harrisonii* in the general collection], slide BR-4819; W, BR • Moosach near München; Kützing sample 921, slide BR-4820; BR.
UNITED KINGDOM • Hull; 15 Jan. 1854; Smith sample s.n., slide BR-4685; BR.

LM description. Frustules in girdle view rectangular, solitary. Valve outline cruciform in larger valves becoming subovoid/rhomboid in smaller specimens, usually showing a rather irregular valve outline. Larger valves subtly heteropolar with one apex slightly wider than the opposite one, becoming distinctly heteropolar in the lower end of the size range. Apices not protracted, broadly rounded. Central inflations broadly rounded with a broad base. Valve dimensions (n = 30): length 10–36 µm, width 7–24 µm. Sternum rather wide, linear to weakly lanceolate. Striae narrower than the virgae, alternating, radiate to weakly curved, 5–6 in 10 µm. Individual lineolae in the striae usually well discernible in LM. Figures 1, 2A–M.

SEM description. Valve surface uneven. Virgae with clearly raised transapical ridge. Striae uniseriate, composed of long, apically elongated areolae (= lineolae). Vimines broader than the areolae, becoming shorter towards the sternum and on the valve mantle. Spines irregular, rudimentary, grouped as verrucae-like structures on the valve face/mantle junction, located on the virgae in pit-like, shallow depressions. Apical pore fields very large, present on both apices, with both pore fields almost equal in size. Pore fields composed of a large number of parallel rows of very small, double, slit-like pores. Internally, valve surface more or less flat, with broad virgae and depressed series of areolae. Volae on the striae bifurcate, emerging from the longer inner side of the vimines. Figure 2N–Q.

Associated diatom flora. The lectotype population was observed in a fossil sample (Polierschiefer = layered diatomaceous earth) collected in the surroundings of Cassel, a town in central Germany (Hesse, Germany). According to Ehrenberg (1854), the silver-grey

material has a Tertiary origin and is composed of freshwater organisms. Although highly fragmented, it is possible to identify several species in the sample such as *Planothidium joursacense* (Hérib.) Lange-Bert., *Cavinula scutelloides* (W.Sm.) Lange-Bert., and several species of *Pseudostaurosira* and *Navicula*. This species composition indicates more alkaline, mesotrophic, β-mesosaprobic conditions (Lange-Bertalot et al. 2017). The type population of *O. harrisonii* in Hull is almost a monoculture of *S. harrisonii* with nearly 100% of the observed diatom flora belonging to this species. The Moosach populations, however, are more diverse and dominated by taxa such as *Achnanthidium exile* (Kütz.) Heib., *Cocconeis pseudothumensis* E.Reichardt, *Denticula kuetzingii* Grunow, *D. tenuis* Kütz., *Ellerbeckia arenaria* (Moore) Dorofeyuk & Kulikovskiy, *Eunotia alkalibiontica* Lange-Bert., *Grunowia tabellariae* (Grunow) Rabenh., *Odontidium mesodon* (Ehrenb.) Kütz., *Staurosirella neopinnata* E.Morales et al., *S. leptostauron* (Ehrenb.) D.M.Williams & Round, and various species of *Delicata*, *Cymbella*, and *Gomphonema*. This species composition is usually found in oligo- to mesotrophic, calcium-bicarbonate enriched, alkaline conditions (Lange-Bertalot et al. 2017).

Staurosirella informis (W.Sm.) Van de Vijver, **comb. nov.**

Fig. 3, Supplementary material 4

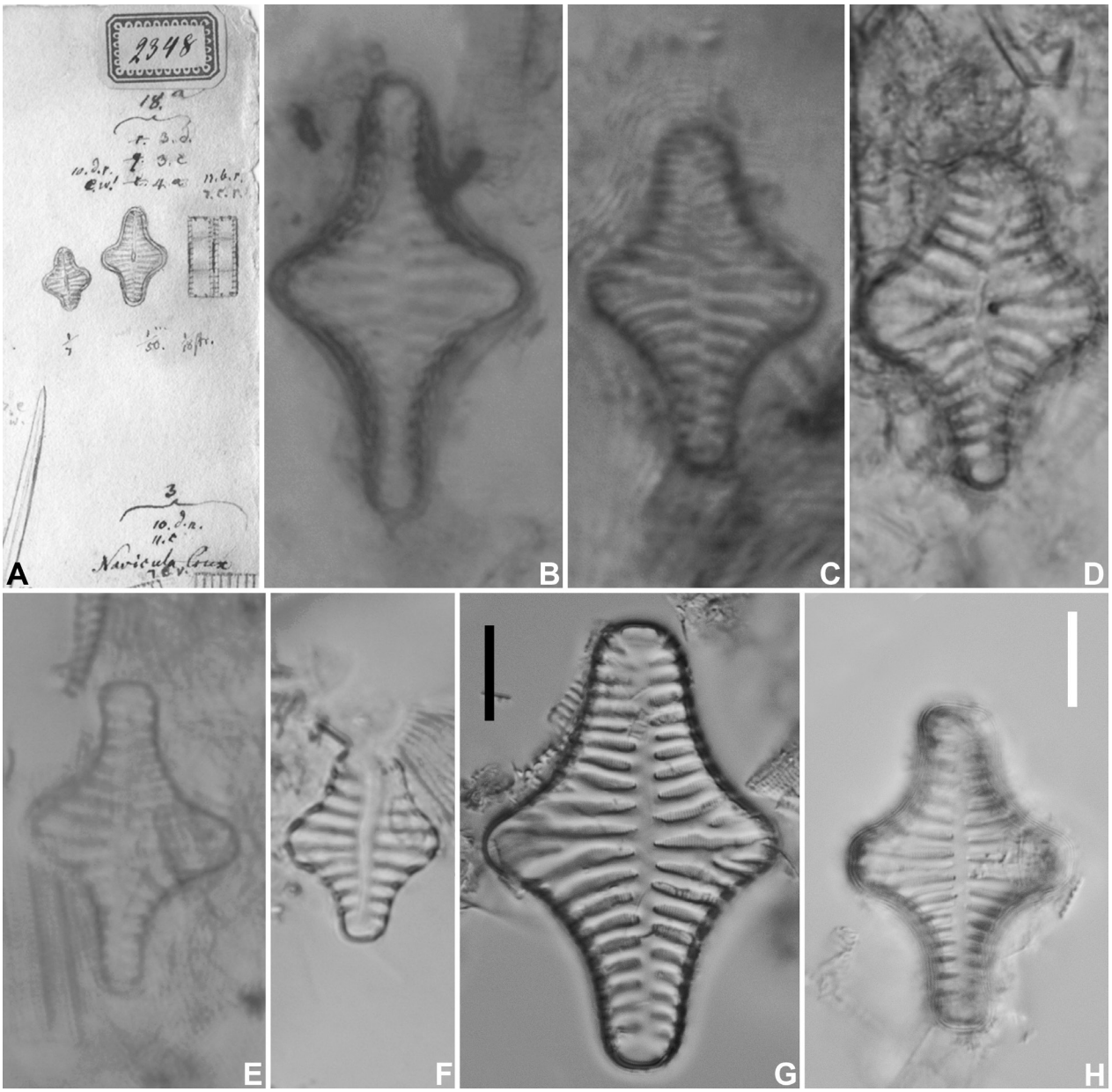

Figure 1. *Staurosirella crux* (Ehrenb.) Van de Vijver & Kusber comb. nov., LM micrographs taken from the original Ehrenberg sample 2726 (Polirschiefer bei Cassel, Germany). **A**. Original drawing 2348 from the Ehrenberg Collection (Berlin, Germany). **B**–**E**. LM pictures of valves in valve face view from the original mica conserved in BHUMP, Berlin, Germany. **F**–**H**. LM pictures of prepared unmounted Ehrenberg material. Scale bar = 10 µm.

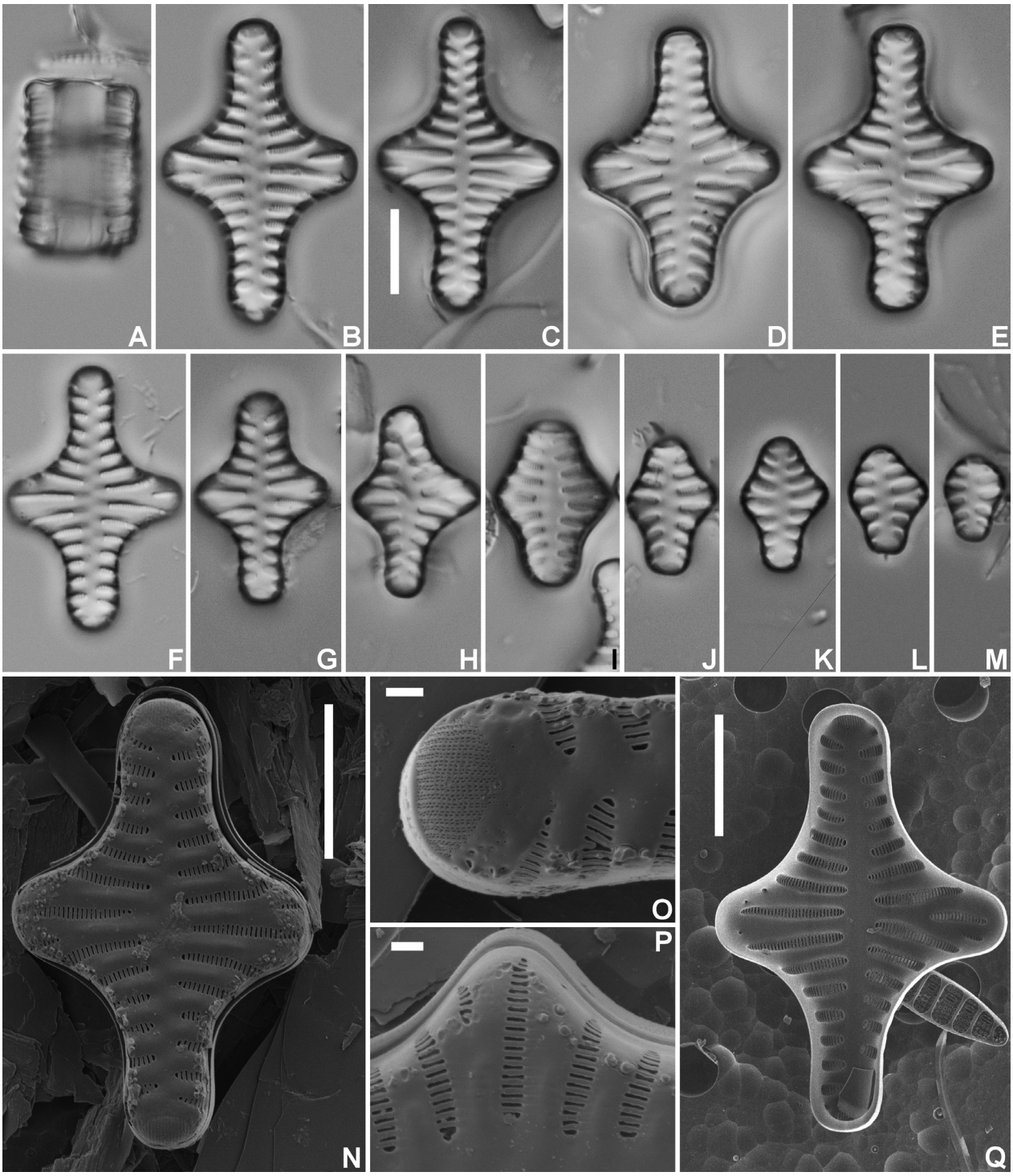

Figure 2. *Staurosirella crux* (Ehrenb.) Van de Vijver & Kusber comb. nov., LM and SEM micrographs taken from the original Smith type material for *Odontidium harrisonii* (BR-4685, Hull, United Kingdom). **A**. LM picture of a frustule in girdle view. **B**–**M**. LM pictures of valves in valve face view in decreasing length. **N**. SEM external view of a complete valve. **O**. SEM external detail of the footpole showing the large apical pore field. **P**. SEM external detail of part of the central area with the marginal spines, the large virgae and the vimines. **Q**. SEM internal view of a complete valve. Scale bar = 10 µm (A–N, Q), 1 µm (O–P).

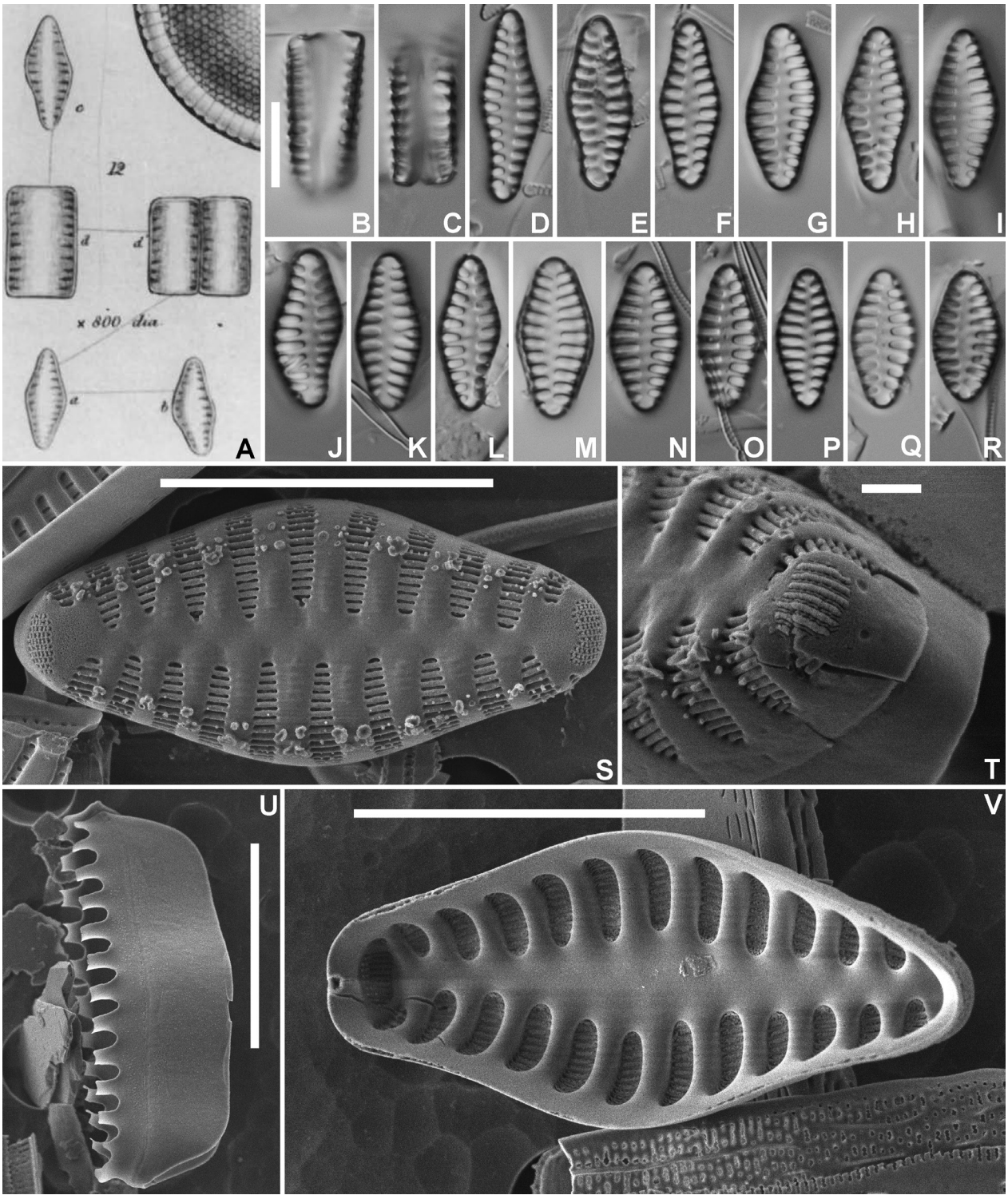

Figure 3. *Staurosirella informis* (W.Sm.) Van de Vijver comb. nov., LM and SEM micrographs taken from the original Smith material (BR-4821, Cauterets, Gave de Lizez, France). **A**. Original drawing from Smith (1857: fig. 12). **B**–**C**. LM pictures of two frustules in girdle view. **D**–**R**. LM pictures of valves in valve face view in decreasing length. **S**. SEM external view of a complete valve. **T**. SEM external detail of the footpole showing the large apical pore field. **U**. SEM view of the valvocopula with the fimbriate extensions. **V**. SEM internal view of a complete valve. Scale bar = 10 μm (B–S, U–V), 1 μm (T).

Odontidium informe W.Sm. (**basionym**), Annals and Magazine of Natural History, second series 19: 10, plate II, fig. 12a–c. 1857. (Smith 1857)

Type locality. Gave de Lizez, Cauterets, Pyrenees Mountains, France, Jul. 1856.

Lectotype. BR-4821 (**designated here**), slide made from Smith sample Gave de Lizez. Figure 2N illustrates the lectotype.

Registration for the new combination. http://phycobank.org/103339

Registration for the typification. http://phycobank.org/103842

Analysed material. FRANCE • Cauterets, Gave de Lizez; William Smith sample Gave de Lizez, slide BR-4821; BR • Gave de la Reine; William Smith sample Gave de la Reine, slide BR-4822; BR.

UNITED KINGDOM • Redesdale, Hermits Well; Aug. 1856; leg. R.K. Greville; Walker Arnott sample S445, slide BR-4823; BR.

LM description. Frustules rectangular in girdle view, solitary, but occasionally forming short band-like chains. Valves isopolar, rhombic-lanceolate in larger valves, becoming more strictly lanceolate in smaller specimens. Apices not protracted, cuneately to broadly rounded. Valve dimensions (n = 20): length 15–22 µm, width 7–9 µm. Sternum moderately broad, lanceolate, slightly widened near the centre. Striae not broader than the virgae, weakly radiate throughout the entire valve, 6–7 in 10 µm. Areolae occasionally weakly discernible in LM (e.g. Fig. 3H–I). Figure 3B–R.

SEM description. Sternum and vimines externally raised above the striae. Weakly raised parallel ridges present on the virgae. Single or double, irregularly shaped spines present on the virgae, with a large number of small granules present between the spines on virgae and vimines. Striae composed of linear, slit-like areolae, separated by thin vimines. Areolae diminishing in length near the sternum. Apical pore fields present on both apices, equal in size and shape, composed of at least 7 long rows of small, rounded pores, covered occasionally by small silica plates. Valvocopula very large, plain, with distinct fimbriae. Internal areola occlusions formed by finely branched volae. Figure 3S–V.

Associated diatom flora. The type population was found in a sample from the Gave de Lizez, a stream in the French Pyrenees (region de Bigorre, Haute-Pyrenées, France). The sample is dominated by *Achnanthidium gracillimum* (F.Meister) Lange-Bert., *A. trinode* Ralfs, *Brachysira neoexilis* Lange-Bert., *Denticula tenuis*, *Fragilaria perdelicatissima* Lange-Bert. & Van de Vijver, *Staurosirella neopinnata*, and *Staurosira tabellaria* (W.Sm.) Leud.-Fortm., together with several species of *Cymbella*, *Delicata*, and *Gomphonema*. According to Lange-Bertalot et al. (2017), this diatom community points to an alkaline, oligo- to weakly mesotrophic, carbonate-enriched substrate. The Walker Arnott population from Redesdale, a valley in the western part of Northumberland, (northeast England, United Kingdom) closely resembles this species composition, with high numbers of *Brachysira neoexilis*, *Delicata delicatula* (Kütz.) Krammer, *Denticula tenuis*, *Eucocconeis flexella* (Kütz.) F.Meister, and *Fragilaria* cf. *amphicephaloides* Lange-Bert., indicating almost similar conditions, though the listed species thrive more in standing waterbodies such as larger lakes (Lange-Bertalot et al. 2017).

Staurosirella leptostauron (Ehrenb.) D.M.Williams & Round

Fig. 4, Supplementary materials 2K–Z, 3C–F, 5–7

Biblarium leptostauron Ehrenb. (**basionym**) (Ehrenberg 1854: 8, plate VII, figs 35–36)

Fragilaria harrisonii var. β *rhomboides* Grunow (Grunow 1862: 368)

Fragilaria leptostauron (Ehrenb.) Hust. (Hustedt 1931: 153)

Fragilaria leptostauron var. *rhomboides* (Grunow) Hust. (Hustedt 1931: 154)

Staurosirella rhomboides (Grunow) E.Morales & Manoylov (Morales et al. 2010a: 43)

Staurosira leptostauron (Ehrenb.) Kulikovskiy & Genkal (Kulikovskiy et al. 2011: 363)

Type locality. Germany, Polierschiefer bei Cassel, Ehrenberg BHUPM drawing sheet 2347, BHUPM sample 2726.

Epitype locality. Moosach near Munich, Grunow Moosach sample s.n., material conserved at BR! and W!.

Lectotype. BHUPM drawing sheet 2347 "Cassel." (**designated here** by Kusber & Van de Vijver), valve original annotated in black colour "10. δ.bl.", subsequently annotated in red colour "31" [icon!], the image represents a specimen on Mica BHUPM 420310 δ r that could not be found during the recent studies at BHUPM. The lectotype here selected was published in Ehrenberg (1854), see our Fig. 2A "36".

Epitype. BR-4819 (**designated here** by Van de Vijver for the above lectotype), slide made from the Grunow Moosach sample s.n. Figure 4C illustrates the epitype.

Isoepitype. W0164841 (**designated here** by Schuster & Van de Vijver for the above lectotype), raw Grunow Moosach material s.n. at W.

Registration for the typification. http://phycobank.org/104203

Analysed material. GERMANY • Polierschiefer bei Cassel, Ehrenberg sample 2726, [icon!] drawing sheet 2347; BHUPM • Moosach near München; Grunow Moosach sample s.n., slide BR-4819; BR • Moosach near München; Kützing sample 921, slide BR-4820; BR.

UNITED KINGDOM – **England** • Burnham, Norfolk; William Smith sample; 1 Jan. 1854; leg. Mr. Brookes; slide BR-4824; BR • Redesdale, Hermits Well; Walker Arnott sample S445; Aug. 1856; leg. R.K. Greville; slide BR-4823; BR.

IRELAND • William County Clare; Smith sample Lough Derg; 24 Jul. 1854; leg. W. Smith; slide BR-4825; BR.

Description note. As the search for *S. leptostauron* in Ehrenberg's sample 2726 was not successful, the following morphological description is based on the epitype material from Moosach.

LM description. Frustules in girdle view rectangular, impossible to get into focus entirely due to protruding central parts. Valves isopolar to weakly heteropolar with weakly narrower footpole (Fig. 4B, F, L), distinctly cruciform throughout its entire cell cycle. Apices

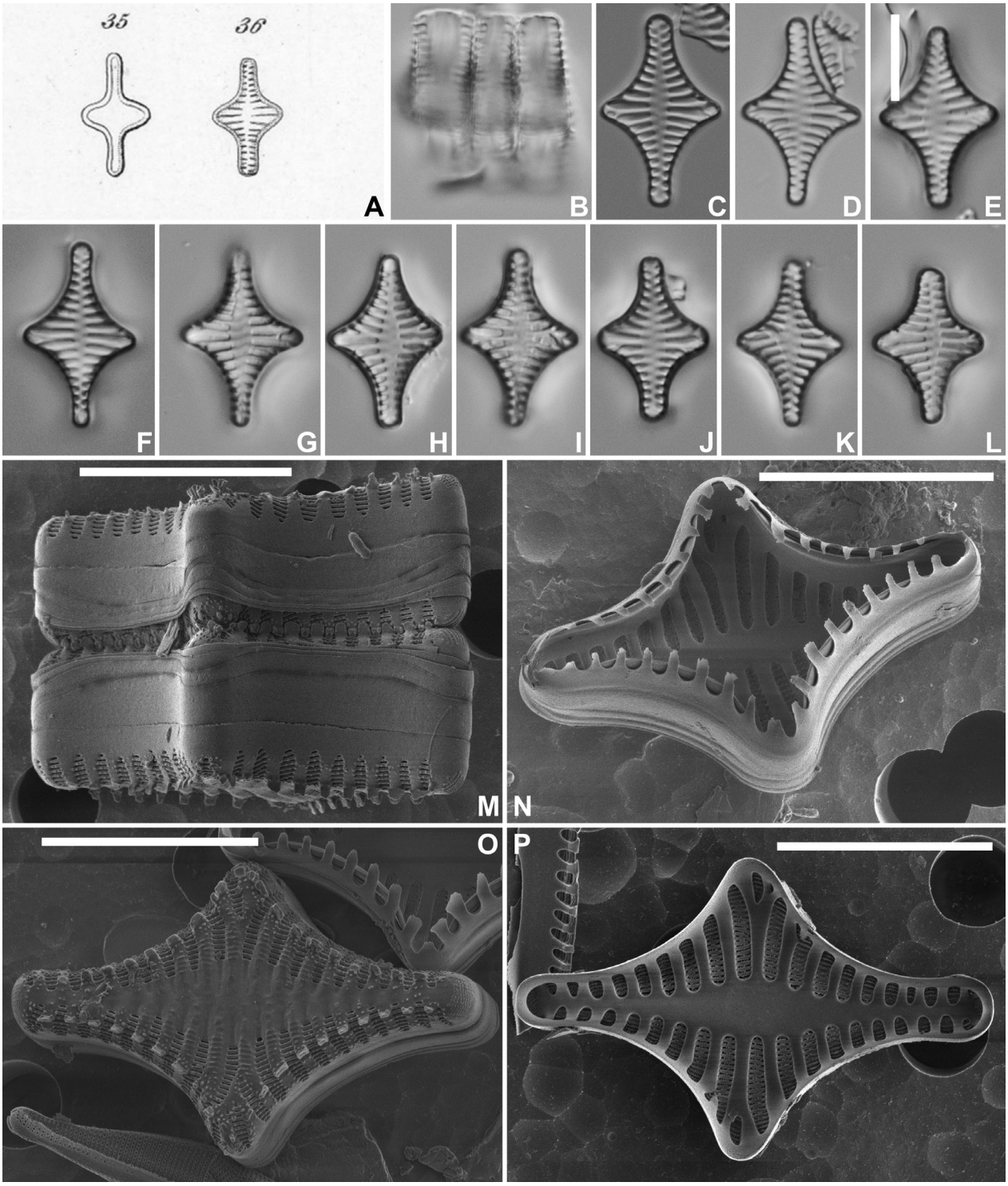

Figure 4. *Staurosirella leptostauron* (Ehrenb.) D.M.Williams & Round, LM and SEM micrographs taken from Grunow's Moosach sample (BR-4819, Moosach, Germany). **A**. Published images in Ehrenberg (1854: figs 35–36) after original drawing from C.G. Ehrenberg in BHUPM 2347. **B**. LM picture of three connected frustules in girdle view. **B**–**L**. LM pictures of valves in valve face view in decreasing length. **M**. SEM external view of two connected frustules in girdle view. **N**. SEM view of the valvocopula connected to the girdle showing the fimbriate extensions. Scale bar = 10 µm.

elongated, narrow, acutely rounded. Central inflation on both margins, acutely rounded. Valve dimensions (n = 25): length 15–23 µm, width 10–16 µm. Sternum broad, distinctly lanceolate, widened near the valve centre, often showing irregular markings (see for instance Fig. 4IK and N). Striae parallel to weakly radiate at the centre, becoming more radiate towards the apices, clearly wider than the virgae, ca 9 in 10 µm. Individual areolae only rarely discernible in LM. Figure 4A–L.

SEM description. Valve face not flat, showing clear topography with raised virgae and sternum and depressed striae. Distinct short, parallel ridges present on the virgae, in line with the vimines separating the linear areolae. In eroded valves, ridges less prominently present to even absent. Sternum often irregularly raised. Large, flattened, irregularly shaped marginal blunt spines placed on the virgae. Numerous, irregular, often very small granules present on the virgae between the spines and the vimines. Apical pore fields present on both apices, clearly different in size and shape, giving the valves an heteropolar appearance. Pore field at the footpole composed of more than 8 long rows of small, rounded to squarish pores. At the headpole, pore field smaller, with a maximum of 5–6 short rows of small pores. Observations of valve interior in the Moosach material showing typical finely branched volae (Fig. 4N). Valvocopula with well-developed fimbriae. Figure 4M–P.

Associated diatom flora. The Moosach population is quite diverse and dominated by taxa such as *Achnanthidium exile* (Kütz.) Heib., *Cocconeis pseudothumensis*, *Denticula kuetzingii* Grunow, *D. tenuis* Kütz., *Ellerbeckia arenaria* (Moore) Dorofeyuk & Kulikovskiy, *Eunotia alkalibiontica* Lange-Bert., *Grunowia tabellaria* (Grunow) Rabenh., *Odontidium mesodon* (Ehrenb.) Kütz., *Staurosirella neopinnata* E.Morales et al., *S. leptostauron* (Ehrenb.) D.M.Williams & Round, and various species of *Delicata*, *Cymbella*, and *Gomphonema*. This species composition is often found in oligo- to mesotrophic, calcium-bicarbonate enriched, alkaline conditions (Lange-Bertalot et al. 2017). In the Smith sample s.n. from Lough Dern (Scotland, United Kingdom), the dominant species include *Encyonopsis cesatii* (Rabenh.) Krammer, several smaller species of *Encyonopsis* and *Cymbella*, *Denticula tenuis*, and *Cymatopleura solea* (Bréb.) W.Sm. The Walker Arnott population from Redesdale, a valley in the western part of Northumberland, (northeast England, United Kingdom) presents a similar species composition with very high numbers of *Brachysira neoexilis*, *Delicata delicatula*, *Denticula tenuis*, *Eucocconeis flexella* (Kütz.) F.Meister, and *Fragilaria* cf. *amphicephaloides*. All analysed UK populations indicate alkaline, mesotrophic calcium-bicarbonate enriched lake conditions (Lange-Bertalot et al. 2017).

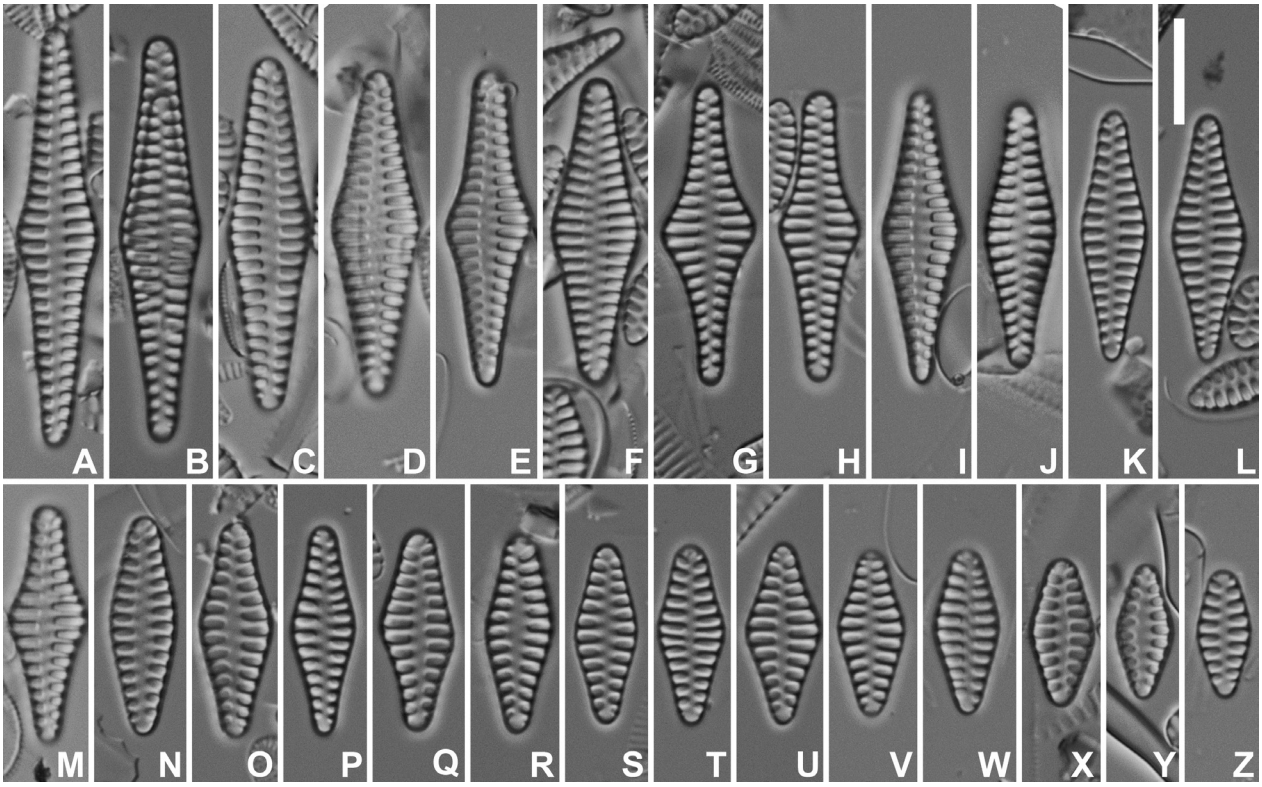

Figure 5. *Staurosirella moralesii* Van de Vijver, Jüttner & D.M.Williams sp. nov., LM micrographs taken from the type material (ANSP G.C 100049b, Willow Creek, United States). **A**–**Z**. LM pictures of valves in valve face view in decreasing length. Note the change in valve outline in the smaller valves. Scale bar = 10 µm.

Staurosirella moralesii Van de Vijver, Jüttner & D.M.Williams, **sp. nov.**

Figs 5, 6, Supplementary material 8

Type locality. Willow Creek, Waushara, Wisconsin, USA Western Lake Michigan Drainage study Unit, 1993 (ANSP G.C 100049b).
Holotype. ANSP G.C 100049b (Academy of Natural Sciences, Philadelphia). Figure 5F illustrates the holotype.
Registration. http://phycobank.org/103340
Analysed material. UNITED STATES • Willow Creek, WI; sample ANSP G.C 100049b, material kept at The Academy of Natural Sciences, Philadelphia, new slide deposited as BR-4826; BR, ANSP.
LM description. Valves almost isopolar, with a slightly larger footpole, rhombic throughout the entire cell diminution series. Larger specimens more elongated than smaller, more compact valves. Apices acutely rounded, not protracted. Valve dimensions (n = 25): length 10–40 µm, width 5–9 µm. Sternum variable, moderately broad, mostly lanceolate, to narrow and linear in some valves (Fig. 5T). Striae much broader than the virgae, parallel in the middle, becoming weakly radiate at the apices, 7–8 in 10 µm. Areolae not discernible in LM. Figure 5.
SEM description. Valve face irregular with weakly raised virgae bearing parallel very low ridges. Series of large, flattened marginal spines present on the virgae, due to erosion often split into several parts (Fig. 6B). In non-eroded valves, granules scattered all over valve mantle and the valve margin, usually located on the vimines (Fig. 6C). Striae composed of linear, slit-like areolae, separated by thin vimines. Striae much broader than the virgae. Areolae gradually diminishing in length towards the sternum and the valve face/mantle junction, widening again slightly on the mantle (Fig. 6A). Apical pore fields present on both apices. At the footpole, pore field rather

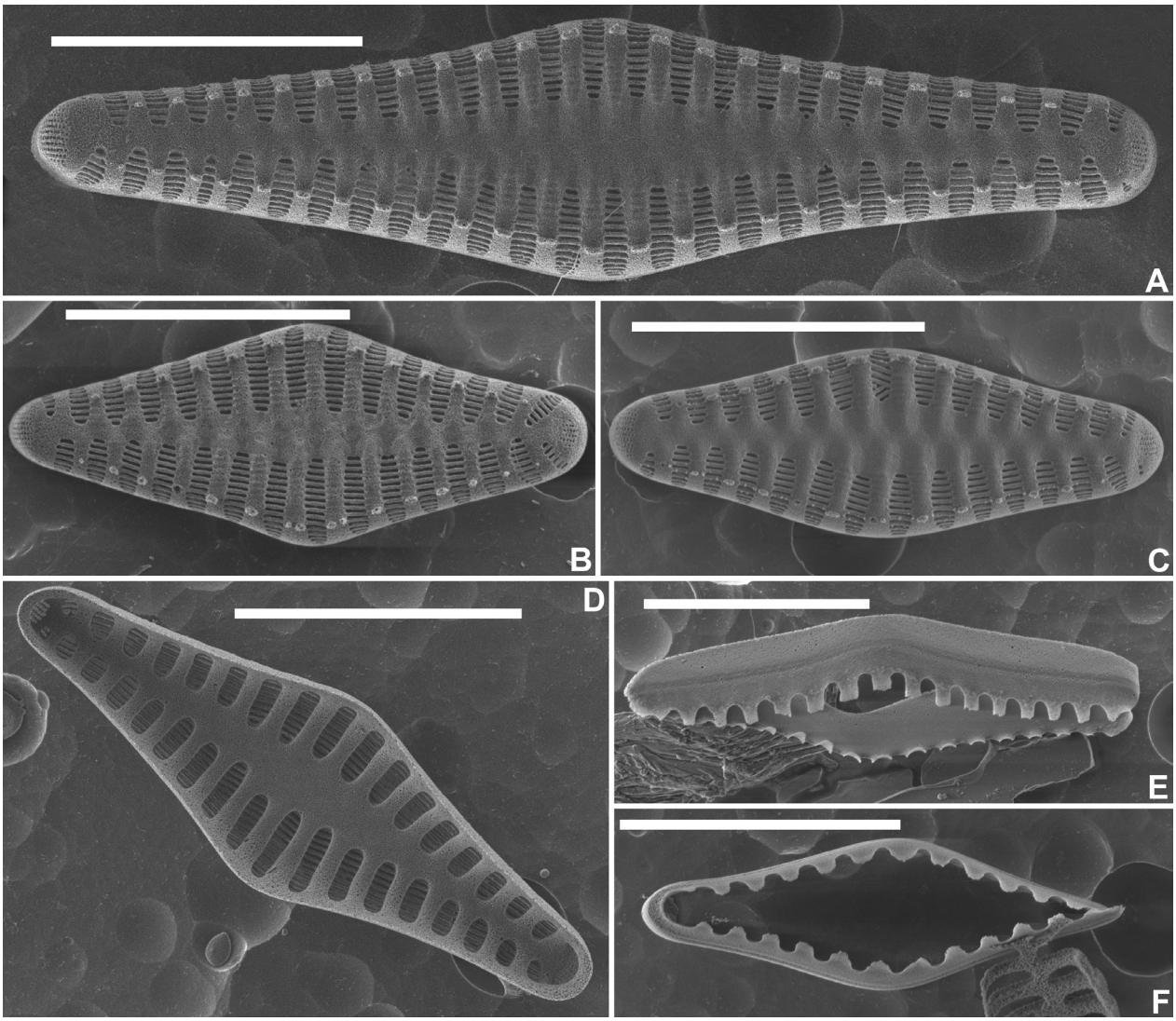

Figure 6. *Staurosirella moralesii* Van de Vijver, Jüttner & D.M.Williams sp. nov., SEM micrographs taken from the type material (ANSP G.C 100049b, Willow Creek, United States). **A**–**C**. SEM external view of three complete valves, showing the variation in the shape and size of the sternum, the differences in shape and size in apical pore field between head- and footpole. **D**. SEM internal view of a complete valve. **E**–**F**. SEM view of the valvocopula with the fimbriate extensions in oblique and frontal view. Scale bar = 10 µm.

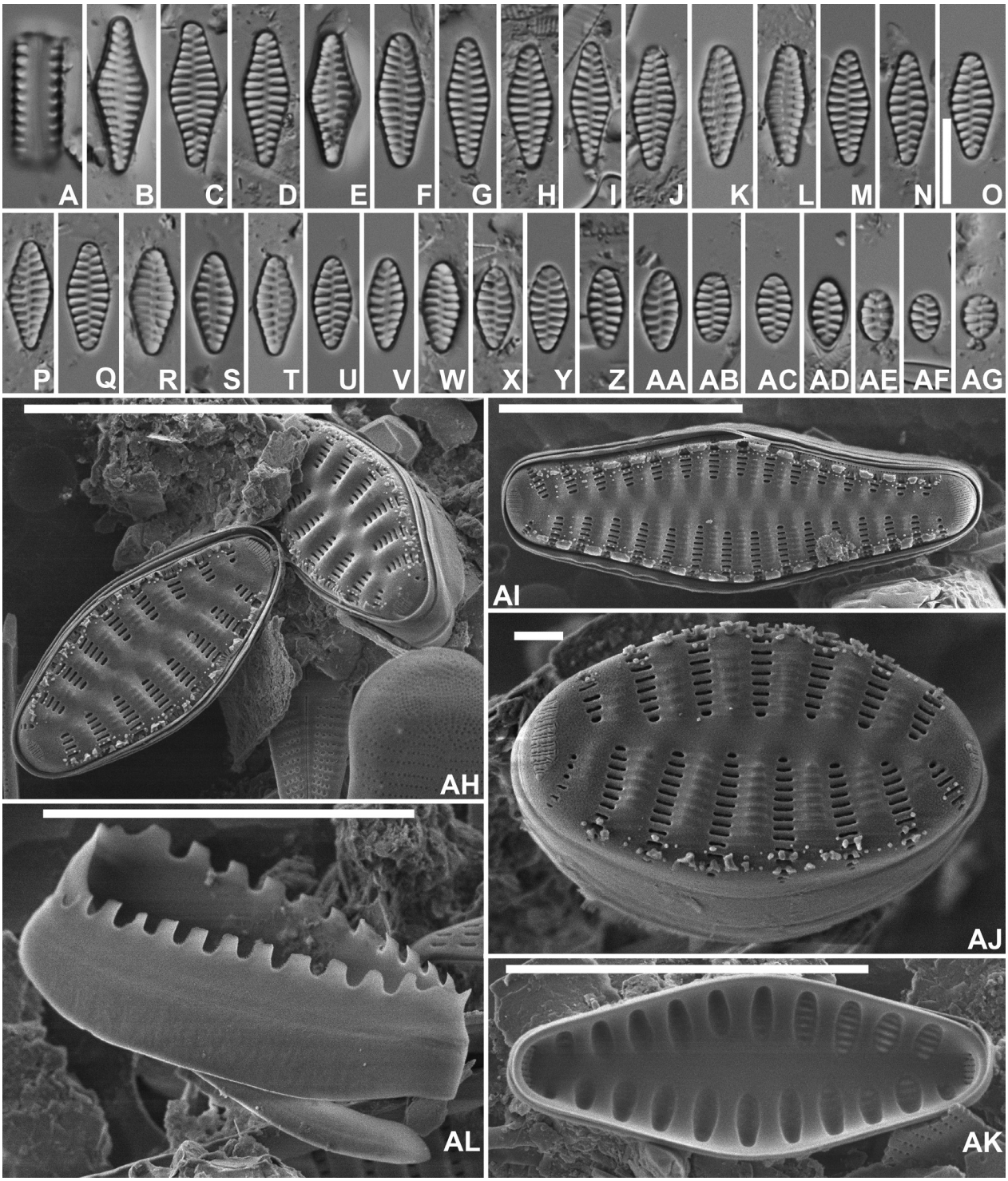

Figure 7. *Staurosirella neorhomboides* Van de Vijver & Jüttner sp. nov., LM and SEM micrographs taken from the type material (BR-4827, Killen Burn, United Kingdom). **A**. LM picture of a frustule in girdle view. **B**–**AG**. LM pictures of valves in valve face view in decreasing length. **AH**–**AJ**. SEM external view of several valves, clearly showing the irregular spines and papillae on the valve margins. **AK**. SEM internal view of a complete valve. **AL**. SEM view of the broad valvocopula with the fimbriate extensions. Scale bar = 10 µm (A–AI, AK–AL), 1 µm (AJ).

large, composed of at least 7 long rows of small, rounded pores, covering the entire foot pole (Fig. 6C). Pore field at the headpole smaller, located on the weakly depressed headpole (Fig. 6A–C). Internally sternum flat connected to the virgae (Fig. 6D). Apical pore fields clearly visible with a distinct difference in size between footpole (larger) and headpole (smaller), indicating the heteropolarity of the valves. Valvocopula with distinct fimbriae, often with dentated edge (although possibly a result of weak valve erosion) (Fig. 6E–F). Figure 6.

Etymology. The species is named after the late Dr Eduardo A. Morales (University of Evora, Portugal) who suddenly passed away in May 2023. Eduardo was a world-renowned specialist of the taxonomy and morphology of small-celled araphid genera and described many species in the genera *Staurosirella*.

Associated diatom flora. The Willow Creek sample is entirely dominated by several species of *Staurosirella*. Apart from *S. moralesii*, *S. ovata* E.Morales & Manoylov and *S. manoyloviana* had high relative abundances. However, Morales and Manoylov (2006b) pointed out that the low proportion of *S. moralesii* (reported as *S. rhomboides*) they observed was an indication that they did not have their optimal conditions in this river. In contrast, our observations of the type slide showed a rather high abundance of *S. moralesii*. According to Morales and Manoylov (2006b), Willow Creek in Wisconsin has relatively warm (19.5°C) and basic (pH 8.2) waters with medium conductivity (348 µS/cm), a nitrate and nitrite concentration of 1.20 mg/L, and an orthophosphate concentration of 0.10 mg/L. Other frequent species in the sample include *Amphora indistincta* Levkov, *Cocconeis pediculus* Ehrenb., *C. pseudothumensis*, *Geissleria acceptata* (Hust.) Lange-Bert. & Metzeltin, several species of *Gomphonema*, *Karayevia clevei* (Grunow) Bukht., *Navicula tripunctata* (O.F.Müll.) Bory, and *Psammothidium lauenburgianum* (Hust.) Bukht. & Round. Most of these species are characteristic for alkaline waterbodies with higher trophic levels (meso-eutrophic) (Lange-Bertalot et al. 2017).

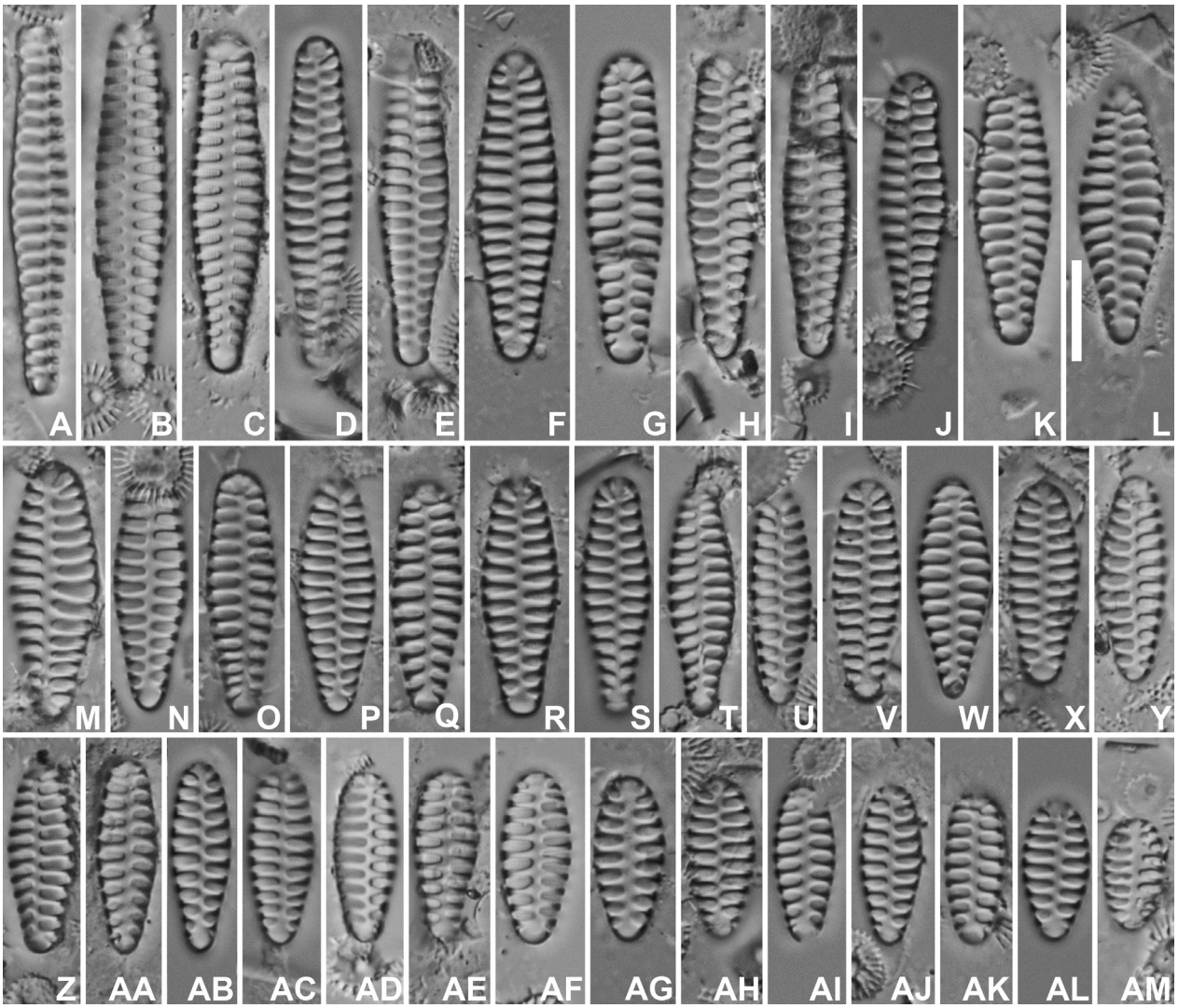

Figure 8. *Staurosirella martyi* (Hérib.) E.Morales & Manoylov, LM micrographs taken from the type material (BR-4829, Dépôt de Neussargues, Cantal, France). **A**–**AM**. LM pictures of valves in valve face view in decreasing length. Note the change in valve outline in the smaller valves. Scale bar = 10 µm.

Staurosirella neorhomboides Van de Vijver, Kusber & Jüttner, sp. nov.

Fig. 7

Type locality. Killen Burn, Highland, Scotland, UK.
Holotype. BR-4827 (Meise Botanic Garden, Belgium), slide made from original Killen Burn material. Figure 7G illustrates the holotype.
Isotype. Slide 435 (University of Antwerp, Belgium).
Analysed material. UNITED KINGDOM – **Scotland** • Killen Burn, Highland; slide BR-4827; BR.
Registration. http://phycobank.org/103341
LM description. Frustules rectangular in girdle view, solitary (Fig. 7A). Valves weakly heteropolar with slightly broader headpoles and more acute footpoles, rhombic-lanceolate in larger valves, becoming more strictly lanceolate to even elliptical in smaller specimens. Apices not protracted in smaller valves, cuneately to broadly rounded, elongated in longer specimens. Valve dimensions (n = 60): length 5–20 µm, width 3.5–7.0 µm. Sternum variable, moderately broad, lanceolate, slightly widened near the centre to very narrow, linear. Striae narrower than the virgae, weakly radiate throughout the entire valve, 9–10 in 10 µm. Areolae not discernible in LM. Figure 7A–AG.

SEM description. Sternum and virgae externally raised above the striae. Weakly raised parallel ridges present on the virgae. Single or double, irregularly shaped spines present on the virgae, with a large number of small granules present between the spines on virgae and vimines. Striae narrower than the virgae, composed of linear, slit-like areolae, separated by thin vimines. Areolae diminishing in length near the sternum. Both apices not depressed. Apical pore fields present on both apices, on the footpole larger than on the headpole. On the footpole, pore field composed of at least 7 long rows of small, rounded pores, covered by small, but distinct, silica plates. Valvocopula very large, plain, with distinct fimbriae. Internal areola occlusions formed by finely branched volae. Figure 7AH–AK.
Etymology. The specific epithet refers to *Staurosirella rhomboides* (now considered a synonym of *S. leptostauron*), the name that was used in the past to identify this species.
Associated diatom flora. The sample from Killen Burn is dominated by species of *Achnanthidium*, *Navicula lanceolata* (C.Agardh) Ehrenb., *N. tripunctata*, *Planothidium reichardtii* Lange-Bert. & Werum, and *Tabellaria flocculosa* (Roth) Kütz. with *Cocconeis pseudothumensis*, *Frustulia vulgaris* (Thwaites) De Toni, *Gomphonema exilissimum* (Grunow) Lange-Bert. &

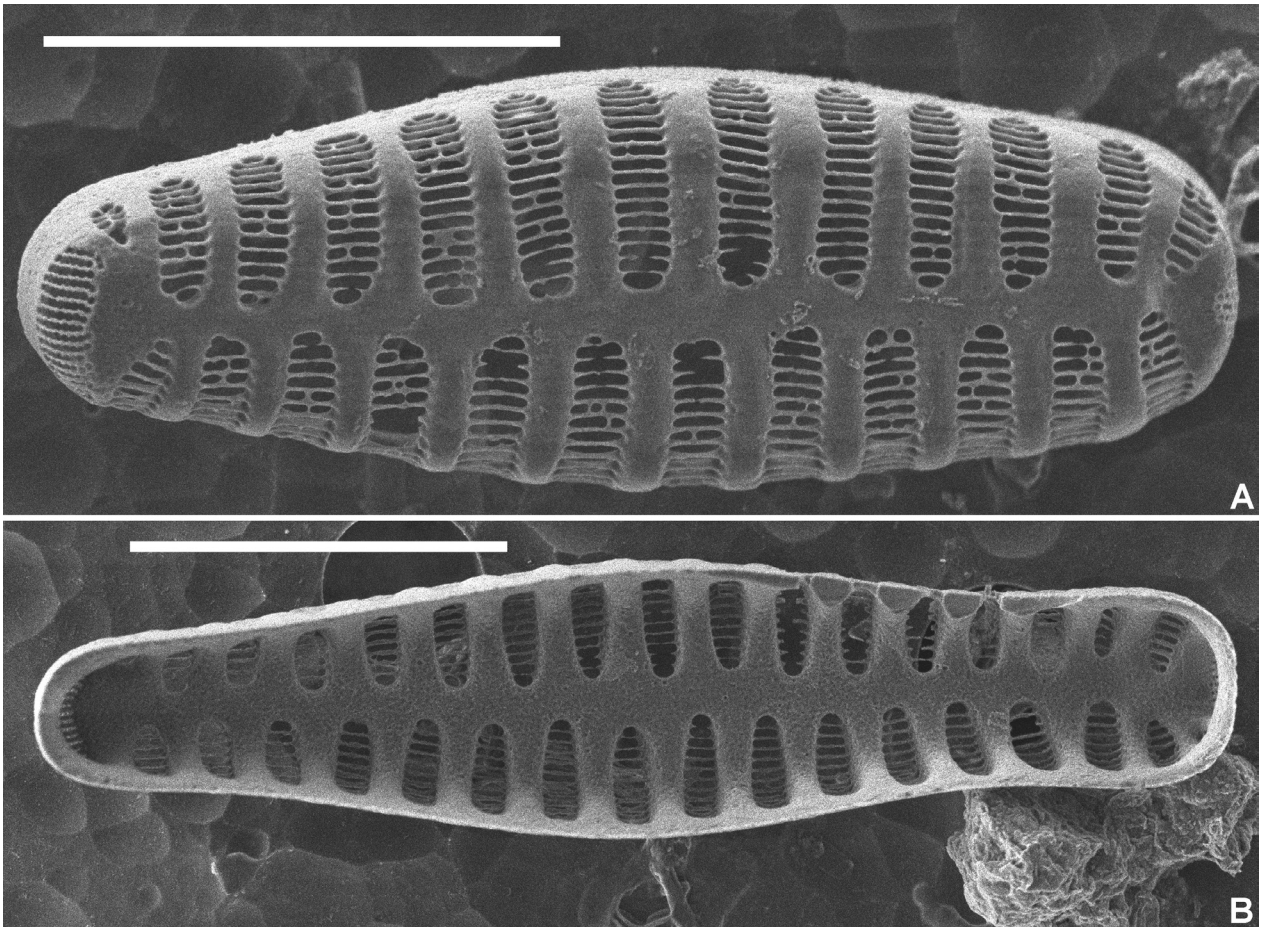

Figure 9. *Staurosirella martyi* (Hérib.) E.Morales & Manoylov, SEM micrographs taken from the (highly eroded) lectotype material (BR-4829, Dépôt de Neussargues, Cantal, France). **A**. SEM external view of an entire valve. **B**. SEM internal view of an entire valve. Scale bar = 10 µm.

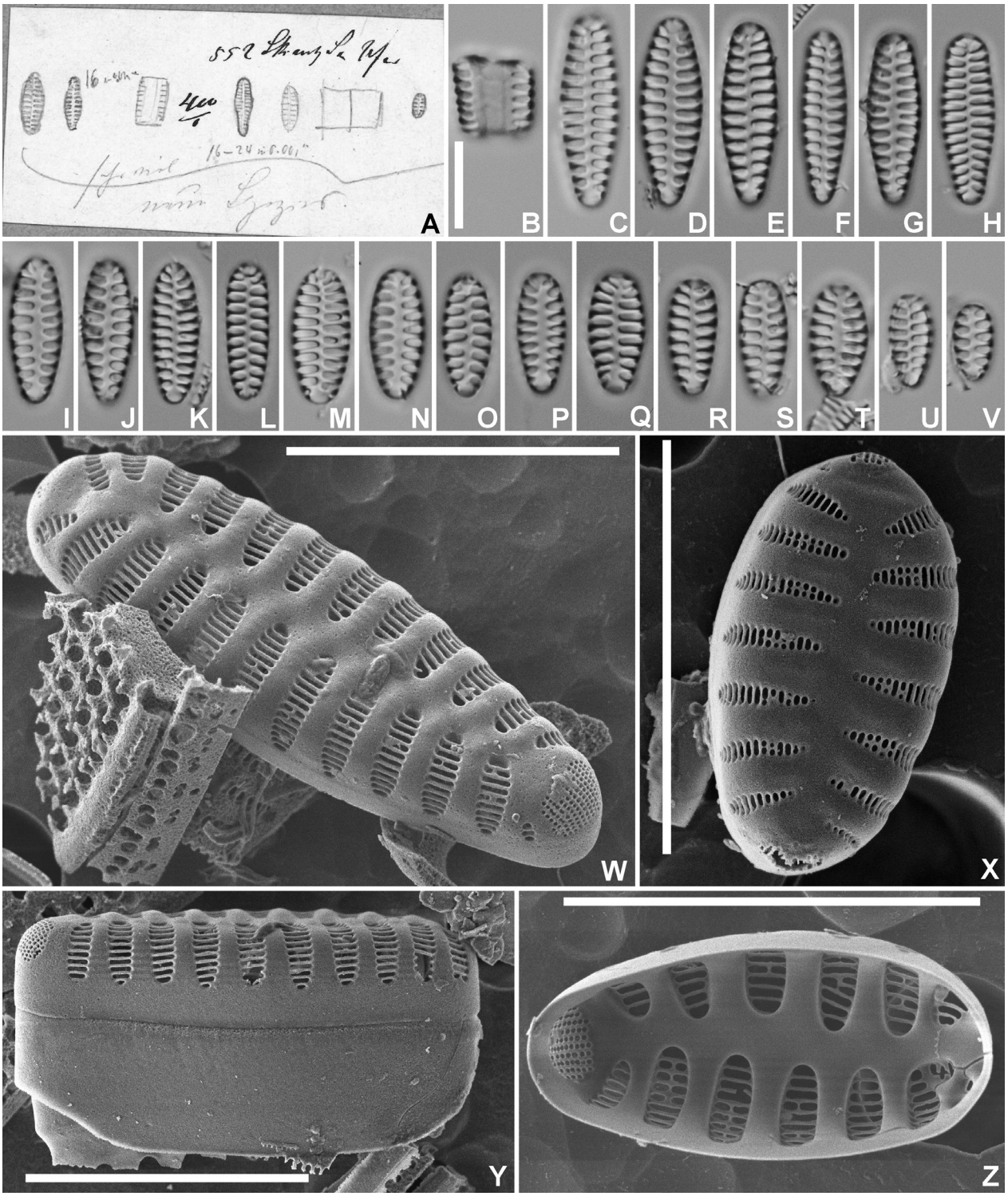

Figure 10. *Staurosirella martyi* (Hérib.) E.Morales & Manoylov, LM and SEM micrographs taken from the epitype material (BR-4828, Grunow sample 552, Stienitz See, Berlin, Germany). **A**. Original drawing from the Grunow Collection in W. **B**. LM picture of a frustule in girdle view. **C**–**V**. LM pictures of valves in valve face view in decreasing length. **W**–**X**. SEM external view of several valves. **Y**. SEM girdle view of a valve and its connected valvocopula. **Z**. SEM internal view of an entire view. Scale bar = 10 µm.

E.Reichardt, *Navicula gregaria* Donkin, *Planothidium lanceolatum* (Bréb.) Lange-Bert., and *Reimeria sinuata* (W.Greg.) Kociolek & Stoermer showing lower abundances. According to Lange-Bertalot et al. (2017) and Werum and Lange-Bertalot (2004), this community indicates alkaline, higher nutrient conditions.

Staurosirella martyi (Hérib.) E.Morales & Manoylov 2006b

Figs 8–11, Supplementary material 9

Opephora martyi Hérib., 1902 (**basionym**) (Héribaud 1902: 43)

Fragilaria harrisonii var. γ *dubia* (Grunow 1862: 368)

Staurosira harrisonii var. *dubia* (Grunow) Cleve (Cleve and Grunow 1880: 9)

Opephora martyi var. *capitata* Hérib. (Héribaud 1903: 30)

Opephora cantalense Hérib. (Héribaud 1903: 30)

Opephora cantalense var. *capitata* Hérib. (Héribaud 1903: 30)

Fragilaria mutabilis f. *martyi* (Hérib.) A.Cleve (Cleve-Euler 1932: 23)

Martyana martyi (Hérib.) Round (Round et al. 1990: 673)

Fragilaria martyi (Hérib.) Lange-Bert. (Lange-Bertalot 1993: 46)

Staurosirella leptostauron var. *dubia* (Grunow) Edlund (Edlund 1994: 12)

Staurosira martyi (Hérib.) Lange-Bert. (Krammer and Lange-Bertalot 2000: 586)

Staurosirella dubia (Grunow) E.Morales & Manoylov (Morales et al. 2010a: 43)

Staurosira dubia Grunow, nom. inval. (Cleve and Möller 1879: no. 270–271)

Type locality. Dépôt de Neussargues, sample collected between the train station and L'Allagnon (Héribaud 1902: 41), Cantal, France.

Epitype locality. Grunow sample 552, "zwischen *Aegagropila Sauteri* aus dem Stienitz See bei Berlin" (Leg. amic. Reinhardt), material conserved at W! Two samples of cleaned material (W0164812 and W0164813, the latter sampled) are filed in the general collection under *Fragilaria intermedia*.

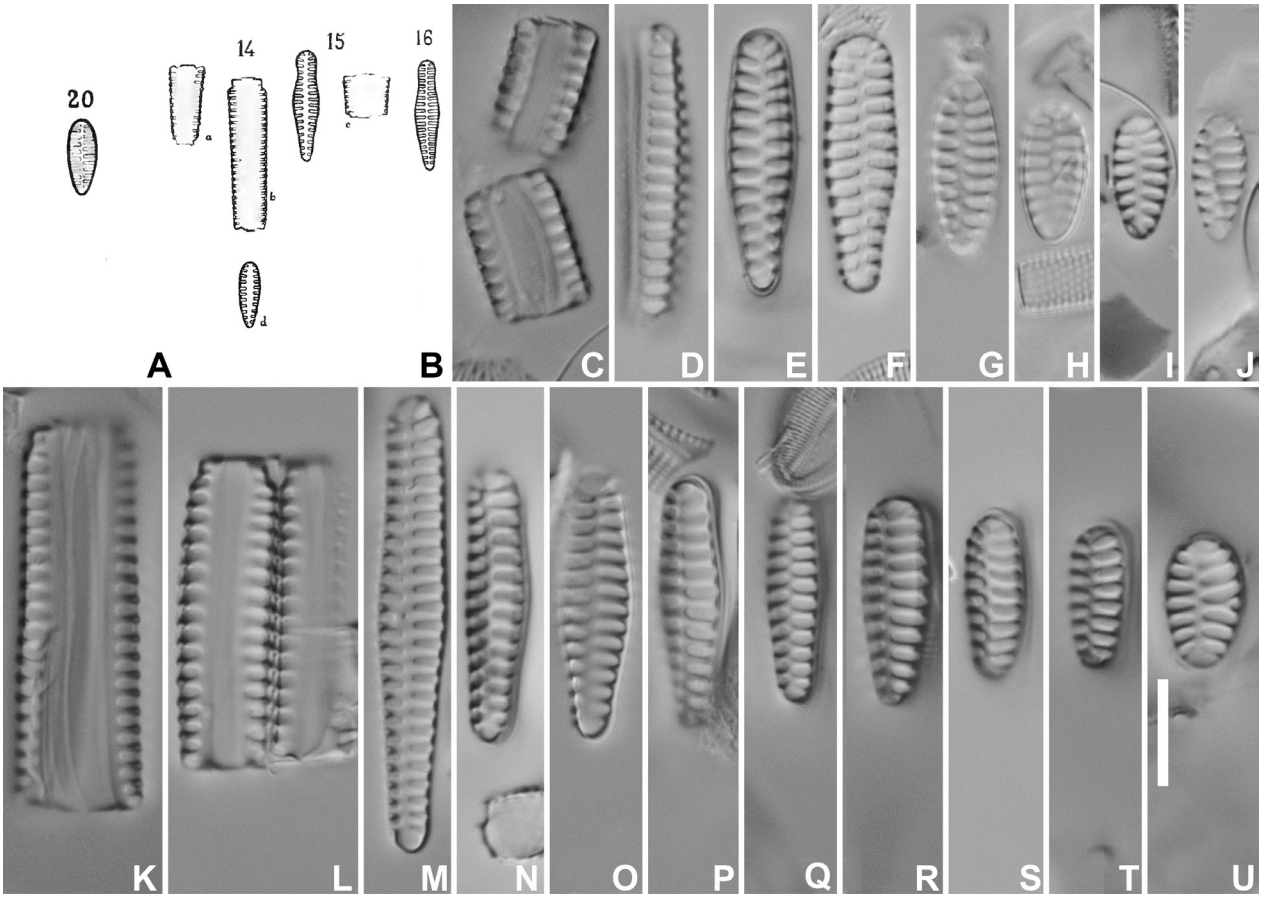

Figure 11. *Staurosirella martyi* (Hérib.) E.Morales & Manoylov, LM micrographs taken from the original material for *Opephora cantalense* Hérib. (C–J) and *O. cantalense* var. *capitata* (K–U) (BM68398, Dépôt de Joursac, Cantal, France). **A**–**B**. Original drawings from Héribaud (1903) representing *O. cantalense* and *O. cantalense* var. *capitata*. **C**–**D**. LM picture of a frustule and valve in girdle view of *O. cantalense*. **E**–**J**. LM pictures of valves in valve face view in decreasing length. **K**–**L**. LM picture of a frustule and valve in girdle view of *O. cantalense* var. *capitata*. **M**–**U**. LM pictures of valves in valve face view in decreasing length. Scale bar = 10 μm.

Lectotype (designated here). BR-4829, slide made from Héribaud sample Dépôt de Neussargues. Figure 8C illustrates the lectotype.

Epitype (designated here for the above selected lectotype). BR-4828, slide made from Grunow sample 552. Figure 10D illustrates the epitype.

Registration. http://phycobank.org/103844

Analysed material. FRANCE • Dépôt de Neussargues, sample collected between the train station and l'Allagnon, Cantal, France; slide BR-4829; BR • Dépôt de Joursac, Cantal, France, slide Collection Tempère & Peragallo (2^{e} edition) BM 68398; BM • zwischen *Aegagropila Sauteri* aus dem Stienitz See bei Berlin; leg. amic. Reinhardt; Grunow sample 552, slides BR-4828, W0164812 and W0164813; BR, W.

UNITED KINGDOM • Ormesby, Norfolk; 10 Apr. 1853; leg. M. Bridgeman, Smith sample s.n., slide BR-4830; BR.

LM description. Frustules rectangular in girdle view, solitary, band-like colonies at present not observed. Valves heteropolar, larger valves with clear constriction between valve middle and headpole, smaller valves ovoid in shape. Headpole broadly rounded, and more acute footpole. Valve outline lanceolate in larger valves, elliptic to elliptic-lanceolate in smaller valves. Valve dimensions (n = 40): length 9–38 µm, width 5–10 µm. Sternum narrow to moderately broad, linear to lanceolate. Striae broad, wider than the virgae, parallel in the middle becoming gradually weakly radiate towards the apices, 6–7 in 10 µm. Individual areolae often discernible in LM (Fig. 8B, C). Figure 8.

SEM description. Headpole clearly depressed. Sternum and vimines externally weakly raised above the striae. Areolae linear, slit-like, separated by narrow vimines, the latter occasionally interconnected subdividing the areolae in two or three smaller areolae. Spines absent. Apical pore

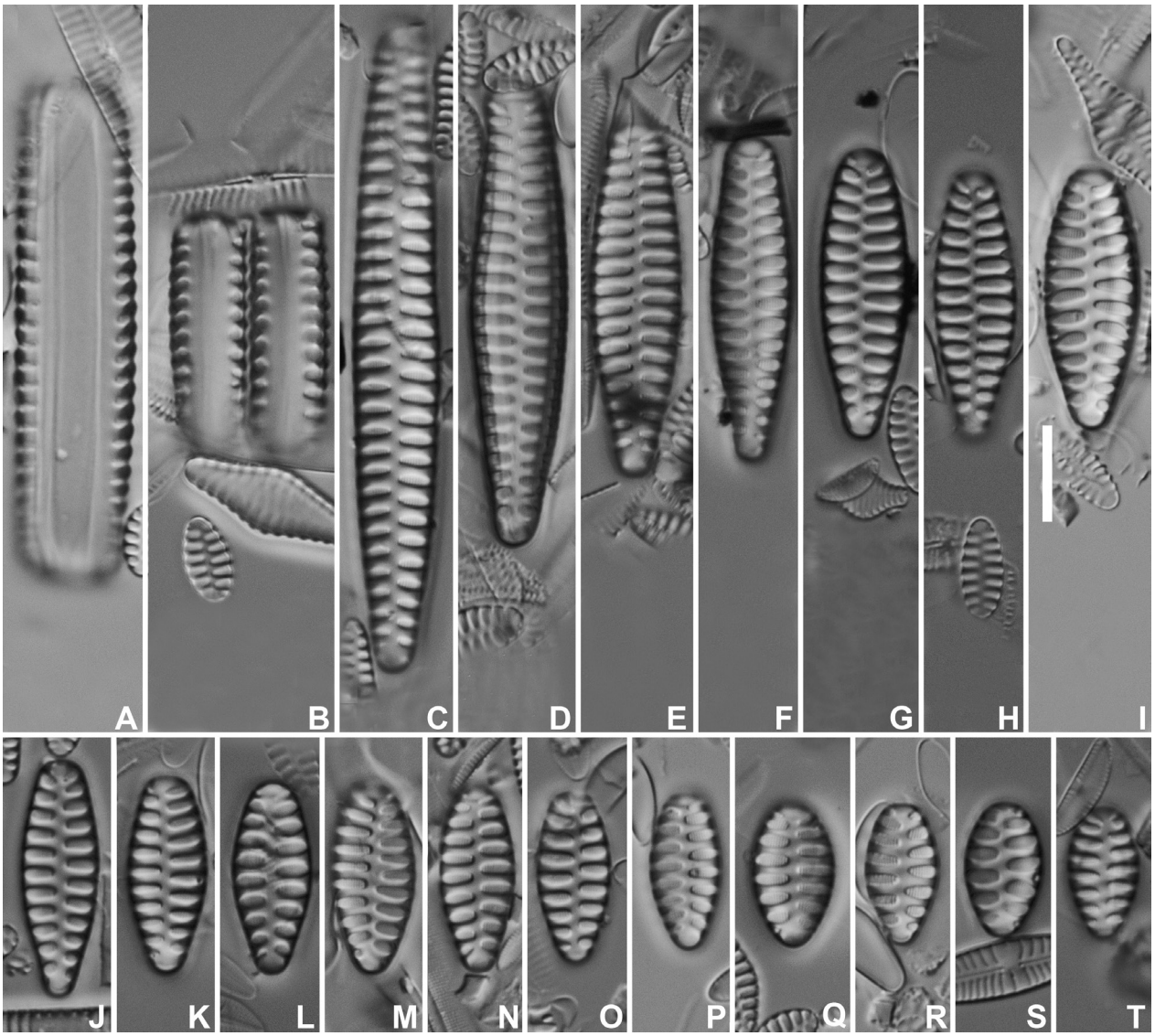

Figure 12. *Staurosirella manoyloviana* Van de Vijver, Jüttner & D.M.Williams sp. nov., LM micrographs taken from the type material (ANSP G.C 100049b, Willow Creek, United States). **A**–**B**. LM pictures of two frustules in girdle view. **C**–**T**. LM pictures of valves in valve face view in decreasing length. Note the change in valve outline in the smaller valves. Scale bar = 10 µm.

field at footpole very large, composed of more than eight long rows of small, rounded to squarish pores, extending from valve face to mantle. Apical pore field much smaller at headpole, restricted to a compact group of a few small pores. Internally, small pseudoseptum present at footpole contrary to headpole lacking pseudoseptum. Internal areola occlusions eroded due to age of material (Miocene), making observations not possible. Valvocopula very large, plain, open. Figure 9.

Associated diatom flora. Héribaud (1902) listed several species of *Navicula* for the Dépôt de Neussargues including *Navicula bouhardi* Hérib., *N. dariana* var. *miocenica* Hérib. & Perag., *N. malinvaudi* Hérib., *N. sculpta* Ehrenb. together with *Eunotia gracilis* var. *capitata* Perag. & Hérib. and *Melosira boulayana* Perag. These species are most likely all extinct and their ecological preferences are currently not known. The epitype sample (Grunow sample 552) is almost entirely dominated by araphid species. *Fragilaria vaucheriae* (Kütz.) J.B.Petersen is the most frequently observed, followed by *Staurosira* cf. *binodis* (Ehrenb.) Lange-Bert., *Gomphonema capitatum* Ehrenb., *Nitzschia amphibia* Grunow, and *Pinnularia brebissonii* (Kütz.) Rabenh. Based on Lange-Bertalot et al. (2017), these species are usually found in alkaline water bodies with moderate to higher electrolyte contents and higher trophic levels.

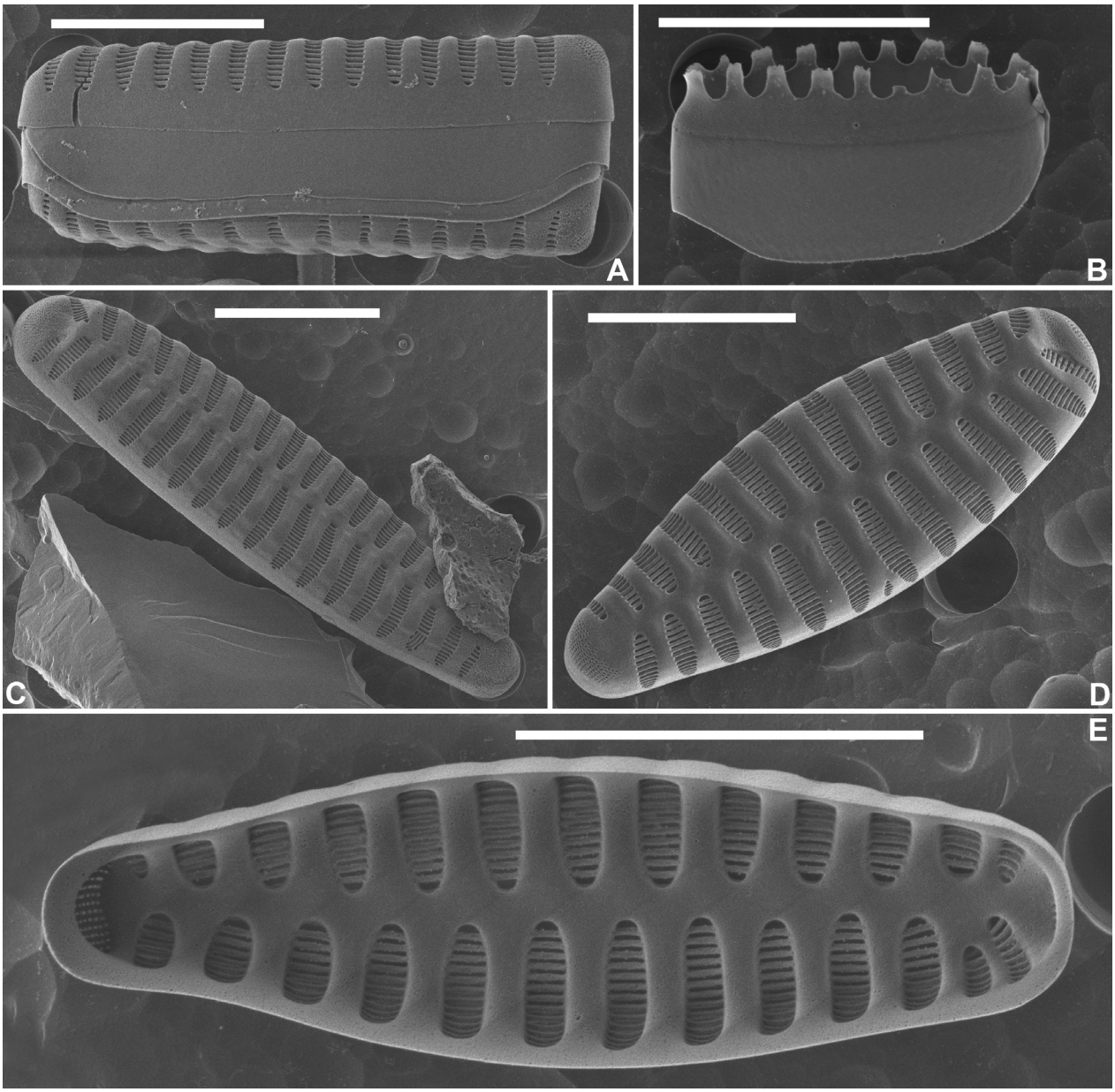

Figure 13. *Staurosirella manoyloviana* Van de Vijver, Jüttner & D.M.Williams sp. nov., SEM micrographs taken from the type material (ANSP G.C 100049b, Willow Creek, United States). **A**. SEM view of a frustule in girdle view. **B**. SEM view of the valvocopula with the fimbriate extensions. **C**–**D**. SEM external view of two complete valves. **E**. SEM internal view of a complete valve. Scale bar = 10 µm (C–E), 5 µm (A–B).

Staurosirella manoyloviana Van de Vijver, Jüttner & D.M.Williams, **sp. nov.**

Figs 12–13

Type locality. Willow Creek, Waushara, Wisconsin, USA, Western Lake Michigan Drainage study Unit, 1993 (ANSP G.C 100049b).

Holotype. ANSP G.C 100049b (Academy of Natural Sciences, Philadelphia). Figure 12E illustrates the holotype.

Registration. http://phycobank.org/103342

Analysed material. UNITED STATES • Willow Creek, WI; sample ANSP G.C 100049b, material kept at The Academy of Natural Sciences, Philadelphia, new slide made BR-4826; BR.

LM description. Frustules rectangular in girdle view, solitary or in pairs, band-like colonies at present not observed. Valves distinctly heteropolar, ovoid in shape throughout the entire cell diminution series. Larger valves slightly more elongated. Headpole not protracted, broadly rounded. Footpole more acutely rounded. Valve dimensions (n = 20): length 15–70 µm, width 8–10 µm. Sternum narrow, linear, very rarely lanceolate. Striae as broad as, or narrower than the virgae, alternating, parallel throughout to weakly radiate towards the apices, 5–6 in 10 µm. Individual areolae clearly discernible in LM. Figure 12.

SEM description. Observations based on Morales and Manoylov (2006b: figs 102–103). Headpole depressed. Marginal spines absent. Striae composed of linear, slit-like areolae, separated by very thin vimines. Areolae only weakly diminishing in length near the sternum. Apical pore fields present on both apices, much larger on the footpole, the latter composed of 5– 7 long rows of small, rounded pores, entirely situated on the valve mantle. Valvocopula very large, plain. Figure 13.

Etymology. The species is named after Prof. Dr Kalina Manoylov (Georgia College, USA), co-author of Morales and Manoylov (2006b) discussing several species of *Staurosirella*.

Associated diatom flora. The Willow Creek sample is entirely dominated by several species of *Staurosirella*. Apart from *S. manoyloviana*, *S. ovata* and *S. moralesii* had high relative abundances, with *S. manoyloviana* being the least abundant. Morales and Manoylov (2006b) state that Willow Creek in Wisconsin is relatively warm

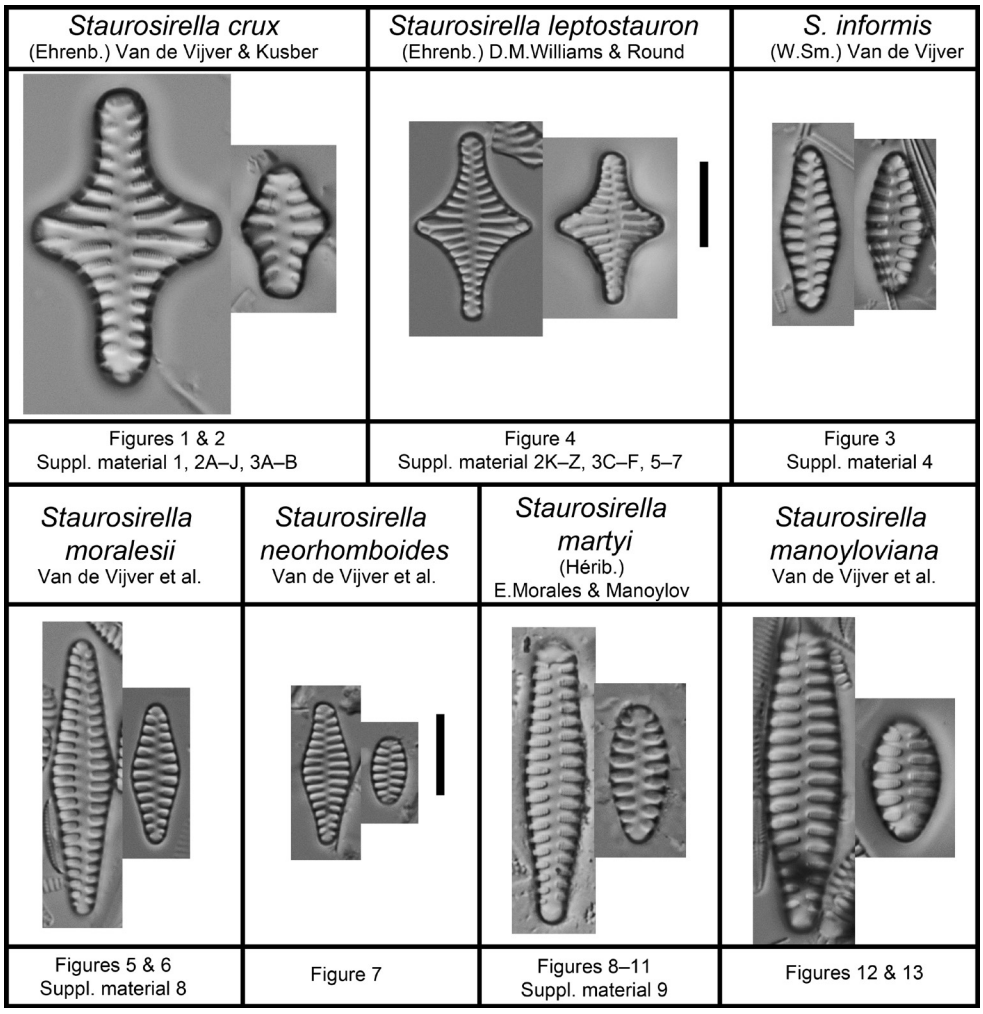

Figure 14. Selected largest and smallest valves of al *Staurosirella* taxa in LM, discussed in this paper. Images from original material. The Figures and Supplementary materials numbers indicate all illustrations of the species. Scale bars = 10 µm.

(19.5°C) and basic (pH 8.2) and has medium conductivity (348 µS/cm), a nitrate and nitrite concentration of 1.20 mg/L, and an orthophosphate concentration of 0.10 mg/L. Other frequent species in the sample include *Amphora indistincta*, *Cocconeis pediculus*, *C. pseudothumensis*, *Geissleria acceptata*, several species of *Gomphonema*, *Karayevia clevei*, *Navicula tripunctata*, and *Psammothidium lauenburgianum*. Most of these species are characteristic for alkaline waterbodies with higher trophic levels (meso-eutrophic) (Lange-Bertalot et al. 2017).

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SUPPLEMENTARY MATERIALS

Supplementary material 1

Staurosirella crux (Ehrenb.) Van de Vijver & Kusber comb. nov., LM micrographs taken from Grunow's Moosach sample (BR-4819, Moosach, Germany). **A**–**E**. LM pictures of valves in valve face view in decreasing length. **F**. SEM external view of a complete valve. **G**. SEM internal view of a complete valve. Scale bar = 10 µm.
https://doi.org/10.5091/plecevo.119907.suppl1

Supplementary material 2

Staurosirella crux (Ehrenb.) Van de Vijver & Kusber comb. nov. (A–J, left specimen), and *S. leptostauron* (Ehrenb.) D.M.Williams & Round (J–Z, right specimen). LM micrographs taken from Kützing's Moosach sample 921 (BR-4820, Moosach, Germany). **A**–**J**. LM pictures of valves in valve face view in decreasing length of *S. crux*. **J**–**Z**. LM pictures of valves in valve face view in decreasing length of *S. leptostauron*. Scale bar = 10 µm.
https://doi.org/10.5091/plecevo.119907.suppl2

Supplementary material 3
Staurosirella crux (Ehrenb.) Van de Vijver & Kusber comb. nov. (A–B), and *S. leptostauron* (Ehrenb.) D.M.Williams & Round (C–F). SEM micrographs taken from Kützing's Moosach sample 921 (BR-4820, Moosach, Germany). Note the structural differences between both species. **A**. SEM external view of a complete valve of *S. crux*. **B**. SEM internal view of a complete valve of *S. crux*. **C**–**D**. SEM external view of two complete valves of *S. leptostauron*. **E**. SEM view of the valvocopula with the fimbriate extensions. **F**. SEM internal view of a complete valve of *S. crux*. Scale bar = 10 µm.
https://doi.org/10.5091/plecevo.119907.suppl3

Supplementary material 4
Staurosirella informis (W.Sm.) Van de Vijver comb. nov. LM and SEM micrographs taken from Walker Arnott's sample S445 (BR-4823 Redesdale, Hermits Well, United Kingdom). **A**. LM picture of three connected frustules in girdle view. **B**–**T**. LM pictures of valves in valve face view in decreasing length. **U**. SEM external view of a complete valve. **V**. SEM external detail of the valve apices of a complete frustule. **W**. SEM external view of the valve apex showing the apical pore field. **X**. SEM internal view of a complete valve. Scale bar = 10 µm (A–U, W–X), 5 µm (V).
https://doi.org/10.5091/plecevo.119907.suppl4

Supplementary material 5
Staurosirella leptostauron (Ehrenb.) D.M.Williams & Round, LM and SEM micrographs taken from Smith's original sample for *Odontidium harrisonii* var. β (BR-4824, Burnham, United Kingdom). **A**. Original drawing from Smith (1856: fig. 374). **B**–**H**. LM pictures of valves in valve face view in decreasing length. **I**. SEM external view of a complete valve. **J**. SEM view of the valvocopula with the fimbriate extensions. Scale bar = 10 µm.
https://doi.org/10.5091/plecevo.119907.suppl5

Supplementary material 6
Staurosirella leptostauron (Ehrenb.) D.M.Williams & Round, LM and SEM micrographs taken from Smith's original sample for *Odontidium harrisonii* var. β (BR-4825, Lough Dern, United Kingdom). **A**. Original drawing from Smith (1856: fig. 374). **B**–**O**. LM pictures of valves in valve face view in decreasing length. **P**. SEM external view of a complete valve. **Q**. SEM internal view of an entire valve. Scale bar = 10 µm.
https://doi.org/10.5091/plecevo.119907.suppl6

Supplementary material 7
Staurosirella leptostauron (Ehrenb.) D.M.Williams & Round, LM and SEM micrographs taken from Walker Arnott's sample S445 (BR-4823, Redesdale, Hermits Well, United Kingdom). **A**–**O**. LM pictures of valves in valve face view in decreasing length. **P**. SEM external view of a complete valve. **Q**. SEM internal view of an entire valve. Scale bar = 10 µm.
https://doi.org/10.5091/plecevo.119907.suppl7

Supplementary material 8
Staurosirella moralesii Van de Vijver, Jüttner & D.M.Williams sp. nov., LM micrographs taken from the type material (ANSP G.C 100049b, Willow Creek, United States). **A**–**L**. LM pictures of several very large valves. Scale bar = 10 µm.
https://doi.org/10.5091/plecevo.119907.suppl8

Supplementary material 9
Staurosirella martyi (Hérib.) E.Morales & Manoylov, LM and SEM micrographs taken from Smith's material of Ormesby (BR-4830, Ormesby, United Kingdom). **A**–**B**. LM pictures of two frustules in girdle view. **C**–**Z**. LM pictures of valves in valve face view in decreasing length. **AA**. SEM external view of a complete valve. **AB**. SEM external detail of the footpole showing the large apical pore field. **AC**. SEM internal view of an entire valve. **AD**. SEM view of the valvocopula with the fimbriate extensions. Scale bar = 10 µm (A–AC), 1 µm (AD).
https://doi.org/10.5091/plecevo.119907.suppl9