Unraveling the identity of *Fragilaria pinnata* Ehrenberg and *Staurosira pinnata* Ehrenberg: research in progress on a convoluted story

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Abstract – *Fragilaria pinnata* Ehrenberg is one of the most commonly reported taxa in floristic and ecological works from around the world. Yet, the images published for this taxon reveal that its identity is not well defined and that several morphological variants have been ascribed to it. The present manuscript includes a preliminary analysis of the literature and type material housed in the Ehrenberg Collection, Berlin, Germany. The nomenclatural history of the taxon, a critical examination of original drawings, and results of the examination of type material lead to the conclusion that *Fragilaria pinnata* (current synonym: *Staurosirella pinnata* (Ehrenberg) D.M.Williams & Round) is not an araphid diatom, but rather an organism with links to the genus *Denticula* Kützing. The history of another taxon, *Staurosira pinnata* Ehrenberg, was also investigated to determine its actual relationship to *Fragilaria pinnata* since recent publications present these two names as synonyms. *Staurosira pinnata* also has an entangled history and a dubious current concept. Although, we have not examined type material for this taxon yet, based on examination of the nomenclatural history and original drawings, we were able to conclude that it is indeed an araphid diatom, but that the current synonymy with *Fragilaria pinnata* is incorrect.

Diatoms / Bacillariophyceae / Fragilaria pinnata / Staurosira pinnata / Denticula / Nomenclature / taxonomy / species concept drift

Résumé – *Fragilaria pinnata* Ehrenberg est l'un des taxons les plus communément répertoriés dans les travaux floristiques et écologiques. Cependant, les images publiées pour ce taxon révèlent que son identité n'est pas bien définie et que plusieurs variantes morphologiques lui ont été attribuées. Notre étude inclut une analyse préliminaire de la littérature et du matériel type conservé dans la collection d'Ehrenberg à Berlin en Allemagne. L'histoire nomenclaturale de ce taxon, un examen critique des dessins originaux et les résultats de l'examen du matériel type permettent de mener à la conclusion que *Fragilaria pinnata* (synonyme actuel : *Staurosirella pinnata* (Ehrenberg) D.M.Williams et Round) n'est pas une diatomée araphidée, mais plutôt un organisme lié au genre

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Denticula Kützing. L'histoire d'un autre taxon, Staurosira pinnata Ehrenberg, a également été étudiée afin de déterminer ses liens avec Fragilaria pinnata étant donné le fait que de récentes publications présentent ces deux noms comme étant des synonymes. Staurosira pinnata a également une histoire compliquée et un concept actuel douteux. Bien que nous n'ayons pas encore examiné le matériel type de ce taxon, sur la base d'un examen approfondi de l'histoire nomenclaturale et des dessins originaux, nous sommes en mesure de pouvoir conclure qu'il s'agit de fait d'une diatomée araphidée, mais que la synonymie avec Fragilaria pinnata est incorrecte.

Diatomées / Bacillariophyceae / Fragilaria pinnata / Staurosira pinnata / Denticula / Nomenclature / taxonomie / dérive du concept spécifique

INTRODUCTION

In recent years, a number of publications appeared concentrating on the study of type material to clarify the identity of several diatom taxa, especially of those that are frequently reported in the ecological literature. With increased use of diatoms as indicators of ecosystem health, establishing the identity of at least the most common taxa could improve the accuracy of ecological diagnostic tools relying heavily on the most inclusive taxonomic categories as the basic units expressing environmental change.

Araphid diatoms are frequent components of freshwater planktonic and benthic communities and are often reported as important indicators expressing past (e.g., Servant, 1970; Watchorn et al., 2008) and recent (e.g., Kawecka & Robinson, 2008; Karst-Riddoch et al., 2009) changes in aquatic systems. Species in genera formerly associated to Fragilaria Lyngbye, e.g., Staurosirella D.M.Williams et Round, Fragilariforma D.M.Williams et Round, Punctastriata D.M.Williams et Round, etc. (Williams & Round, 1987) are backed by a rather extensive number of published images. However, lack of taxonomic consistency is evident from these illustrations. A quick compilation of images of Fragilaria pinnata Ehrenberg or its current synonym Staurosirella pinnata (Ehrenberg) D.M.Williams et Round, for example, puts in evidence that the concept of this taxon is not well defined and that at least (conservatively) half a dozen morphological variants have been assigned this particular name. Compare, for example, scanning and transmission electron microscopy images in the references listed under "Fragilaria pinnata" in Gaul et al. (1993) and Henderson & Reimer (2003).

The case of *Staurosira pinnata* Ehrenberg is also confusing and the current interpretation of this name and the organism to which it should be applied is not clear from the literature. It suffices to trace the nomenclatural history of this taxon in the Catalogue of Diatom Names (2011) and in Guiry & Guiry (2011) to see that this name is currently associated with two different accepted genera: *Dimeregramma* Ralfs and *Staurosira* Ehrenberg. What is more, *Staurosira pinnata* is now being used in some current literature as a synonym of *Fragilaria pinnata*, see, for example, Schmidt *et al.* (2004).

As part of a larger research project focusing on the study of type material of key diatom taxa from collections around the world and a palaeoenvironmental assessment in an Argentinian Andean lake, we began investigating precisely the case of *Fragilaria/Staurosirella pinnata*. We write this contribution to show that the process of unraveling the identity of a taxon is not always straightforward

and that matters are complicated by species concept drift (the change in the original concept of a taxon over time or the continuous change and broadening of original descriptions of certain species; i.e., the constant broadening of the original diagnosis to fit aberrant populations). This phenomenon appears deeply rooted and fairly widespread in diatom taxonomy (Van de Vijver *et al.*, 2009, 2010).

MATERIALS AND METHODS

One of us (JMG) visited the Ehrenberg collection housed in the *Institut für Paläontologie, Museum für Naturkunde* in Berlin and had the chance to inspect part of the micas containing material identified by Ehrenberg as including specimens of *Fragilaria pinnata*. Ehrenberg (1843) explicitly designated (p. 415, using an exclamation mark at the end of the protologue) a gathering from "Moctezuma Flüss", México, Sample 1229 as type material and drew several frustules and valves, which now constitute the iconotype of *F. pinnata* (pl. 3 (6), figs 8 a-e; illustrated here in Figs 1a-e). Ehrenberg prepared with this material several micas arranged in strips. The strips and micas analyzed for the present work were:

- Mica strip 20-04-01: micas 3, 4, and 5, and
- Mica strip 20-04-02: micas 2 and 4.

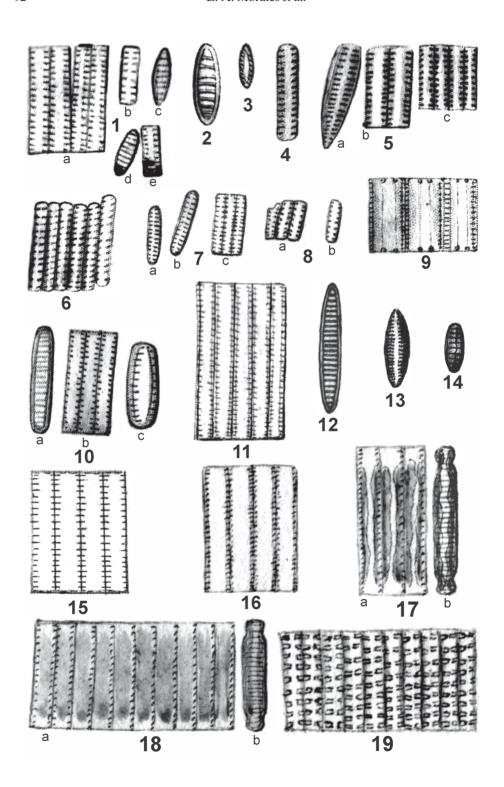
Photographs were taken at 400X using an Olympus BX51 light microscope and a Canon PowerShot A640 color digital camera.

After review of this material we did an extensive literature search to find the original description and drawings of *Fragilaria pinnata* made by Ehrenberg. We also started a search for *Staurosira pinnata* Ehrenberg, although the type material of this taxon in the Ehrenberg Collection remains to be analyzed. Our literature search included subsequent publications by other authors containing interpretations of Ehrenberg's taxa. Image extracts of plates including drawings made by Ehrenberg taken from the Alga Terra information system (Jahn & Kusber, 2011, where the plates are presented as numbered "draw sheets") and processed using Adobe® Photoshop® CS3, are presented here together with the photographs of specimens found on Ehrenberg's micas in order to support our results and conclusions.

RESULTS AND DISCUSSION

Revising type material in the Ehrenberg Collection

The Ehrenberg Collection is a valuable asset to many fields of biological and geological research. In a set of articles published in a rather informative volume (Williams & Huxley, 1998), several authors highlighted many of the qualities of this collection. For diatom taxonomists, the collection represents a plethora of opportunities to work on type material of a set of taxa that happen to be among the most frequently reported in current literature. The usefulness of the collection in clarifying genera and species has been demonstrated repeatedly



(Lange-Bertalot & Jahn, 2000; Jahn, 2004; Jahn & Kusber, 2004, 2005; Jahn et al., 2009; among others). In the case of freshwater araphid diatoms, the Ehrenberg collection holds the types of taxa appearing in almost every other checklist and flora published today from any part of the world (e.g., Staurosira construens (Ehrenberg) D.M. Williams et Round, Staurosira construens var. binodis (Ehrenberg) P.B. Hamilton, Staurosira venter (Ehrenberg) Cleve et J.D. Möller, and Staurosirella pinnata, among others).

As discussed by Lazarus (1998) and shown in the work of Jahn and collaborators (see references above), the information and micas prepared by Ehrenberg are not easy to handle, but reliable information can be recovered and, in most cases, sound taxonomic conclusions can be generated.

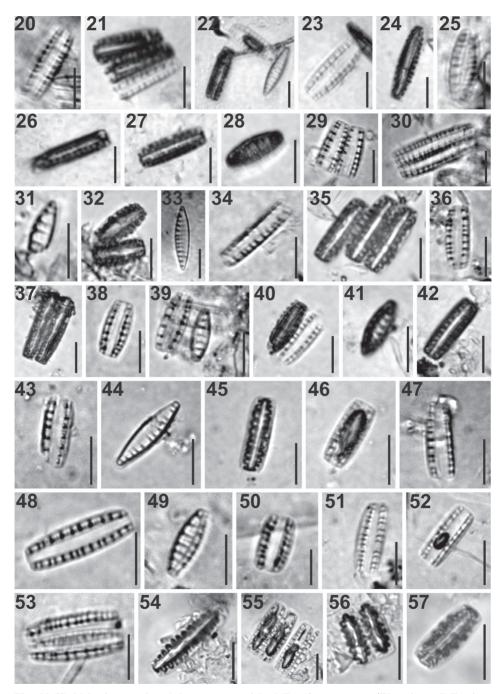
Nomenclatural history of Fragilaria pinnata Ehrenberg

Current name: Staurosirella pinnata (Ehrenberg) D.M. Williams et Round 1987, p. 274.

Basionym: Fragilaria pinnata Ehrenberg 1843, p. 415, pl. 3 (6), figs 8 a-e. Here as Figs 1a-e.

The name *Fragilaria pinnata* had already been used in 1841 by Ehrenberg (p. 144), but it was not until 1843 that he provided a description and an illustration.

Figs 1-19. Drawings of Fragilaria pinnata, F. striata and F. striolata from several of Ehrenberg's publications. Origin of materials is presented here in German, as they appear in Ehrenberg's publications. Figs 1a-e: Iconotype of Fragilaria pinnata (Ehrenberg, 1843, pl. 3 (6), figs 8a-e). Moctezuma Flüss, Mexico. Figs a (colony), b and e, girdle views; figs c and d valve views. Fig. 2: Fragilaria striata (Ehrenberg, 1843, pl. 1, fig. 9). Süd-Amerika, Peru. Valve view of single valve. Fig. 3: Fragilaria pinnata (Ehrenberg, 1854, pl. 1 (3), fig. 7). Kieselguhr von Isle de France, Mascarenen Inseln. Probably an upper view of girdle band. Fig. 4: Fragilaria pinnata (Ehrenberg, 1854, pl. 3 (3), fig. 18). Kieselguhr von Spencer, Massachusetts, Nord-Amerika. Girdle view of frustule. Figs 5a-c: Fragilaria pinnata (Ehrenberg, 1854, pl. 5 (2), figs 27a-c). Torf von Newhaven, Connecticut, Nord-Amerika. Fig. a, girdle band; figs b and c, girdle views of colonies. Fig. 6: Fragilaria pinnata (Ehrenberg, 1854, pl. 5 (3), fig. 48). Torf-Erde von Bridgwater, Massaschusetts, Nord-Amerika. Girdle view of colony. Figs 7a-c: Fragilaria pinnata (Ehrenberg, 1854, pl. 6 (1), figs 45a-c). Bergmehl Von Santafiora, Italien. Figs a and b, girdle bands; fig c, girdle view of colony. Figs 8a-b: Fragilaria pinnata (Ehrenberg, 1854, pl. 6 (2), figs 24a-b). Mergel von Morea, Griechenland. Fig. a, colony in girdle view; fig. b, girdle band. Fig. 9: Fragilaria pinnata (Ehrenberg, 1854, pl. 11, fig. 11). Polirschiefer, Saugschiefer und Halbopal von Bilin, Böhmen. Colony in girdle view. Figs 10a-c: Fragilaria pinnata (Ehrenberg, 1854, pl. 18, figs 75a-c). Grauer Polirschiefer und Tripel von Richmond, Virginien. Fig. a, valve view of single valve; fig. b, girdle view of colony; fig. c, girdle band. Fig. 11: Fragilaria pinnata (Ehrenberg, 1854, pl. 18, fig. 76). Grauer Polirschiefer und Tripel von Richmond, Virginien. Girdle view of colony. Fig. 12: Fragilaria pinnata (Draw sheet n° 638). Salt Lake City, USA. Valve view of single valve. Fig. 13: Fragilaria striolata (Ehrenberg, 1854, pl. 19, fig. 24). Griechische Inseln. Girdle band. Fig. 14: Fragilaria pinnata (Draw sheet n° 623). New Haven, USA. Valve view of single valve. Fig. 15: Fragilaria striolata (Ehrenberg, 1839a, pl. 2, fig. 11). Thames Estuary, London. Girdle view of colony. Fig. 16: Fragilaria striolata (Ehrenberg, 1839b, pl. 3, fig. 11). Freiberg (Schwarzenberg) in Schasen. Girdle view of colony. Figs 17-18: Fragilaria striolata Ehrenberg (Draw sheet n° 632). Freiberg (Schwarzenberg) in Schasen. Figs marked "a" correspond to colonies in girdle view, whereas figs marked "b" are depictions of single valves in valve view. Notice closer resemblance of valve view depictions to the genus Diatoma instead of Denticula as is the case for other drawings on this plate. Fig. 19: Fragilaria syriaca Ehrenberg (Draw sheet n° 632). Relative sizes are the same as those presented in Ehrenberg's original drawings.



Figs 20-57. LM micrographs of the type material of *Fragilaria pinnata* (Ehrenberg Collection, Sample 1229: Moctezuma Flüss; mica strips 20-04-01 and 20-04-02). Notice that all of these valves depict *Denticula*-like morphological features. Scale bars equal 10 µm.

Apparently two subsequent combinations, other than *Staurosirella pinnata*, were presented for this taxon by Kützing (1844) and later by Kuntze (1898):

- ≡ Odontidium pinnatum (Ehrenberg) Kützing 1844, p. 44;
- = Nematoplata pinnata (Ehrenberg) Kuntze 1898, p. 416.

In the same publication of 1843, Ehrenberg presented a second taxon bearing the epithet "*pinnata*":

- Staurosira pinnata Ehrenberg 1843, p. 424.

This taxon name had also been used in 1841 by Ehrenberg (p. 144), but only as part of a list without an illustration. After his description in 1843, the first illustration of *S. pinnata* that we could find dates from 1854 (Ehrenberg, 1854, pl. 5 (2), fig. 24; reproduced here in Fig. 58). This taxon was subsequently combined by Ralfs (Pritchard, 1861), and by Schumann (1867); the latter author placed it as a variety of *Staurosira construens* Ehrenberg (1854, pl. 5, figs 23a-e, here depicted in Figs 59a-e) as follows:

≡ *Dimeregramma* (*Dimerogramma*) *pinnatum* (Ehrenberg) Ralfs *in* A. Pritchard 1861, p. 791, pl. 8, fig. 4 (parenthesis in *Dimerogramma* denote an orthographic correction; the taxon was incorrectly first published under this name);

≡ Staurosira construens var. pinnata (Ehrenberg) Schumann 1867, p. 41.

Analysis of type material of Fragilaria pinnata Ehrenberg

Figures 20-57 show the results of the inspection made of the micas prepared by Ehrenberg with the material from Moctezuma Flüss, México. Comparison of these light microscopy photographs with the drawings in Ehrenberg (1843, pl. 3 (6), figs 8a-e; here as Figs 1a-e) leads to the conclusion that *Fragilaria pinnata* in the type material is not an araphid diatom, but rather a raphid diatom resembling a species of *Denticula* Kützing. In fact, the drawings made by Ehrenberg (1843) show the costae very well (Figs 1c and 1d show costae in valve view and Figs 1a, b and e in girdle view).

A translation of the description of \hat{F} . pinnata made by Ehrenberg (Ehrenberg, 1843, p. 415) provides further evidence:

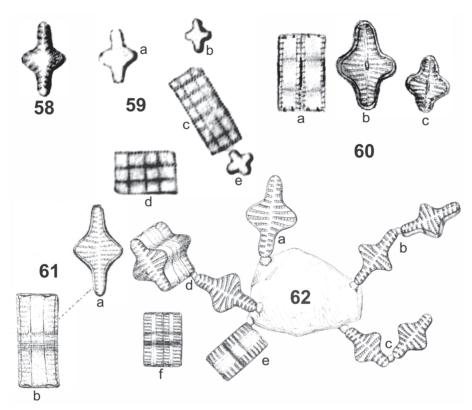
"Fragilaria pinnata: lineari-oblonga striis validis in 1/100 lin. 15, apicibus simpliciter rotundatis. Affinis striolatae et syriacae. Icon!"

Free translation:

"Fragilaria pinnata: [Frustules] linear-oblong, with strong striae, 15 in 1/100 lines, with undivided, rounded apices. Similar to [Fragilaria] striolata and syriaca. See the illustration!" (Notice that the exclamation mark was used in Ehrenberg's time to denote the type, which in this case refers to the Moctezuma Flüss, México material).

F. striolata (as "F.? striata") appears in the next description, following the one for F. pinnata (Ehrenberg, 1843, p. 415). At the end of that description, Ehrenberg clarified that the correct name for striolata is striata. The latter taxon appears illustrated in Ehrenberg (1839a, pl. 2, fig. 11 [four attached frustules in girdle view, reproduced here as Fig. 15]). The description for F. striata (as F. striolata) was presented in Ehrenberg (1839b, p. 129): "Fragilaria striolata, striata, bacillis angustis 8-10ies longioribus quam latis, a latere linearibus subacutis."

A second illustration of *F. striata* was published in Ehrenberg (1843, pl. 1 (3), fig. 9 [valve view]; presented here as Fig. 2). The latter illustration clearly shows a valve of a *Denticula*-like organism with clearly drawn costae. *Fragilaria striata* appears illustrated again in Ehrenberg (1854, pl. 22, fig. 57) and it also



Figs 58-62. Taxa historically associated to *Staurosira pinnata* Ehrenberg. **Figs 58:** *Staurosira pinnata* Ehrenberg (1854, pl. 5(2), fig. 24), from New Haven Connecticut, USA. Draw sheet n° 1093; **Figs 59a-e:** *Staurosira construens* Ehrenberg (1854, pl. 5(2), fig. 23a-e) from the draw sheet n° 1093, New Haven Connecticut, USA; **Figs 60a-c:** *Biblarium leptostauron* (Draw sheet n° 2348). Biolithische süsswasser-bildung, Lockere Felmasse, Tertiär-Gerbirg, Deutschland. **Figs 61a-b:** *Odontidium harrisonii* W.Smith (Roper, 1854, pl. 6, figs 6a, b). **Figs 62a-f:** *Odontidium harrisonii* W.Smith (Smith, 1856, pl. 60, fig. 373).

corresponds to a *Denticula*-like organism, although the costae are faint in this case. In the legend for Plate 22 of this same 1854 publication, Ehrenberg establishes the synonymy of one of his prior identifications under the name *F. pinnata* with *F. striata*: "...Fragilaria pinnata 1844 S 82 = Frag. striolata 1838", which further supports the conclusion that Ehrenberg conceived and attributed the name *Fragilaria pinnata* to an organism that would be currently placed in *Denticula* (notice that the drawing for "...Frag. striolata 1838" alluded to by Ehrenberg (1854), effectively appeared in Ehrenberg (1839a).

A comparison of the first drawing of *F. striata* in valve view (Fig. 2, with clear association to *Denticula*) with other illustrations identified as *F. striolata* (e.g., Figs 17b and 18b) suggest that Ehrenberg had a broad concept of this taxon. Figures 17b and 18b suggest a rather closer relationship to the genus *Diatoma* Bory. This was also noted and illustrated by Dana (1863, fig. 792B).

To our knowledge, Ehrenberg never published an illustration for *F. syriaca*, only a description (Ehrenberg, 1840, p. 211) based on material from the

marine coast of Syria. There is however an Ehrenberg (unpublished) figure of *F. syriaca* in draw sheet n° 641 (reproduced here as Fig. 19). The morphology of the depicted colony in girdle view also suggests a close relationship to the genus *Diatoma. Fragilaria syriaca* was later transferred by Kützing (1844) to the genus *Odontidium* Kützing as *O. syriacum* (Ehrenberg) Kützing and by Kuntze (1898) to the genus *Nematoplata* Bory as *N. syriaca* (Ehrenberg) Kuntze. These three names (*F. syriaca*, *O. syriacum* and *N. syriaca*) are all presented as valid in the Catalogue of Diatom Names (2011).

As long as type material of *F. striata* and *F. syriaca* is not evaluated using light and scanning electron microscopy, it will be difficult to determine their appropriate identities in the context of current diatom taxonomy.

Figures 1-19 include many of the drawings that Ehrenberg provided for F. pinnata and what he considered associated taxa in several of his publications and from different parts of the world. These drawings rather consistently show Denticula-like valves in both valve and girdle views. In several cases he drew what appear to be connective bands (e.g., Figs 5a, 7a and b, 10c, and 13). These drawings of connective bands and striation pattern, together with colonies often shown in girdle view (e.g., Figs 1a, b, e, 4, 5b, c, and 6) may have been the reason for subsequent confusion and inclusion of this taxon in the "fragilarioid" group. It is possible that the girdle bands depicted by Ehrenberg were interpreted as elliptical valves of the araphid type, which together with the short colonies could have been easily associated with Fragilaria. Ehrenberg was careful, however, to depict not only the fimbriate bands and colonies, but he also stressed the striation pattern, depicted as profuse dots in both valve and girdle view drawings (see Figs 5a, 10c and 13, for example). It is possible that Ehrenberg lumped several morphological variants under his Fragilaria pinnata (compare the different shapes of valve view drawings identified as F. pinnata in Figs 1, 3-12 and 14), but because of the characteristics highlighted above, all of these variants seem to belong to the genus Denticula and not to Fragilaria.

The inclusion of *Denticula* within the family "Fragilarieae" around the time of Ehrenberg and the concept of *Denticula* as a genus containing species of solitary habit might have facilitated the association of *F. pinnata* with *Fragilaria* by subsequent authors. Works such as the one by Rabenhorst (1864) establish a clear distinction between *Denticula* and *Fragilaria* based on the inability to form chains and the presence of costae in *Denticula*. As we have observed in type material (Figs 20-57), *F. pinnata* does form chains and does present conspicuous costae. It follows that Ehrenberg might have based his decision to place *pinnata* in *Fragilaria* rather than in *Denticula* on the ability of this species to form band-like colonies although this was not expressed in the protologue (see above).

It is not clear to us yet which current *Denticula* taxa would be associated to *F. pinnata sensu* Ehrenberg. A quick comparison of Figures 20-57 with published material suggests that the complex of *Denticula kuetzingii* Grunow and related taxa such as *Denticula obtusa* W.Smith, *Denticula inflata* W.Smith, *Denticula decipiens* Arnott and *Nitzschia denticula* Grunow (Krammer & Lange-Bertalot, 1988, p. 143, pls 94, 99 and 100) could be among the taxa included by Ehrenberg under *F. pinnata*. Likewise, the complex *Denticula creticola* (Østrup) Lange-Bertalot *et* Krammer, *Denticula rainierensis* Sovereign, *Denticula subtilis* Grunow, and *Denticula sundaysensis* R.E.M.Archibald possess morphological characteristics similar to those depicted in Ehrenberg's drawings (Lange-Bertalot & Krammer, 1993). As each of these taxa has a nomenclatural history of its own, establishing a clear relationship among them will take some

time and it must surely imply detailed examination of type material under light and electron microscopy.

It is important to notice again that during most part of the 1800s Denticula was classified within the family "Fragilarieae" together with genera such as Amphipleura Kützing, Asterionella Hassall, Ceratoneis Ehrenberg, Diatoma, Fragilaria, Grammonema C.Agardh, Odontidium and Plagiogramma Greville (Pritchard, 1861, p. 773). It is not apparent, why and who decided to retain Fragilaria pinnata as an araphid diatom, and why the link with the current concept of Denticula was never established until now. What is certain is that the misinterpreted concept stuck easily among diatomists and that the error was maintained through time. An extreme case of the confusion caused by the lack of a clear interpretation of Ehrenberg's original concept is found in the plates included by Hustedt (1913) in the Schmidt's Atlas (Schmidt et al., 1874-1959), in which this author developed a broad concept of F. pinnata, including in it a rather wide range of morphological variants (see his pl. 297, figs 47-72 and pl. 298, figs 47-60, 66, 68, 71-73).

When Williams & Round (1987) erected the genus *Staurosirella*, they transferred *F. pinnata* to this new genus, but without examination of Ehrenberg's type material. In their discussion of their transfer, Williams & Round cited Haworth's (1975) work on Scottish material, which consisted of light and scanning electron micrographs of what she considered to be *F. pinnata*. Haworth's work was influential until the publication of Williams & Round's 1987 review. Her identifications of *F. pinnata* were in turn largely influenced by Hustedt's (1931, 1959) concept, which represents a much different concept from that presented in the Schmidt's Atlas. Haworth (1975) had studied Ehrenberg's drawings, but erroneously interpreted the Santafiora, Italy (Figs 7a-c) instead of the Moctezuma Flüss, Mexico (Figs 1a-e) drawings as the iconotype of *F. pinnata*. It is clear to us that identifications and taxonomic decisions presented by both Haworth (1975) and Williams & Round (1987) are incorrect and failed to make the connection with the original Ehrenberg intention.

We gave careful consideration to the idea that a possible solution caused by the concept change for *F. pinnata* would be a conserved name with a conserved type. However, as indicated previously, the name is currently associated with at least half a dozen different morphological variants. Additionally, Grunow (1862), Krammer & Lange-Bertalot (1991) and Guiry & Guiry (2011) suggest several other synonyms that require careful scrutiny before they are accepted as true synonyms. Thus, a prior careful characterization of these variants/synonyms under light and scanning electron microscopy is required. Also, it should be considered that if the current taxonomic and ecological data available in the literature are based on such a broad concept of *F. pinnata*, a deep reevaluation of these data should be made, especially considering that *pinnata*-like variants are often reported in water quality assessment and palaeoecological (for example) publications throughout the world.

The case of Staurosira pinnata Ehrenberg

Guiry & Guiry (2011) include a note for this taxon that states: "Status of name: This name [Staurosira pinnata Ehrenberg] is currently regarded as a taxonomic synonym of Staurosirella leptostauron (Ehrenberg) D.M.Williams et Round" (brackets added by us).

However, Staurosirella leptostauron has the following nomenclatural history:

Current name: Staurosirella leptostauron (Ehrenberg) D.M.Williams et Round 1987, p. 276, figs 22 & 23.

Basionym: *Biblarium leptostauron* Ehrenberg 1854, p. 8, pl. 12, figs 35 & 36 (here as Figs 60a-c).

Grunow (1862) considered *B. leptostauron* as a synonym of: *Odontidium harrisoni* W.Smith 1856, p. 18, pl. 60, fig. 373 (here as Figs 62a and b). But thought that *O. harrisoni* would be better placed in *Fragilaria* as: *Fragilaria harrisoni* (W.Smith) Grunow 1862, p. 368.

Hustedt (1931) considered *Staurosira pinnata* as a species of *Fragilaria*, but could not make the combination in the latter genus due to the existence of *Fragilaria pinnata* Ehrenberg. Hustedt then used the epithet of the earliest synonym *Biblarium leptostauron* to provide the combination:

Fragilaria leptostauron (Ehrenberg) Hustedt 1931, p. 153, figs 668 a-f.

There is a major nomenclatural problem to be solved regarding the use of the name *Odontidium harrisoni*, since the Catalogue of Diatom Names (2011) attributes it to two different authors other than Smith (1856):

1) Odontidium harrisonii Roper 1854, pl. 6, figs 6a and b (here as Figs 61a and b).

In this case, Roper discussed his use of the name to some extent and provided a rather clear drawing of it (Roper, 1854, pl. 6, figs 6a and b; Figs 61a and b herein). Roper wrote: "Fig. 6 a and b represents a small cross-shaped valve that occurs sparingly, which Mr. Smith, from a drawing, thought might be referred to his *Odontidium tabellaria...*" As an added footnote, Roper wrote at the bottom of p. 77: "From specimens I have lately seen of *Odontidium Harrisonii*, W.S., I am inclined to believe that this may be a small form of that species rather than *O. tabellaria*. As it is a doubtful form I have not included it in the lists."

2) Odontidium harrisoni W.Gregory 1855, p. 37.

This corresponds to a mention of the taxon by name, but no figure was provided. The name is part of a table (p. 37) and it is accompanied by a footnote stating "A beautiful form lately detected by Mr. Harrison."

When Smith described *O. harrisoni* (Smith, 1856, p. 18, pl. 60, fig. 373; depicted here as Figs 62a and b) he stated that it had been found in "Fresh water. Near Hull, April 1852, Aug. 1849 and Jan. 1854, Mr. R. Harrison". He later added: "The larger form [referring to the nominate variety of this taxon] has alone occurred in the locality where it was first discovered by Mr. Harrison; the smaller [referring to his variety β, which he considered to be the same as Roper's *O. harrisoni*] appears widely distributed, as it is sparingly present in almost every alpine or subalpine gathering with which I am acquainted" (brackets added by us).

Therefore, it seems likely that although Harrison had not published (nor named) formally his observed taxon, he had shown it in public. Roper (1854) and Gregory (1855) mention the taxon and refer to it as *O. harrisoni* probably because Smith had also shown his work and his intention to describe the taxon as a new species before its publication. Since it is Smith (1856) who presented a first formal description and accompanying drawings of the taxon, very similar to that diagrammed by Roper (1854), this taxon should be attributed to Smith.

Based solely on words and drawings, it is nearly impossible to demonstrate with clarity whether *Staurosira pinnata*, *Biblarium leptostauron* and *Odontidium harrisoni* are true synonyms. Study of type materials using light and scanning electron microscopy seems to be the only possible way to solve this nomenclatural morass.

For the time being, we can state that the current usage of the name *Staurosira pinnata* in place of *Staurosirella pinnata* is erroneous because these taxa are based on two different types. Therefore, the taxonomy and synonymy presented in references such as Schmidt *et al.* (2004) merit reconsideration.

Some preliminary conclusions and implications of the present work

Use of *Fragilaria pinnata* as basionym of *Staurosirella pinnata* (being *Staurosirella* an araphid genus within the Fragilariaceae) is inappropriate since *F. pinnata* was first illustrated, and thus typified, by a specimen in the "Moctezuma Flüss" material, specimen that in fact corresponds to a *Denticula* sp. Thus, the current concept of *F. pinnata* does not correspond with the original concept developed by Ehrenberg.

We currently do not know what the araphid commonly referred to as *Fragilaria/Staurosirella pinnata* really is. Examination of type material of entities, morphologically similar to the *F. pinnata* concept of Hustedt (1931, 1959), Haworth (1975), Podzorski (1985) and Williams & Round (1987), could elucidate the identity of some morphological variants currently included under these names. It is possible that some of these variants may have to be described as new taxa.

Undoubtedly, Fragilaria pinnata and Staurosira pinnata cannot be regarded as synonyms.

Until type materials of *Staurosira pinnata*, *Biblarium leptostauron* and *Odontidium harrisoni* are analyzed, their synonymy is not proven and, therefore, all these names should be handled with extreme care.

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REFERENCES

CATALOGUE OF DIATOM NAMES, 2011 — California Academy of Sciences, On-line Version updated 23 Sept. 2011. Compiled by Elisabeth Fourtanier & J. Patrick Kociolek. Available online at http://research.calacademy.org/research/diatoms/names/index.asp.

DANA J.D., 1863 — Manual of geology. 1st ed. Philadelphia. 798 p.

EHRENBERG C.G., 1839a — Über das im Jahre 1686 in Curland vom Himmel gefallene Meteorpapier und über dessen Zusammensetzung aus Conferven und Infusorien. Abhandlungen der Königlichen Akademie der Wissenschaften zu Berlin 1838, pp. 45-58.

EHRENBERG C.G., 1839b — Über die Bildung der Kreidefelsen und des Kreidemergels durch unsichtbare Organismen. Abhandlungen der Königlichen Akademie der Wissenschaften zu Berlin 1838, pp. 59-147.

EHRENBERG C.G., 1840 — Characteristik von 274 neuen Arten von Infusorien. Bericht über die zur Bekanntmachung geeigneten Verhandlungen der Königlich-Preussischen Akademie der Wissenschaften zu Berlin 1840, pp. 197-219.

- EHRENBERG C.G., 1841 Über Verbreitung und Einfluss des mikroskopischen Lebens in Südund Nordamerika. Bericht über die zur Bekanntmachung geeigneten Verhandlungen der Königlich-Preussischen Akademie der Wissenschaften zu Berlin 1841, pp. 139-144.
- EHRENBERG C.G., 1843 Verbreitung und Einflufs des mikroskopischen Lebens in Süd- und Nord- Amerika. Abhandlungen der Königlichen Akademie der Wissenschaften zu Berlin 1841, pp. 291-445, 4 pls.
- EHRENBERG C.G., 1854 Mikrogeologie, Einundvierzig Tafeln mit über viertausend grossentheils
- colorirten Figuren, Gezeichnet vom Verfasser. [Atlas]. Leopold Voss, Leipzig, 40 pls. GAUL U., GEISSLER U., HENDERSON M., MAHONEY R. & REIMER C.W., 1993 Bibliography on the fine-structure of diatom frustules (Bacillariophyceae). *Proceedings of the academy of natural sciences of Philadelphia* 144: 69-238.
- GREGORY W., 1855 On a post-Tertiary lacustrine sand, containing Diatomaceous exuviae, from Glenshira, near Inverary. Quarterly journal of microscopical science, London 3: 30-43, pl. 4.
- GRUNOW A., 1862 Die österreichischen Diatomaceen nebst Anschluss einiger neuen Arten von andern Lokalitäten und einer kritischen Uebersicht der bisher bekannten Gattungen und Arten. Erste Folge. Epithemieae, Meridioneae, Diatomeae, Entopyleae, Surirelleae, Amphipleureae. Zweite Folge. Familie Nitzschieae. Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien 12: 315-472, 545-588, 7 pls.
- GUIRY M.D. & GUIRY G.M., 2011 AlgaeBase. World-wide electronic publication, National University of Ireland, Galway, http://www.algaebase.org; searched on 11 October 2011.
- HAWORTH E.Y., 1975 A scanning electron microscope study of some different frustule forms of the genus Fragilaria found in Scottish late-glacial sediments. British phycological journal 10:
- HENDERSON M.V. & REIMER C.W., 2003 Bibliography on the fine structure of diatom frustules (Bacillariophyceae). II. (+Deletions, addenda and corrigenda for bibliography I). Diatom monographs 3: 1-377.
- HUSTEDT F., 1913 Plates 72-75. In: Schmidt A. et al. (eds), Atlas der Diatomaceen-kunde, bergründer von A. Schmidt. Aschersleben-Leipzig.
- HUSTEDT F., 1931 Die Kieselalgen Deutschlands, Österreichs und der Schweiz unter Berücksichtigung der übrigen Länder Europas sowie der angrenzenden Meeresgebiete. In: Rabenhorst L. (ed.), Kryptogamen Flora von Deutschland, Österreich und der Schweiz. Band 7, Teil 2, Lief. 1. Leipzig, Akademische Verlagsgesellschaft m.b.h., 176 p.
- HUSTEDT F., 1959 Die Kieselalgen Deutschlands, Österreichs und der Schweiz unter Berücksichtigung der übrigen Länder Europas sowie der angrenzenden Meeresgebiete. In: Rabenhorst L. (ed.), Kryptogamen Flora von Deutschland, Österreich und der Schweiz. Band 7, Teil 2. Champaign, Koeltz Scientific Books & Dehra Dun, Bishen Singh Mahendra Pal Singh, 845 p. (Reprint 1991).
- JAHN R., 2004 Discovery of the type specimen of *Pinnularia gastrum* Ehrenberg, the type species of the genus *Placoneis* Mereschkowsky. *Diatom research* 19 (2): 229-234.
- JAHN R. & KUSBER W.-H., 2004 Algae of the Ehrenberg Collection: 1. Typification of 32 names of diatom taxa described by C.G. Ehrenberg. Willdenowia 34 (2): 577-595.

 JAHN R. & KUSBER W.-H., 2005 — Reinstatement of the genus Ceratoneis Ehrenberg and
- lectotypification of its type specimen: C. closterium Ehrenberg. Diatom research 20 (2): 295-304.
- JAHN R. & KUSBER W.-H. (eds), 2011 AlgaTerra Information System [online]. Botanic Garden and Botanical Museum Berlin-Dahlem, Freie Universität Berlin. 10 October 2011. Available from http://www.algaterra.org>.
- JAHN R., KUSBER W.-H. & ROMERO O.E., 2009 Cocconeis pediculus Ehrenberg and C. placentula Ehrenberg var. placentula (Bacillariophyta): Typification and taxonomy. Fottea 9 (2): 275-288.
- KARST-RIDDOCH T.L., MALMQUIST H.J. & SMOL J.P., 2009 Relationship between freshwater sedimentary diatoms and environmental variables in Subarctic Icelandic lakes. Archiv für Hydrobiologie 175 (1): 1-28.
- KAWECKA B. & ROBINSON C.T., 2008 Diatom communities of lake/stream networks in the Tatra Mountains, Poland, and the Swiss Alps. Oceanological and hydrobiological studies 37:
- KRAMMER K. & LANGE-BERTALOT H., 1988 Bacillariophyceae 2. Teil: Bacillariaceae, Epithemiacae, Surirellaceae. *In*: Ettl H., Gerloff J., Heynig H. & Mollenhauer D. (eds), Süßwasserflora von Mitteleuropa 2/2. Stuttgart – New York, Gustav Fisher Verlag, 596 p. KRAMMER K. & LANGE-BERTALOT H., 1991 – Bacillariophyceae 3. Teil: Centrales,
- Fragilariaceae, Eunotiaceae. In: Ettl H., Gerloff J., Heynig H. & Mollenhauer D. (eds), Süßwasserflora von Mitteleuropa. 2/3. Gustav Fisher Verlag, Stuttgart – New York, 576 p. KUNTZE O., 1898 – Revisio Generum Plantarum. Part III. Leipzig. 576 p.
- KÜTZING F.T., 1844 Die Kieselschaligen. Bacillarien oder Diatomeen. Nordhausen. 152 p., 30 pls.

- LANGE-BERTALOT H. & JAHN R., 2000 On the identity of Navicula (Frustulia) rhomboides and Frustulia saxonica (Bacillariophyceae). Systematics and geography of plants 70: 255-261.
- LANGE-BERTALOT H. & KRAMMER K., 1993 Observations on Simonsenia and some small species of Denticula and Nitzschia. In: Sims P.A. (ed.), Progress in diatom studies, Contributions to taxonomy, ecology and nomenclature. Special volume in honour of Robert Ross on the occasion of his 80th Birthday. Nova Hedwigia, Beiheft 106: 121-131.
- LAZARUS D., 1998 The Ehrenberg Collection and its curation. *In*: Williams D.M. & Huxley R. (eds), Christian Gottfried Ehrenberg (1795-1876). The man and his legacy. The Linnean Society of London, Special Issue No. 1. London, Academic Press Limited, pp. 31-48.
- PODZORSKI A.C., 1985 An illustrated and annotated checklist of the diatoms from the Black River Waterways, St. Elisabeth, Jamaica. Bibliotheca diatomologica 7, 177 p.
- PRITCHARD A., 1861 A history of infusoria, including the Desmidiaceae and Diatomaceae, British and foreign. Fourth edition. Enlarged and revised by Arlidge J.T., Archer W., Ralfs J., Williamson W.C. and the author. London, Whittaker and Co. 968 p., 40 pls.
- RABENHORST L., 1864 Flora Europaea Algarum aquae dulcis et submarinae. Sectio I. Algas diatomaceas complectens, cum figuris generum omnium xylographice impressis. Apud Eduardum Kummerum, Lipsiae. 359 p.
- ROPER F.C.S., 1854 Some observations on the Diatomaceae of the Thames. Transactions of the microscopical society, new series, London 2: 67-80, pl. 6.
- SCHMIDT A. et al. (eds), 1874-1959 Atlas der Diatomaceen-kunde. Heft 1-120, Tafeln 1-460 (Tafeln 1-213 A. Schmidt; 213-216 M. Schmidt; 217-240 F. Fricke; 241-244 H. Heiden; 245, 246 O. Müller; 247-256 F. Fricke; 257-264 H. Heiden; 265-268 F. Fricke; 269-472 F. Hustedt). Aschersleben-Leipzig.
- SCHMIDT R., KAMENIK C., LANGE-BERTALOT H. & KLEE R., 2004 Fragilaria and Staurosira (Bacillariophyceae) from sediment surfaces of 40 lakes in the Austrian Alps in relation to environmental variables, and their potential for palaeoclimatology. Journal of limnology 63 (2): 171-189.
- SCHUMANN J., 1867 Preussische Diatomeen. Schriften der Königlichen Physikalisch-Ökonomischen Gesellschaft zu Konigsberg 8 (Abh.): 37-68, pls 1-3.
- SERVANT S., 1970 Répartition des diatomées dans les séquences lacustres holocènes au nord-est du Lac Tchad. Cahiers ORSTOM, sér. Géol. 2 (1): 115-126.
- SMITH W., 1856 Synopsis of British Diatomaceae. London, John Van Voorst, Vol. 2. 107 p.,
- pls 32-60, 61-62, A-E. VAN DE VIJVER B., LANGE-BERTALOT H. & COMPÈRE P., 2009 Two new freshwater diatom species (Bacillariophyceae) from a small pool in the National Botanic Garden of
- Belgium. Belgium journal of botany 142 (2): 194-203. VAN DE VIJVER B., MATALONI G., STANISH L. & SPAULDING S.A., 2010 New and interesting species of the genus Muelleria (Bacillariophyta) from the Antarctic region and South Africa. Phycologia 49 (1): 22-41.
- WATCHORN M.A., HAMÍLTON P.B., ÁNDERSON T.W., ROE H.M. & PATTERSON R.T., 2008 Diatoms and pollen as indicators of water quality and land-use change: a case study from the Oak Ridges Moraine, Southern Ontario, Canada. Journal of paleolimnology 39: 491-509.
- WILLIAMS D.M. & HUXLEY R. (eds), 1998 Christian Gottfried Ehrenberg (1795-1876). The man and his legacy. The Linnean Society of London, Special Issue No 1, London, Academic Press Limited, 88 p.
- WILLIAMS D.M. & ROUND F.E., 1987 Revision of the genus Fragilaria. Diatom research 2 (2): 267-288.