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Placoneis Mereschkowsky (Bacillariophyta) revisited: resolution of several typification and nomenclatural problems, including the generitype

EILEEN J. COX*

Department of Botany, The Natural History Museum, Cromwell Road, London, SW7 5BD

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The identity of three naviculoid diatoms originally described by Ehrenberg and now placed in the genus *Placoneis* was investigated. Type specimens and material from both the Ehrenberg Collection (Berlin) and the diatom collection at the Natural History Museum, London, were examined with LM and also SEM where possible. The concept of each species had changed since Ehrenberg named them. The current understanding of *Placoneis gastrum* and *Navicula semen* can be traced back to Donkin, and that of *Placoneis placentula* to Grunow. LM and SEM studies of *N. semen* support its transfer to *Placoneis*. It is proposed that the specific epithets *gastrum* and *placentula* should be conserved with conserved types to maintain established practice, and the name *P. navicularis* applied to *N. semen sensu* Donkin. Type material of *Placoneis elginensis* and *Placoneis anglica* was re-examined from slides in the Natural History Museum and it was concluded that *P. elginensis* has been incorrectly applied to specimens of a second species, for which the name *P. anglica* was appropriate. The delimitation of these species, *P. pseudanglica*, and others previously included in *P. elginensis* is reviewed. LM and SEM observations of *Navicula abiskoensis* and *Navicula amphibola* support their transfer to *Placoneis*. Six new combinations are made for additional taxa belonging to *Placoneis*: *P. constans*, *P. insignita*, *P. interglacialis*, *P. porifera*, *P. rostrata* and *P. subgastriformis*. The systematic position of the genus *Placoneis* is reviewed. A revised generic description and a summary of the species currently assigned to *Placoneis* are included. *Botanical Journal of the Linnean Society*, 2003, **141**, 53–83.

ADDITIONAL KEYWORDS: diatom – Ehrenberg – *Navicula abiskoensis* – *Navicula amphibola* – *Navicula semen* – taxon delimitation – type collections.

INTRODUCTION

When the diatom genus *Placoneis* Mereschkowsky (Cox, 1987) was re-erected, *Placoneis gastrum* (Ehrenberg) Mereschkowsky was chosen as the type species, in preference to *P. exigua* (Gregory) Mereschkowsky, because delineation and nomenclature of the latter were confused (Krammer & Lange-Bertalot, 1986). *Placoneis gastrum* apparently presented less difficulty and agreed with Mereschkowsky's protologue of the genus (Mereschkowsky, 1903). However, comparing various published illustrations and descriptions, it is clear that the concept of *P. gastrum* has shifted since Ehrenberg (1843) first described and illustrated it (as *Pinnularia gastrum*). Patrick & Reimer (1966: p. 518) commented that 'one cannot be sure that the taxon which Ehrenberg and Kützing had in mind is the same as the one we recognize as *N. gastrum* today'. The delimitation of *Placoneis placentula* (Ehrenberg) Heinzerling, which was originally described at the same time (Ehrenberg, 1843), is perhaps even more problematical. Although Ehrenberg's illustrations showed different shaped cells with either radiate (Ehrenberg, 1838) or parallel (Ehrenberg, 1843) striae, Kützing (1844) and Rabenhorst (1853) only reproduced an example with parallel striae, which conflicts with the current understanding of this species (*cf.* Patrick & Reimer, 1966; Germain, 1981; Krammer & Lange-Bertalot, 1986).

The causes of such conceptual shifts are understandable. Many early descriptions (e.g. Ehrenberg, 1843; Kützing, 1833, 1844) are extremely brief with small illustrations. Subsequent workers did not always see original material but allocated specimens

*E-mail: e.j.cox@nhm.ac.uk

to described taxa based on the published descriptions only (Cox, 1998, 1999a). Thus, Cleve & Grunow (1880), while explicitly following Donkin's concept (Donkin, 1873) of *Navicula gastrum* (Ehrenberg) Kützing, questioned whether this is the species illustrated by Ehrenberg (1843). However, Donkin (1873) was basing his interpretation of the species on a later figure in Ehrenberg's *Mikrogeologie* (Ehrenberg, 1854) and on specimens in Lough Mourne material. To add to the confusion, the cited figures differ from those given by Ehrenberg (1873, 1875) in a later documentation of original descriptions and figures.

Mereschkowsky (e.g. 1902; 1903) described several new genera on the basis of their chloroplast types, referring to known species, but sometimes without seeing the original publication, let alone specimens of original material. Clearly, such reliance on published literature can easily result in nomenclatural problems. The solution of these then requires either the formal description of new taxa, e.g. *Craspedostauros* E. J. Cox for *Stauronella* Mereschkowsky (Cox, 1999a) and *Parlibellus* E. J. Cox for *Libellus* Cleve (Cox, 1988), neotypification or conservation, e.g. *Navicula cuspidata* Kützing and *N. ambigua* Ehrenberg (Cox, 1998).

In order to establish the identities of *P. gastrum* and *P. placentula*, drawings and original material in the Ehrenberg collection (Museum für Naturkunde, Berlin) were examined. Slides and material from other historical diatom collections held in the Natural History Museum, London, were also studied. In the course of this investigation, specimens of *Navicula semen* Ehrenberg (*sensu* Donkin) and *Navicula amphibola* Cleve were encountered and their similarity to *Placoneis* recognized. The morphology of these taxa was therefore investigated more closely to confirm their taxonomic position, and a search for specimens in original material was undertaken to resolve the identity of the taxa that Ehrenberg had named, and to confirm the identity of *N. amphibola* (Table 1).

When *Placoneis* was re-established (Cox, 1987), several other species were transferred to the genus on the basis of their chloroplasts, but type material was not examined. Several of the types are held in the Natural History Museum and have now been examined with both LM and SEM. The lectotypification of some of these is reviewed. Recently, Metzeltin & Lange-Bertalot (1998) and Rumrich, Lang-Bertalot & Rumrich (2000) described several new species of *Placoneis* and have also transferred other taxa to the genus. An evaluation of their decisions and an update of the systematics of *Placoneis* are provided.

MATERIAL AND METHODS

Original drawings, preparations, slides and material were examined from the Ehrenberg collection in the Museum für Naturkunde, Berlin (BHU) and collections in the Natural History Museum, London (BM) (Appendix 1). Subsamples of some Ehrenberg and W. Smith material were cleaned for light and electron microscopy by heating in nitric acid. For LM, cleaned frustules were mounted in Naphrax, or, for SEM, mounted on stubs and coated with gold-palladium. A Zeiss Universal photomicroscope and Kodak T Max or 100 Delta pro film were used to take light micrographs, and scanning electron micrographs were taken on a Philips XL 30 SEM using Kodak Tri-X 400 pro film.

Terminology of valve structure follows Ross *et al*. (1979) and Cox & Ross (1981), particularly the use of virgae (Cox & Ross, 1981), rather than interstriae (Ross *et al*., 1979), to describe the solid silica between the striae. Vimines (Cox & Ross, 1981) is used to describe the cross connections between pores within a stria. Terminology for the pore occlusions follows Mann (1981).

OBSERVATIONS

PINNULARIA GASTRUM EHRENBERG

Ehrenberg (1843) described and illustrated *Pinnularia gastrum* (Fig. 1) from Vera Cruz, Mexico (Ehrenberg, 1843: 421, pl. 3, VII, fig. 23), but also recorded it from Newhaven, Connecticut (USA) and Iceland (Ehrenberg, 1843: 384). Later, he (Ehrenberg, 1875) referred to an illustration of a specimen from Down, Mourne Mountains (Ireland) (Fig. 2) (pl. 15, fig. 23) in his *Mikrogeologie* (Ehrenberg, 1854), indicating that *Pinnularia gastrum* was a synonym of *Navicula gastrum*. An illustration of *P. gastrum* from Iceland (Fig. 3) was also included (pl. 5, I, fig. 12) in the *Mikrogeologie* (Ehrenberg, 1854). Kützing (1844) transferred *P. gastrum* to *Navicula* and presumably copied (Fig. 4, Kützing, 1844: pl. 28, fig. 56) Ehrenberg's drawing (*cf.* Fig. 1). All four illustrations show valves with protracted apices, radiate to more or less parallel striae and a clearly defined central nodule. Rabenhorst (1853: pl. 6, fig. 15) (Fig. 5) appears to have followed Ehrenberg (1843) (Fig. 1) and Kützing (1844) (Fig. 4), but minimized the protracted shape of the apices (*cf.* Figs 1,5). However, it should be noted that *P. gastrum* from Vera Cruz came from a marine sample, whereas the later illustrated specimens of *N. gastrum* from Mourne, Iceland and Newhaven were from freshwater samples.

Although he cited all the above illustrations, Donkin (1873: pl. 3, fig. 10) illustrated his account of *N. gastrum* Ehrenberg with a diatom (Fig. 6) from 'Loch-Mourne' (sic) which had slightly more protracted, broadly rounded, apices, radiating striae with a few slightly shorter striae inserted opposite the central area. Donkin (1873) specified that he

Table 1. Summary information on availability of type material and location of type slides of *Placoneis* species

Species	Original author	Date	Cited locality (original)	Original material	Specimens in material	Type slide	Locality of slide
P. abiskoensis	Hustedt	1942	Abisko, Sweden	Hustedt Coll.	?	N1/2	Abisko, Sweden
P. amphibola	Cleve	1891	Erlafsee near Mariazell	Grunow coll.?	?	?	(Austria)
P. anglica	Ralfs, in Pritchard	1861	Bramley near Guildford	none	none	BM 23510	Guildford, England
P. clementioides	Hustedt	1944	Schalkenmehrener Maar in der Eifel	Hustedt Coll.	?	N11/59	Schalkenmehrener Maar (Germany)
P. clementis	Grunow	1882	Dúbravica bei Neusohl, Ungarn	Grunow coll.?	?	?	(Hungary)
P. constans	Hustedt	1944	Oberohe, Lüneburger Heide	Hustedt Coll.	?	N14/22	Oberohe, Germany
P. demeraroides	Hustedt	1966	Demerara River	Hustedt Coll.	?	N2/54	Demerara River (Guyana)
P. elginensis	Gregory	1856	none	none	none	BM 11751	Elgin, Scotland
P. exigua	Gregory	1854	Diatomaceous earth, Mull	BM?			Scotland
P. explanata	Hustedt	1948	Gaj, Konin. Warthegau	Hustedt Coll.	?	N2/91	Gaj, Konin., Poland
P. gastrum	Ehrenberg (conserved)	1843	Vera Cruz, Mexico	BHU	none	none	–
			Iceland	BHU	yes	BHU + BM	Brenn Torf, Iceland
			Newhaven,Conn.	BHU	none	none	–
			Lough Mourne	BM	none	BM 12187	Lough Mourne, Ireland
P. ignorata	Schimanski	1978	Zufluß zur Zettleitz von der Kastenleite (Frankenwald)	Coll. Schimanski	?	Nr 231.11	Tributary of Zettleitz, Germany
P. insignita	Hustedt	1942	Laguna de Bay, Luzon	Hustedt Coll.	?	163/27a	Laguna de Bay, Luzon, Philippines
P. interglacialis	Hustedt	1944	Oberohe, Lüneburger Heide	Hustedt Coll.	?	N10/17	Oberohe, Germany
P. jatobensis	Krasske	1951	Brazilien	Coll. Krasske, Kassel, Germany	?	D IV 96	Brazil

Table 1. *Continued*

Species	Original author	Date	Cited locality (original)	Original material	Specimens in material	Type slide	Locality of slide
P. molesta	Metzeltin & Lange-Bertalot	1998	Rio Tapajós, Brazilien	Coll. Lange-Bertalot	?	AmS-568	Rio Tapajós, Brazil
P. navicularis	Ehrenberg	1854	Pelham, Massachusetts	BHU	yes	Eco-006	Pelham, USA
P. paraelginensis	Lange-Bertalot, in Rumrich *et al.*	2000	Hattenprice, nr Springhead Hill, England	?	?	VH Types 43	Hattenprice, England
P. pellaifa	Lange-Bertalot, & Rumrich	2000	Lago Pellaifa, Chile	Coll. Lange-Bertalot	?	AmS-Ch 132	Lago Pellaifa, Chile
P. placentula	Ehrenberg (conserved)	1843	Vera Cruz, Mexico	BHU	none	–	–
				BM	?	BM 93093	Lilliesleaf Pond, England
P. porifera	Hustedt	1944	Breiter Lucin	Hustedt Coll.	?	N10/55	Breiter Lucin (Feldberg, Germany)
P. pseudanglica	Lange-Bertalot, in Krammer & Lange-Bertalot	1986	none	Hustedt Coll.	?	N11/75	Breiter Lucin (Feldberg, Germany)
P. rostrata	A. Mayer	1917	Donaualtheim, Bavaria	?	?	?	? (Germany)
P. santaremensis	Metzeltin & Lange-Bertalot	1998	Rio Tapajós, Brazilia, bei Santarém	Coll. Lange-Bertalot	?	AmS-563	Rio Tapajós, Brazil
P. scharfii	Lange-Bertalot & Rumrich, in Rumrich *et al.*	2000	Lago Pellaifa, Chile	Coll. Lange-Bertalot	?	AmS-Ch 132	Lago Pellaifa, Chile
P. signata	Hustedt	1944	Breiter Lucin	Hustedt Coll.	?	N11/75	Breiter Lucin, Feldberg, Germany
P. subgastriformis	Hustedt	1945	Prespasee, Macedonien	Hustedt Coll.	?	N1/33	Lake Prespas, Macedonia
P. subplacentula	Hustedt	1930	Tanganyikasee	Hustedt Coll.	?	N8/24	Lake Tanganyika, E. Africa
P. surinamensis	Cleve	1895	Surinam	?	?	?	–
P. tersa	Hustedt	1956	Lake Maracaibo, Venezuela	Hustedt Coll.	?	343/65	Lake Maracaibo, Venezuela
P. undulata	Østrup	1918	Iceland	?	?	?	–

illustrated a specimen from the same deposit as that examined by Ehrenberg (1854). Cleve & Grunow (1880: 31) explicitly followed Donkin's concept of the species, questioning whether Donkin (1873) illustrated the same taxon as Ehrenberg. They (Cleve & Grunow, 1880) also recognized three varieties of the species: *N. gastrum* var. *Jenisseyensis* Grun., *N. gastrum* var. *exigua* Grun. (= *Pinnularia exigua* Greg.), and *N. gastrum* var. *latiuscula* Grun. Comparing Donkin's drawing (Fig. 6) with later illustrations of the species (Figs 7–26, especially Figs 8,9,16–24) confirms that the modern concept of the freshwater species *N. gastrum* (*cf.* Patrick & Reimer, 1966; Germain, 1981; Krammer & Lange-Bertalot, 1986) originated with Donkin (1873). However, some of the specimens illustrated by Hustedt (Figs 10–15,25,26) would be excluded. It should also be noted that Donkin (1873) (mis-)referenced Ehrenberg's illustration as 'Taf. III, VII, 22', i.e. Ehrenberg's drawing of *P. placentula* Ehrenberg (Fig. 33).

The original micas for *P. gastrum* and *N. gastrum* were missing from the Ehrenberg boxed sets (BHU). However, original material from Vera Cruz (marine sediment), Iceland and Newhaven was located and examined with both LM and SEM. No specimens of *N. gastrum* were found although there were a few specimens of *Navicula semen* Ehrenberg *sensu* Donkin and *Navicula amphibola* Cleve in the Iceland material (Figs 91,103,107). The specimens of *N. amphibola* in the Iceland material agree reasonably with Ehrenberg's illustration (Fig. 3) and therefore it may be concluded that this is the taxon illustrated by Ehrenberg (1854: pl. 5, I, fig. 12). Regine Jahn (pers. comm.) considers that a specimen from Newhaven (very similar to that illustrated in Fig. 106) corresponds to Ehrenberg's illustration (Fig. 1) of *N. gastrum* from Vera Cruz (1843: pl.3, VII, fig. 23).

Although all three taxa are members of *Placoneis* (see below for discussion of the taxonomic position of *N. amphibola*), there are significant differences between them. *Placoneis gastrum* has very bluntly rostrate apices, widely spaced (relative to their width), radiating striae throughout the valve, and alternately longer and shorter striae opposite the central area. Its valves are 30–60 μm long and 12–18 μm wide, with 8–10 striae in 10 μm (Figs 27–32, Mann & Stickle, 1995: figs 1–3). *Navicula amphibola* is usually larger, 37–75 μm long, 22–27 μm wide, and has slightly fewer (7–8), more coarsely areolate striae in 10 μm (Figs 103,104). The valves of *N. amphibola* are also more parallel sided at the centre and the apices more acute than those of *P. gastrum*. The unidentified *Placoneis* (Fig. 106) is also broader than *P. gastrum* (about 25 μm rather than <18 μm wide), has almost apiculate apices, and more coarsely areolate striae. Applying the specific epithet *gastrum* to specimens of either (*N. amphibola* or the specimen in Fig. 106) would introduce considerable confusion into the literature. *Navicula gastrum* has been used reasonably consistently since the late 19th century, and particularly in the last 70 years (Hustedt, 1930, 1966; Patrick & Reimer, 1966; Germain, 1981; Krammer & Lange-Bertalot, 1986). It was chosen as the type of *Placoneis* (Cox, 1987) because, out of the taxa included in that genus by Mereschkowsky (1903), *P. gastrum* was considered to present the least difficulty as far as its identity was concerned. Mann & Stickle (1995) have also used its reproductive behaviour as representative of the genus.

In the absence of specimens of *P. gastrum* in original Ehrenberg material, but the possibility that *N. amphibola* or another unnamed *Placoneis* sp. represent the taxon illustrated by Ehrenberg, retention of the established usage of *P. gastrum* requires the formal conservation of that name with a conserved type. Since its modern usage can be traced back unequivocally to Donkin (1873), and Donkin explicitly examined material from the Lough Mourne deposit (Figs 27–30), a Donkin slide from this locality (BM 12187) is the earliest material that can serve as a conserved type. It is therefore proposed that BM 12187, labelled '12 Lough Mourne Deposit. 1870 AS.D.' be conserved as the type of *P. gastrum* Ehrenberg. (BM 12186 is labelled '1 Loch Mourne Deposit. 1870. A.S.D.' but does not contain any specimens of *P. gastrum*.) A formal proposal to accept the conservation of the name *Pinnularia gastrum* Ehrenberg with a conserved type is in preparation.

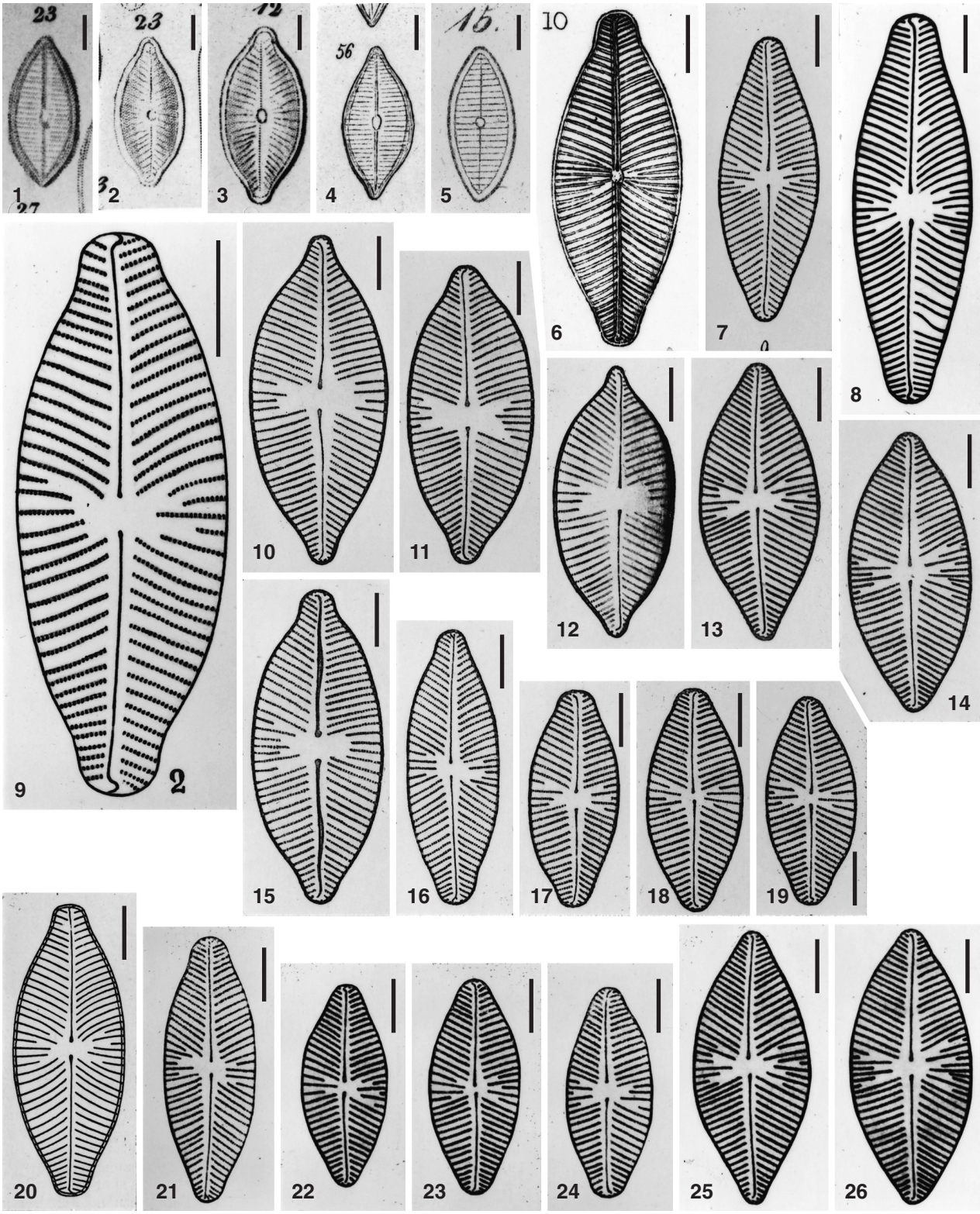
Placoneis gastrum (Ehrenberg) Mereschkowsky (Figs 27–32)

Basionym: Pinnularia gastrum Ehrenberg (1843) Phys. Math. Abhandl. K. Akad. Wiss. Berlin 1841: 421, pl 3, VII, fig. 23.

Type: BM 12187 (Lough Mourne deposit, 1870, Donkin)

Description: Valves broadly lanceolate, sometimes slightly wider on one side than the other, with broadly protracted, bluntly rounded apices, 30–60 μm long, 12–18 μm wide. Striae radiate throughout the valve, 8–10 in 10 μm, alternately longer and shorter around the central area, which is rounded to diamond-shaped. Striae composed of fine, but distinct, areolae and much narrower than the intervening virgae (SEM, cf. Cox, 1987: fig. 35). Raphe slits very slightly curved near the poles, slightly expanded at the centre and unilaterally deflected at the poles, but the polar curvature is difficult to see as it is very close to the apex.

In live material the central bridge of the chloroplast forms a strong curve, abutting the valve margin approximately midway between the valve centre and

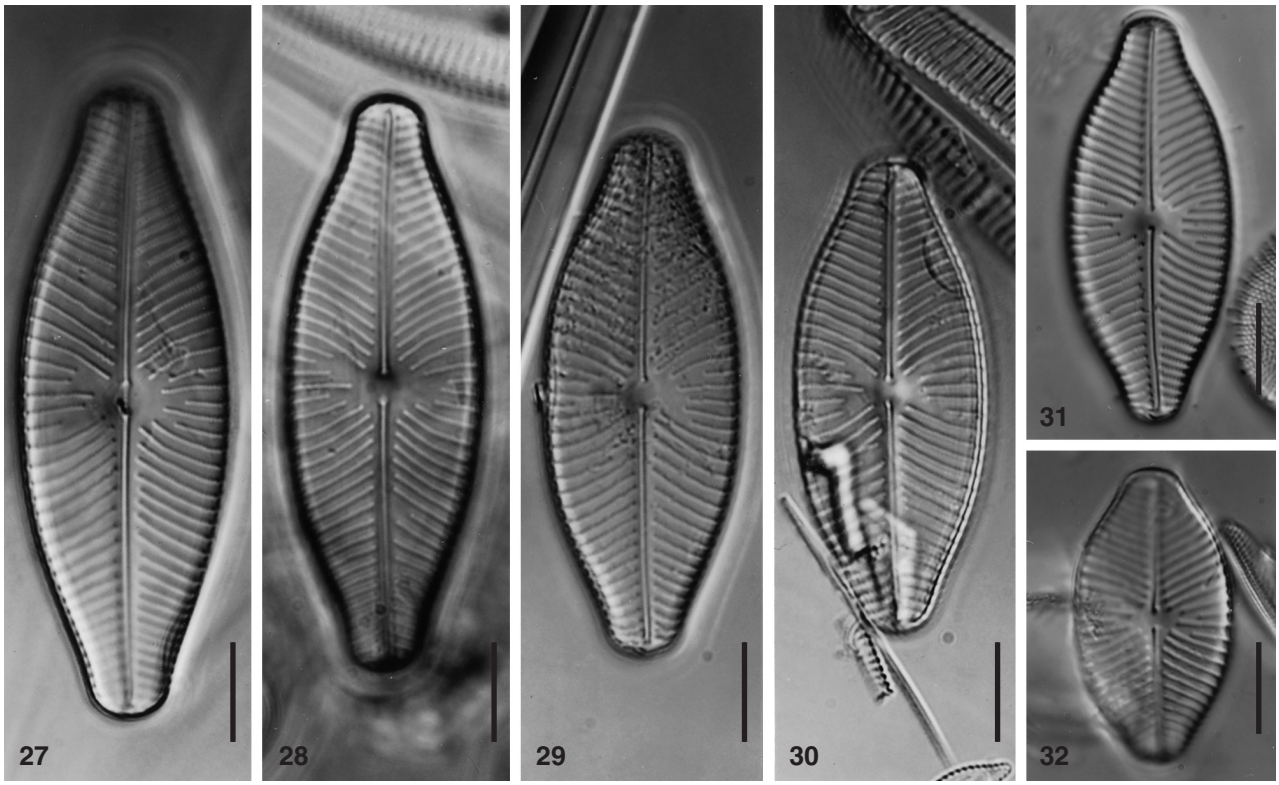


apices, slightly straighter for its central third. Two volutin droplets are often conspicuous and close to the central bridge (Cox, 1987: figs 1–4, Mann & Stickle, 1995: figs 5–8).

Distribution: Fossil and recent freshwater, mesoeutrophic to eutrophic (to slightly brackish) lakes. Lough Mourne deposit; Peterhead deposit; Malta; St Saturnin (Puy de Dôme), France; Gijon, Oviedo, Spain; Willershausen, Harz, Germany (Krasske), Wumme near Bremen, Wernigerode & Lübeck, Germany (Hustedt); Douglas Lake, Michigan, USA (Patrick & Reimer); New Caledonia (Manguin); E. African lakes (Gasse), including Lake Tanganyika; Holstein lakes (Schöhsee, Plußsee, Schluensee), N. Germany (E. J. Cox); Schlei estuary, Germany (Wendker); White Mere, Cheshire, England, Dunsapie & Duddingston Lochs, Edinburgh, Scotland (D. G. Mann).

PINNULARIA PLACENTULA EHRENBERG

Pinnularia placentula was published in 1843 (Ehrenberg, 1843: 421, pl. 3, VII, fig. 22) and illustrated again



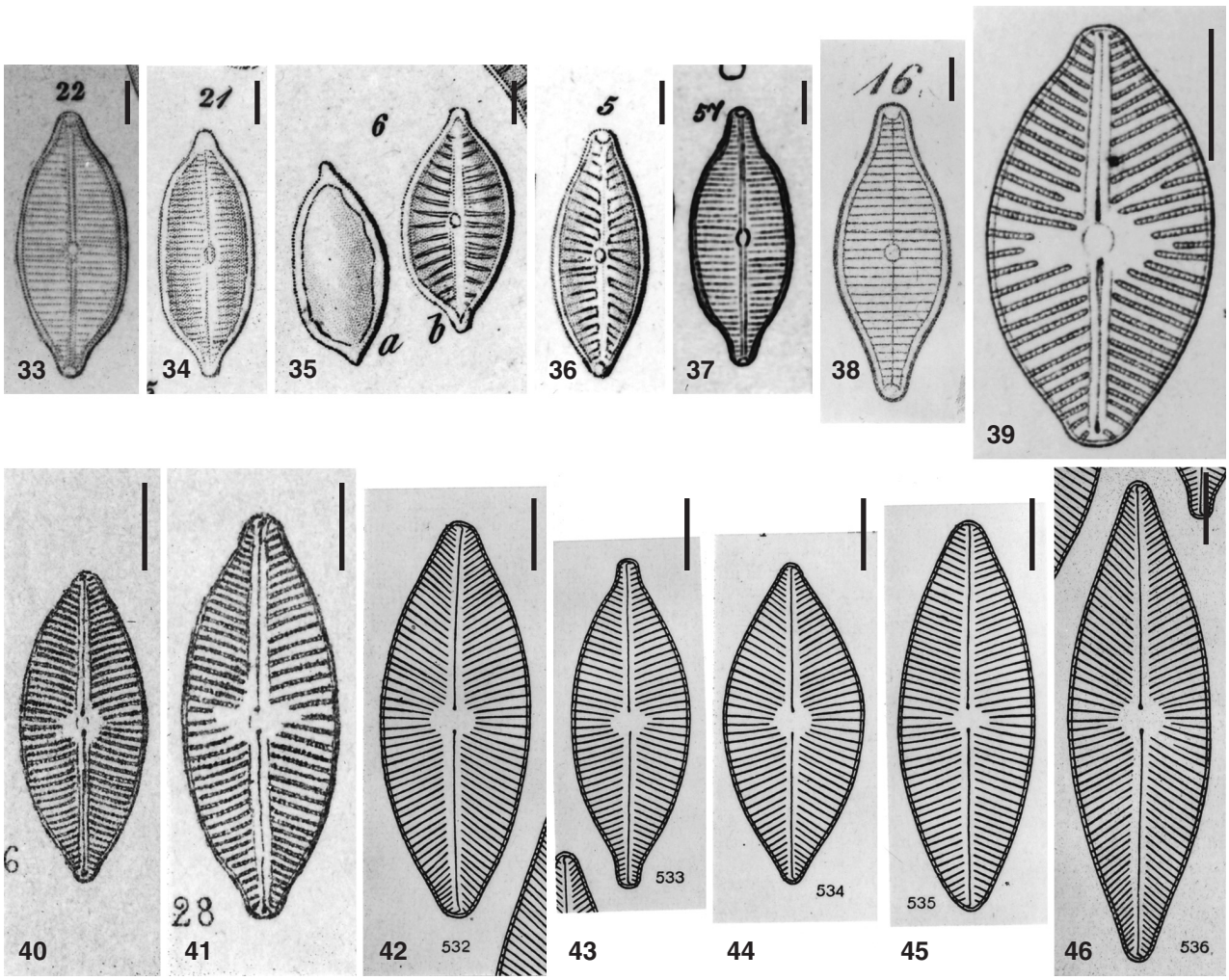
Figures 27–32. Light micrographs of *Placoneis gastrum* from slides in the Natural History Museum, London. Figs 27–30. BM 12187, Lough Mourne. Fig. 31. BM 68866, Gijon, Oviedo (Spain), freshwater fossil deposit. Fig. 32. BM 68953, Malta, freshwater fossil deposit. All scale bars represent 10 μm.

Figure 1–26. Illustrations of *Placoneis gastrum* from 19th century publications and various Hustedt publications. Scale bars = 10 μm. Fig. 1. *Pinnularia gastrum,* Vera Cruz, Mexico, Ehrenberg (1843): pl. 3, VII, fig. 23. Fig. 2. *Pinnularia gastrum,* diatomaceous earth, Mourne Mountains, Ireland, Ehrenberg (1854): pl. 15, fig. 23. Fig. 3. *Pinnularia gastrum,* fuel peat from Iceland, Ehrenberg (1854): pl. 5, I, fig. 12. Fig. 4. *Navicula gastrum*, Kützing (1844): pl. 28, fig. 56. Fig. 5. *Navicula gastrum*, Rabenhorst (1853): pl. 6, fig. 15. Fig. 6. *Navicula gastrum*, Loch Mourne deposit, Donkin (1873): pl. 3, fig. 10. Figs 7–26 Hustedt's illustrations of *N. gastrum*. Figs 8,9. Hustedt in A. Schmidt, Atlas (1934): pl. 398, figs 1,2, Wumme near Bremen, Germany. Figs 7,10–19. Hustedt in A. Schmidt, Atlas (1911): pl. 272, figs 9–19. Fig. 7. Klieken (fossil freshwater). Figs 10. Hainmühlen, Germany (recent freshwater). Figs 11–13. Ireland (fossil freshwater). Figs 14, 15. East Africa (recent freshwater) (III. Tanganyika Expedition). Figs 16. Bremen-Wumme, Germany (recent freshwater). Figs 17. Wernigerode, Germany (recent freshwater). Figs 18–19. Lübeck, Germany (recent freshwater). Fig. 20. Hustedt (1930): fig. 537. Figs 21–26. Hustedt (1966): fig. 771.

in the *Mikrogeologie* (Ehrenberg, 1854: pl. 8, II, fig. 6, pl. 8, III, fig 5 and pl. 15, fig. 21). The earliest figure (Ehrenberg, 1843) (Fig. 33) shows a broadly linear lanceolate valve with apiculate apices and parallel transverse striae from Vera Cruz. The later Ehrenberg figures (Figs 34–36, Mourne [Ireland], Zamuto and Arca [Hungary]) (Ehrenberg, 1854) differ from each other, although two (Figs 35,36) show slightly more radiate striae. Three specimens (Figs 34,35) have apiculate apices, the other (Fig. 36) more bluntly rostrate apices. As with *P. gastrum*, there was no mica for *P. placentula* from Vera Cruz, and no specimens approximating to Ehrenberg's drawing (Ehrenberg, 1843: pl. 3, VII, fig. 22) were found in the material.

Kützing (1844) and Rabenhorst (1853) seem to have reproduced Ehrenberg's first figure (Ehrenberg, 1843) (Fig. 33), but have drawn the apices more bluntly (Figs 37,38). The illustrations in Cleve & Grunow (1880: pl. 2, fig. 36) (Fig. 39) and Van Heurck (1880–1884: pl. 8, figs 26,28) (Figs 40,41) differ from each other, with that in Van Heurck (1880–1884) being closer to our current understanding of the species. Cleve & Grunow (1880) treated *N. placentula* as a species including several varieties, recognizing its close relationship with *N. gastrum*, whereas Ralfs (in Pritchard, 1861) and Van Heurck (1880–1884) treated it as a variety of *N. gastrum*. Patrick & Reimer (1966) wrote that 'Grunow (1880a [i.e. Cleve & Grunow, 1880): 34, pl. 2, fig. 36) was the first to use Ehrenberg's taxon correctly in the genus *Navicula*'.

Cleve & Grunow (1880) did not give any dimensions for *N. placentula* although their drawing shows a valve



Figures 33–46. Illustrations of *Placoneis placentula* from 19th century publications and Hustedt (1930). Scale bars = 10 μm. Fig. 33. Ehrenberg (1843): pl. 3, VII, fig. 22, Vera Cruz. Fig. 34. Ehrenberg (1854): 15, fig. 21, Mourne Mountains. Fig. 35. Ehrenberg (1854): pl. 8, II, fig. 6, Zamuto (Hungary). Fig. 36. Ehrenberg (1854): pl. 8, III, fig. 5, Arca (Hungary). Fig. 37. Kützing (1844): pl. 28, fig. 57. Fig. 38. Rabenhorst (1853): pl. 6, fig. 16. Fig. 39. Cleve & Grunow (1880): pl. 2, fig. 36. Figs 40,41. Van Heurck (1880–1884): pl. 8, figs 26,28. Figs 42–46. Hustedt's (1930) illustrations of *P. placentula*.

that is about 33 μm long and 18 μm wide. Subsequently, Cleve (1895) described *N. placentula* as 'elliptic-lanceolate, with rostrate, obtuse ends', 50–60 μm long, 16–28 μm wide, with 'coarsely lineate or punctate' striae. Although Cleve & Grunow (1880) recorded *N. placentula* from Jenissey, there is no record of this taxon in the index to their exsiccata set, nor of slides made from material collected from Jenissey. They (Cleve & Grunow, 1880: 34) comment that genuine ('authentische') examples (of *N. placentula*) can be found in 'Polirschiefer von Cassel' (polished slate from Kassel, Germany) but that these have little to do with Ehrenberg's illustrations. Slides of this material are not present in the Cleve & Möller series, nor have any yet been found in the NHM after an extensive search of herbarium material.

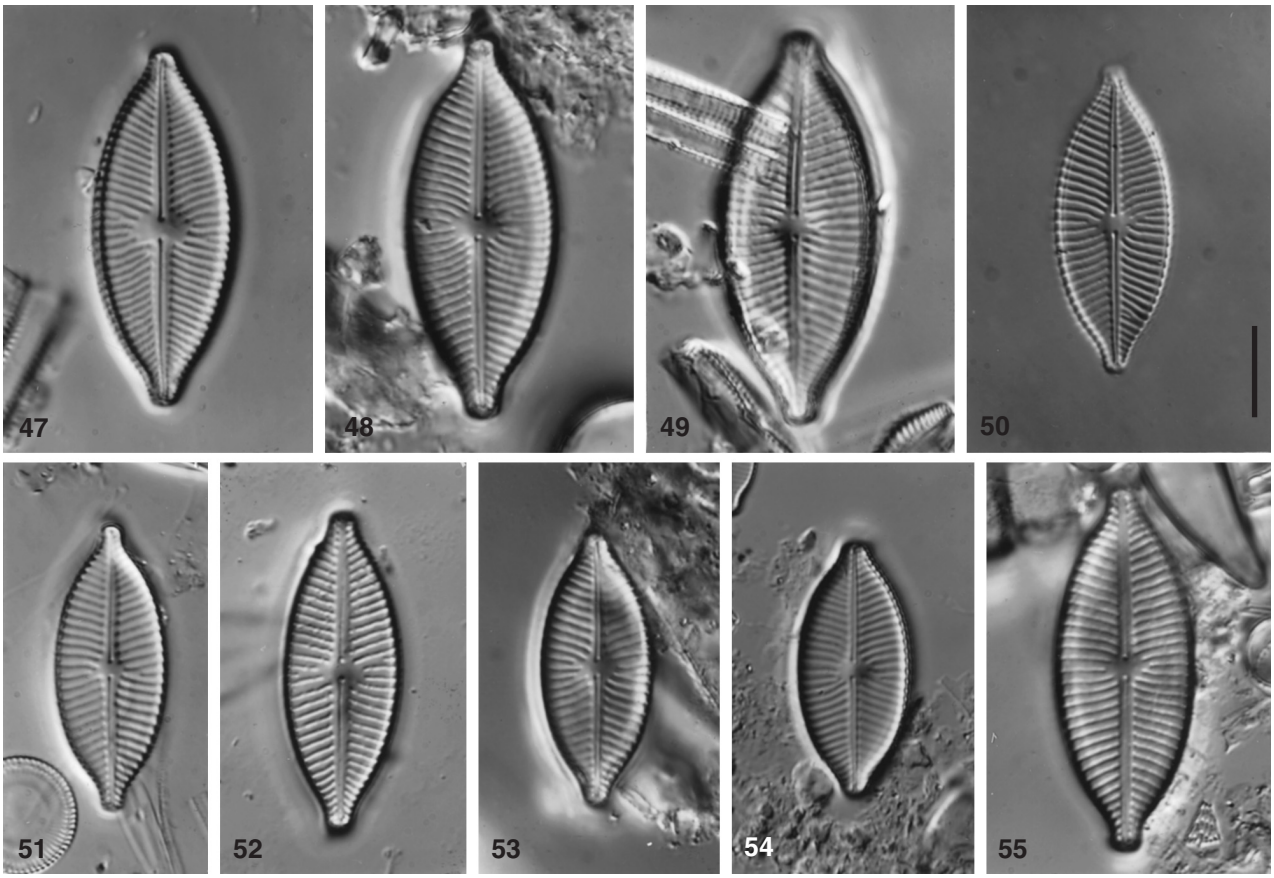
According to Van Heurck (1885), valves are 25–45 μm long and 12.5–17.5 μm wide. His drawings (Figs 40,41) show one valve (Fig. 41) that is approximately 48 μm long and 18 μm wide, and another (Fig. 40) (designated 'forma *minor*') that is about 37 μm long and 15 μm wide. Hustedt (1930), Patrick & Reimer (1966) and Germain (1981) gave a wider size range for this species, 30–70 μm long by 14–28 μm wide (by incorporating Cleve's size range?). However, Patrick & Reimer (1966) illustrated only a smaller specimen, about 33 μm long and 14 μm wide, and Germain (1981) stated that he had seen only smaller cells, about 35 μm long and 12 μm wide.

Krammer & Lange-Bertalot (1986) re-stated the size range as 30–70 μm long by 12–28 μm wide, but their illustrations do not match this range. The largest specimen is 50 μm long by 18 μm wide, the smallest 26 μm long and 12 μm wide (Krammer & Lange-Bertalot, 1986; plate 50). *Navicula subplacentula* Hustedt was treated as a different species, but Krammer & Lange-Bertalot (1986) stated that it shares the characteristics of *N. placentula*, apart from having oppositely deflected polar raphe fissures. However, comparing their illustrations of these taxa with those published by Simonsen (1987), Krammer & Lange-Bertalot (1986) do not appear to have illustrated any genuine specimens of *N. subplacentula* (*cf.* Krammer & Lange-Bertalot, 1986: fig. 50: 1–8 with Simonsen, 1987: pl. 199, figs 3,4, pl. 200, figs 1–3). Krammer & Lange-Bertalot (1986) include diatoms with both rostrate and apiculate apices in *N. placentula* and *N. subplacentula*, including the smallest specimens (20–25 μm long by 10–11 μm wide) under *N. subplacentula*. The lectotype of *N. subplacentula* (Simonsen, 1987: pl. 200, figs 1–3) is 60–65 μm long, 23–28 μm wide, with a distinctively curved inner raphe fissure (*cf.* Schmidt's Atlas, 1930: pl. 370, fig. 7). Thus, while the specimens illustrated (Krammer & Lange-Bertalot, 1986) for these two taxa can be considered representative of *N. placentula sensu lato*, they also highlight the confusion over the identity of this taxon.

The current definition of *P. placentula* allows for considerable variability within the species (Cox, 1986). Not only is the size range extensive, but variation is also observed in valve outline, apical shape and stria arrangement. The differences in size range and stria morphology (described above) suggest that Cleve (1895) had a different taxon in mind from that recognized subsequently by Patrick & Reimer (1966) and Germain (1981), and from the the smaller specimens illustrated by Krammer & Lange-Bertalot (1986). This is also clear from the number of different taxa purportedly belonging to *N. placentula* on the Tempère & Peragallo slides. For example, some valves are broadly lanceolate, tapering to slightly apiculate apices (Figs 47,106). Others are more or less parallel at the centre, narrowing more abruptly to well-defined, rostrate apices (Fig. 105).

Van Heurck (1885) described *N. placentula* as common in brackish water from Antwerp, although he did not produce a Types du Synopsis slide for this taxon. A search was therefore undertaken for other Van Heurck slides from the same locality (Van Heurck, 1885) to determine whether they contained specimens of *N. placentula* and could be used as a neotype for the species. Slide localities were checked in the index to the Types and other taxa recorded as 'saumâtres, Anvers' (brackish, Antwerp) were noted. If the appropriate slide was labelled 'Belgique' (Belgium) it was examined for specimens of *N. placentula*. BM 26422 (Van Heurck Types du Synopsis no. 111) had a few specimens of a small *N. placentula*, about 30 μm long and 12 μm wide (Fig. 51). Examining modern slides from the UK and Germany, predominantly smaller specimens of *N. placentula* were found (Figs 47–50,52–55). However, it is apparent that these probably represent several different morphs. One morph (smallest) is 30–40 μm long and 13–14 μm wide, with about nine striae in 10 μm (Figs 50–54), while the second (largest) is about 50 μm long and 18–19 μm wide, with about eight striae in 10 μm (Figs 47–49). A third 'intermediate' morph is about 45 μm long and 17 μm wide (Fig. 55), with less radiate striae and rather narrower apices than the largest morph. There are additional subtle differences in apex width and separation of the central raphe fissures, but in none of these is it possible to resolve pores within the striae.

Based on the 20th century accounts and illustrations, the current concept of the species seems to be based around specimens like those on the Van Heurck (BM 26422) and J.R. Carter slides (BM 93093, 93177, 95758). It is clear that further investigation of this species is required to determine the taxonomic status of the different morphs, bearing in mind that several genotypes may have been included in *P. placentula* (*cf.*



Figures 47–55. Light micrographs of *Placoneis placentula* from slides in the Natural History Museum, London. All figures to same magnification; scale bar = 10 μm. Fig. 47. BM 68866, Gijon, Oviedo (Spain), freshwater fossil deposit. Fig. 48. BM 93093, Lilliesleaf pond, England. (England finder reference, M39/1). Fig. 49. BM 93177, Wooden Loch, England. Fig. 50. Adams 169c, Würmsee, Germany. Fig. 51 BM 26422, Van Heurck, Types du Synopsis 111. Fig. 52. BM 95758, River Ane, England. Fig. 53. BM 93177, Wooden Loch, England. Fig. 54. Coll. E. J. Cox, Plußsee, Germany. Fig. 55. BM 93177, Wooden Loch, England.

Mann, 1984, 1989; Cox, 1986). Given that *P. placentula* may in future be shown to comprise several taxa, in order to avoid any future confusion over the typification of *N. placentula* (*cf.* Mann, 2001), a specimen of the largest morph (on BM 93093) has been designated as the neotype. The smallest morph (Figs 50–54) probably represents *N. placentula* fo. *minor sensu* Van Heurck (Fig. 40). If it is later shown that different genotypes exist, these should then be discriminated formally from *N. placentula sensu stricto*.

Placoneis placentula (Ehrenberg) Heinzerling (1908: 71, pl. 1, fig. 20 (Figs 47–55)

Basionym: Pinnularia placentula Ehrenberg (1843) Phys. Math. Abhandl. K. Akad. Wiss. Berlin 1841: 421, pl. 3, VII, fig. 22.

Type: BM 93093 (Lilliesleaf Pond), England finder reference M39/1.

Description: Valves broadly lanceolate to linear-lanceolate, 30–50 μm long, 12–20 μm wide, narrowing rather abruptly to apiculate apices, 3–5 μm wide. Striae slightly radiate throughout the valve, 8–11 in 10 μm, but without markedly longer and shorter alternate striae at the centre, although the central striae are slightly shorter opposite the rounded to diamond-shaped central area. The striae are biseriate with offset areolae (visible in SEM, *cf.* Cox, 1987: fig. 40). In LM the areolae cannot be resolved and therefore the striae appear slightly diffuse. Raphe fissures more or less straight throughout the valve, with oppositely deflected polar fissures and very slightly expanded central endings.

In live material the central bridge of the chloroplast is usually straight for most of its length, with a small droplet at each end, close to the chloroplast and to the cell apices (Cox, 1986: figs 3a–d,f–h; 1987: figs 7–10).

Occurrence: Recent and fossil freshwater, circumneutral mesotrophic or eutrophic to slightly brackish lakes. Peterhead deposit, Scotland; Gijon, Oviedo, Spain; Lilliesleaf Pond & Wooden Loch, England (J. R. Carter); Holstein lakes (Großser Binnensee, Kleiner Plöner See, Plußsee, Schluensee, Schöhsee, Tresdorfersee), Germany (E. J. Cox); Schlei estaury, Germany (Wendker); Laptev Sea, Arctic (Cremer); Mackenzie Delta, Canada (Campeau *et al*.); Altmühl, Bavaria, Germany (Reichardt); Bear Island, Arctic (Metzeltin & Witkowski).

Placoneis elginensis (Gregory) E. J. Cox

Gregory (1856) described and illustrated a new freshwater taxon, *Pinnularia elginensis,* which was subsequently transferred into *Navicula* by Ralfs (in Pritchard, 1861). Krammer & Lange-Bertalot (1986) illustrated a lectotype specimen from BM 11751 (designated by R. Patrick), but also included specimens from BM 23510, which is the lectotype for *Navicula tumida* syn. *Navicula anglica* Ralfs (i.e. *N. tumida* W.Sm.) (see below). BM 11751 is labelled '*Pinn. Elginensis*' and 'Elgin, Gregory'. This slide was examined but only one specimen of *P. elginensis* was found (Figs 56,57). However, additional specimens of this species were found on other slides from the same gathering (Fig. 58).

In their discussion of *N. elginensis* (*sensu lato*), Krammer & Lange-Bertalot (1986) argue that the type specimens (Krammer & Lange-Bertalot, 1986: fig. 46: 1–3) do not support the usual discrimination between *N. elginensis* and *N. anglica*, i.e. that diatoms with ± linear valves and a large, rectangular or elliptic-lanceolate, central area belong to *N. elginensis* (Figs 56–58), whereas those with a small central area belong to *N. anglica* (Figs 59–62). However, in considering the specimens on BM 11751 and BM 23510 as a single taxon, the use of valve outline as a means of discriminating between *N. elginensis* and *N. anglica* has been excluded. Krammer & Lange-Bertalot (1986) also failed to note that the central area in *N. elginensis* is angular and tends to occupy more than half the valve width, whereas in *N. anglica* it usually occupies less than half the valve width and is more rounded.

The illustrations of *P. elginensis* in Krammer & Lange-Bertalot (1986: fig. 46: 1–12) show a range of forms, some of which are rather linear, others more elliptical, with associated variation in the shape and extent of the central area. However, more recently Rumrich *et al*. (2000) have suggested that it is possible to recognize a number of taxa within this complex, i.e. *P. elginensis*, *P. paraelginensis* (see below), *Placoneis ignorata* (Schimanski) Lange-Bertalot and *Placoneis undulata* (Østrup) Lange-Bertalot (see p. 73 for discussion of these last two). Rumrich *et al*.'s (2000) argument for distinguishing *P. paraelginensis* from *P. elginensis* by its somewhat linear, rather than elliptical outline, suggests that they have assumed that the elliptical forms included by Krammer & Lange-Bertalot (1986) are true *P. elginensis*, rather than the more linear lectotype. The micrograph of the latter in Krammer & Lange-Bertalot (1986: fig. 46: 1) is poor. Re-examining the specimen on BM 11751 (Figs 56,57) clearly reveals its linear outline, and the data in Table 2 summarize the features distinguishing *P. elginensis* from similar species.

Placoneis elginensis (Gregory) E. J. Cox (1987): 155 (Figs 56–58)

Basionym: Pinnularia elginensis Gregory, 1856: 9, pl. 1, fig. 33

Lectotype: BM 11751 (designated by R. Patrick)

Description: Valves linear, 32 μm long, 9–10 μm wide, with subcapitate apices about 4–4.5 μm wide. Striae porate, 11 in 10 μm, radiate over almost all the valve, the central striae shorter forming a transverse, bow-tie-like, central area occupying more than half the valve width.

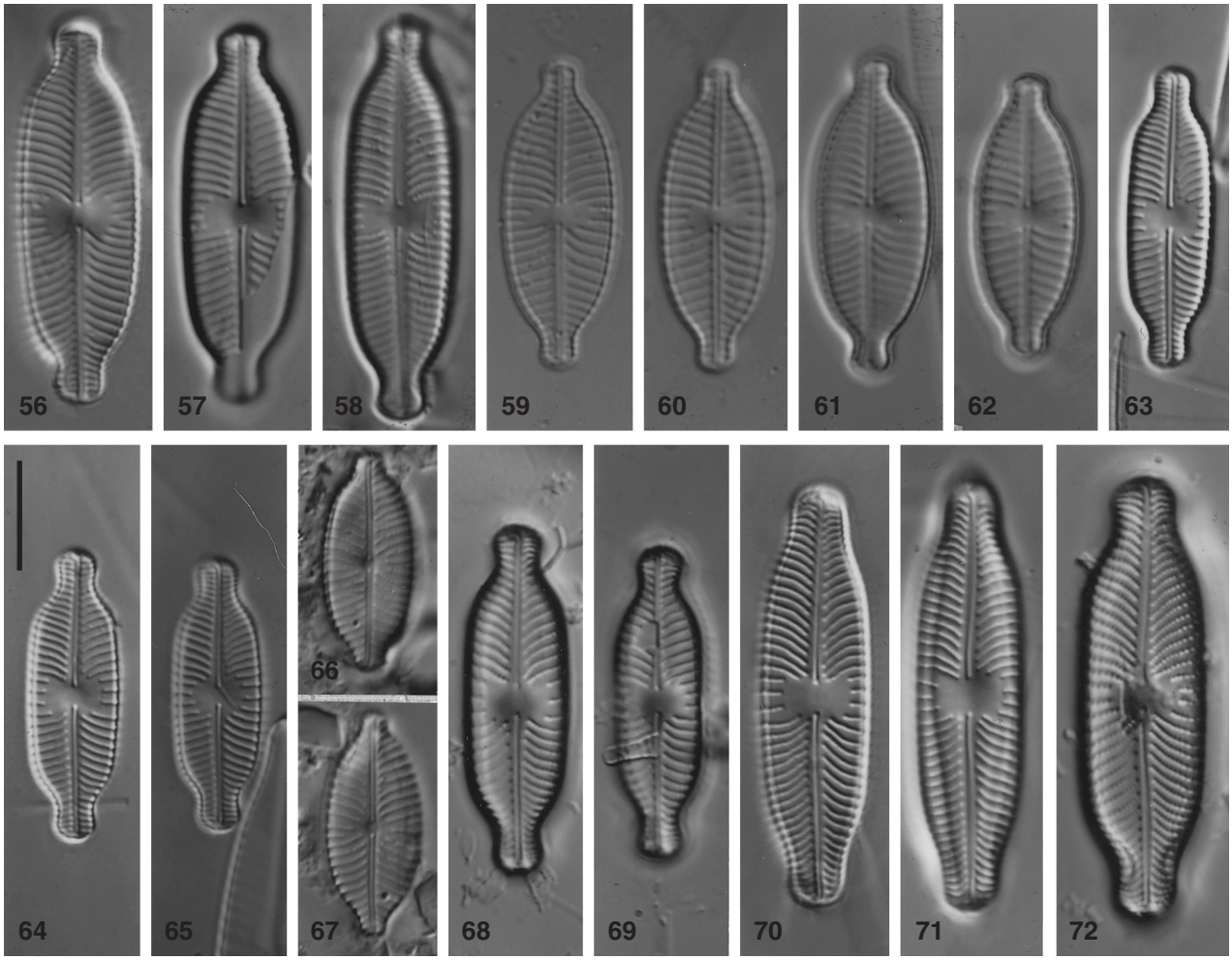
Information on live structure, and SEM illustrations of this taxon are currently lacking.

Distribution: Recent and fossil freshwater. Because a number of different taxa have been included under this name, its distribution requires closer investigation. Elgin, Scotland (Gregory slide); Ouen Thio, near Kouarga, New Caledonia (Manguin); Mittersee, N. Tirol, Austria (Lange-Bertalot & Metzeltin); Andes (Rumrich *et al*.).

Navicula anglica Ralfs

Ralfs (in Pritchard, 1861) first published the name *Navicula anglica* for a diatom based on *Navicula tumida* Wm. Smith. Smith had obtained material from Bramley near Guildford (England), from Capron in November 1850, and BM 23510 was probably made from this gathering. The label states: '*Navicula tumida*, Guildford, J.R. Capron Esq. misit Nov 4 1850'. Specimens on that slide agreeing with Smith's figure (Smith, 1853: pl. 17, fig. 146) are shown in Figs 59–62. The valves are elliptical, with well-defined, rostrate to subcapitate apices, radiating porate striae and a transverse central area. As discussed above, and based on the features documented in Table 2, these more elliptical forms on BM 23510 do not belong to *P. elginensis*, but require another epithet.

At the time Smith (1853) described his species, the same name was already applied to a different diatom, *N. tumida* Brébisson (Kützing, 1849) and therefore illegitimate. If Smith's name had been legitimate, the



Figures 56–72. Light micrographs of *Placoneis elginensis* and its allies from slides in the Natural History Museum, London. All figures to same magnification; scale bar = 10 μm. Figs 56,57. *P. elginensis*, both valves of a single specimen on BM 11751, Elgin, Scotland. Fig. 58. *P. elginensis* on BM 642, Elgin, Scotland. Fig.s 59–62. *P. anglica* on BM 23510, Guildford, England. Figs 63–65. *P. paraelginensis* on BM 26354, VH Types no. 43, England. Figs 66,67. *P. pseudanglica*, Plußsee, Germany. Figs 68,69. *Placoneis* sp. in Ehrenberg material from Iceland. Figs 70,71. *P. rostrata* on BM 26354, VH Types no. 43, England. Fig. 72. *P. abiskoensis* in Ehrenberg material from Iceland.

epithet '*tumida*' would be available for use in *Placoneis*. *Navicula tumida sensu* Brébisson is now placed in *Scolioneis* D. G. Mann. However, Ralfs (in Pritchard, 1861: 900) published the name *Navicula anglica* for Smith's taxon, providing a legitimate and validly published name for the species. Thus, following its transfer into *Placoneis*, the correct name for the species on Smith's slide (BM 23510) is now ***Placoneis anglica*** (Ralfs) E. J. Cox **comb. nov.**

Placoneis anglica (Ralfs) E. J. Cox **comb. nov.** (Figs 59–62)

Basionym: Navicula anglica Ralfs in Pritchard, 1861: 900.

Synonym: Navicula tumida Wm. Smith, 1853: 53, pl. 17, fig. 146.

Lectotype: BM 23510, *Navicula tumida*, Guildford (designated by P. A. Sims)

Description: Valves elliptical, 20–27 μm long, 8–9.5 μm wide, with well-defined, rostrate to subcapitate apices about 3 μm wide. Striae 10–11 in 10 μm, gently radiate over almost all the valve, shorter opposite the central raphe endings forming a transverse area occupying about half the valve width and more rounded than in *P. elginensis*. The central chloroplast bridge is almost straight and the droplets lie one near each apex, midway between the valves when the cell is seen

Table 2. Summary features of species around *Placoneis elginensis*

	P. abiskoensis	*P. anglica*	*P. elginensis*	*P. ignorata*[1]	*P. paraelginensis*	*P. pseudanglica*	*P. rostrata*[2]	*P. undulata*
Valve outline	linear to slightly undulate	elliptical to linear-elliptical	linear	bluntly lanceolate	linear	elliptical to linear-elliptical	linear	elliptic-undulate
Length (μm)	37–46	20–27	30–36	20–35	25–27	19–21	37	18–19
Breadth (μm)	9–12	9–10	9–10	7–10	~7	7–8	~ 9	~ 7
Apex shape	subcapitate	rostrate to subcapitate	subcapitate	tapered	subcapitate	rostrate to subcapitate	rostrate	rostrate
Apex width (μm)	5	2.5–3	4–4.5	n/a	3–3.5	2–3	5	2.5
Raphe path	slightly curved	straight	straight	straight	straight	straight	slightly curved	straight
Central ending separation (μm)	2.5	<2	~2	~2	<2	1.5	~3	1.5
Central area shape	transverse ellipse	transverse	bow-tie	transverse	transverse – bow-tie	rounded	transverse	transverse ellipse
Central area width	>1/2 valve	~1/2 valve	>1/2 valve	>1/2 valve	>1/2 valve	<1/4 valve	~1/2 valve	~1/2 valve
Stria density in 10 μm	10–11	10–11	~11	10–11	11–12	11–12	11–12	12
Pores visible in LM?	yes	no	no	yes	no	no	no	no
Angle of striae to raphe	41°	73–74°	74°	57–64°	68–69°	74–76°	57°	74–76°
Alternately longer/ shorter?	no	yes	no	no	no	yes	no	yes

[1]Based on Krammer & Lange-Bertalot (1986: fig. 46: 10–12)
[2]Based on Rumrich *et al.* (2000: pl. 60, Figs 11,12)

in girdle view (Cox, 1987: figs 18,19). For SEM illustrations, see Cox (1987) figs 34, 45 and 46 (identified as *P. elginensis sensu* Krammer & Lange-Bertalot, 1986).

Occurrence: circumneutral, mesotrophic and slightly eutrophic freshwaters. Guildford, England (W. Smith); Altmühl, Bavaria, Germany (Reichardt); Lake Fidler, Tasmania (Hodgson *et al*.); Julma Ölkky, Finland (Lange-Bertalot & Metzeltin); New Caledonia (Manguin); Holstein lakes (Großer Binnensee, Kleiner Plöner See, Schöhsee, Schluensee, Selenter See) & Hermelinquelle, Breitenbach, Hesse, Germany (E. J. Cox).

PLACONEIS PSEUDANGLICA (LANGE-BERTALOT) E. J. COX

Navicula pseudanglica Lange-Bertalot (Krammer & Lange-Bertalot, 1986) was based on *Navicula anglica* Ralfs *sensu* Hustedt, and separated from *N. elginensis* (*sensu lato*) on the basis of always having a small central area (Figs 66,67). However, Hustedt (1930) says that the central area can be transversely widened because the central striae are shorter, and in fact Krammer & Lange-Bertalot (1986) also state that the central area is rounded to weakly transversely widened. Hustedt (1930) offers a potentially useful criterion in noting that the central striae are not alternately longer and shorter. (Specimens of *N. anglica* from BM 23510 (Fig. 57) sometimes show this.)

Thus, based on the reassessment of *P. elginensis sensu lato* above, *P. pseudanglica* can be separated from *P. anglica*. *Placoneis pseudanglica* has a smaller, more rounded central area than either *P. elginensis* or *P. anglica*. In addition the striae of *P. pseudanglica* are not alternately long and short, nor do they radiate as strongly as in the other taxa (Figs 66,67). The specimens of *P. pseudanglica* illustrated in Krammer & Lange-Bertalot (1986: fig. 46: 13–15) are 21–28 μm long, 7–10 μm wide, with 2–3 μm broad apices, although they give a larger size range, 20–40 (50?) μm long, 8–14 (20?) μm wide. However, the largest of these (op. cit., fig. 46: 13) may represent another taxon, as it has a larger central area, broader apices, less radiate and slightly denser striae. *Navicula anglica* var. *signata* Hustedt (see Simonsen, 1987: pl. 477, figs 8–14) has linear-elliptical valves with rostrate apices, 20–22 μm long, 7–8 μm wide, with 11–12 striae in 10 μm. There is an isolated pore on one side of the central area and the area is rounded rather than transversely expanded.

Placoneis pseudanglica (Lange-Bertalot) E.J. Cox (1987): 155 (Figs 66,67)

= *Navicula pseudanglica* Lange-Bertalot (Krammer & Lange-Bertalot, 1986), *N. anglica sensu* Hustedt (1930)

Slides: Coll. E. J. Cox (Plußsee); var. *signata* Hustedt collection (Hust coll. N11/75. Breiter Lucin. 9 m 14.8.24).

Description: Valves linear-elliptical, 19–20 μm long, 7–8 μm wide, with well defined, rostrate to subcapitate, 2–3 μm broad, apices. Striae are gently radiate throughout, 11–12 in 10 μm, slightly shorter opposite the relatively small, rounded central area (less than quarter valve width approx.). A single isolated pore may be present on one side of the central area (var. *signata* Hustedt). The chloroplast has a fairly straight central bridge and the droplets usually lie close to the valve apices, but not within the rostrate apices (Cox, 1987: figs 11,12,17).

For SEM illustrations, see Cox (1987: figs 37,47,49,50).

Occurrence: Slightly eutrophic to eutrophic freshwater. Breiter Lucin, Mecklenburg, Germany (Hustedt); Holstein lakes (Schluensee, Schöhsee, Selenter See, Plußsee, Trammer See, Tresdorfer See) Germany (E. J. Cox); Mittersee, N. Tirol, Austria (Lange-Bertalot & Metzeltin); E. African lakes (Gasse); Bear Island, Arctic (Metzeltin & Witkowski); Siberia (Lange-Bertalot & Genkal).

PLACONEIS PARAELGINENSIS LANGE-BERTALOT AND ***PLACONEIS ROSTRATA*** (A. MAYER) E. J. COX **COMB. & STAT. NOV**

The illustrations of *P. paraelginensis* (Rumrich *et al*., 2000: pl. 60, figs 17–20), resemble the lectotype of *P. elginensis* (Krammer & Lange-Bertalot, 1986: fig. 46 : 1) in shape and stria arrangement, but, the cells are markedly smaller, suggesting that a different taxon is involved. Closer inspection suggests that Rumrich *et al*. (2000) have subsumed three taxa in the one species.

Van Heurck Types no. 43 (the holotype of *P. paraelginensis*) contains specimens of two diatoms (Figs 63–65,70,71) that are similar to, but not identical with, *P. elginensis*. One (Figs 70,71) is about 37 μm long and 9 μm wide, with broadly rostrate apices, about 5 μm wide, while the other (Figs 63–65) is smaller, 25–26 μm long, about 7 μm wide, with narrower (3.5 μm wide) subcapitate apices. The stria densities are about the same in each, 11–12 in 10 μm. Striae radiate through most of the valve but are shorter opposite the central area. The central raphe slits are more distant in the larger taxon (about 2.7 μm) than the smaller (1.5–1.8 μm). Because of the shape of the cell, i.e. the relative proportions of the

apices and valve dimensions, together with the slightly finer striae, the smaller specimens resemble *P. elginensis* more closely than the larger ones. The larger specimens can be distinguished from the type material of *P. elginensis* by the shape and proportions of the valve apices and the greater separation of the central raphe endings. The smaller specimens represent the taxon that typifies *P. paraelginensis* (Rumrich *et al*., 2000: pl. 60, fig. 18), listed as *Navicula dicephala* Kützing for that slide. The larger specimens resemble *N. elginensis* var. *rostrata* (Mayer) Patrick (Patrick & Reimer, 1966: pl. 50, fig. 6). I have not yet looked for Mayer material, so the description below is based on the specimens on Van Heurck Types du Synopsis no. 43.

The diatom illustrated in Figures 68,69 from Iceland resembles *P. paraelginensis* in shape and size, but has more widely spaced striae (*cf.* also Krammer & Lange-Bertalot, 1986: fig. 48:2; Rumrich *et al*., 2000: pl. 60, fig. 20). The valve apices are also rather subcapitate as opposed to rostrate. The third taxon (from Krasske material) figured under *P. paraelginensis* by Rumrich *et al*. (2000: pl. 60, fig. 17) is slightly narrower than the type specimens, with subcapitate rather than rostrate apices. There may therefore be at least two more taxa within this complex, but further work is required.

Placoneis paraelginensis Lange-Bertalot (Rumrich et al., 2000: 208) (Figs 63–65)

Synonym: Navicula dicephala forma *minor* (Ehr?) W. Smith, in Van Heurck (1880–1884): pl. 8, fig. 33.

Holotype: Van Heurck Types du Synopsis no. 43

Description: Valves linear, 25–27 μm long, about 7 μm wide, with subcapitate apices, 3.5 μm wide. Striae are radiate throughout the valve, 11–12 in 10 μm, slightly wider apart at the centre of the valve, and shorter opposite the central area. The configuration of the valves, including the central area, is very similar to *P. elginensis*, but the smaller dimensions, particularly the width of the valves favour its maintenance as a discrete species. In live cells the central chloroplast bridge forms a strong curve almost to the centre of the cell, and the droplets are central, near the base of the apices (Cox, 1987: figs 5.6).

For SEM illustrations see Figs 108–110, and Cox (1987) figs 36,48 (as *P. dicephala* (W. Smith) Mereschkowsky).

Occurrence: Recent and fossil freshwater (found on more humic sediments than other members of *Placoneis* in N. Germany). Hattenprice, England (Van Heurck slide); Iceland (Ehrenberg material); Holstein lakes (inflow to Großer Binnensee, ditch into Plußsee), Germany (E. J. Cox); Schwarzes Moor, Rhön, Germany (Krammer & Lange-Bertalot); Patagonia (Rumrich *et al*.); Schlei estuary, Germany (Wendker); Papua New Guinea (Vyverman).

Placoneis rostrata (A. Mayer) E. J. Cox **comb. & stat. nov.** (Figs 70,71)

Basionym: Navicula dicephala var. *rostrata* A. Mayer, 1917: 114, pl. 1, figs 42a,b.

Synonyms: Navicula elginensis var. *rostrata* (A. Mayer) Patrick in Patrick & Reimer (1966): 526, pl. 50, fig. 5; *Navicula dicephala* var. *chilensis* Hustedt (1927): 244, pl. 7, fig. 30, Simonsen (1987): pl. 167, figs 14–16; *Navicula abiskoensis* Hustedt *sensu* Krammer & Lange-Bertalot (1986): fig. 48:1.

Slides: BM 26357, Van Heurck Types du Synopsis no. 43; Hustedt Coll. 234/21. Loa, Chile. 11.o.

Description: Valves linear, about 37 μm long and 9 μm wide, with broadly rostrate apices, about 5 μm wide. Striae are radiate throughout the valve, 11–12 in 10 μm, shorter opposite the central area, which is consequently transversely expanded. The raphe slits are slightly curved, unlike *P. elginensis* and *P. paraelginensis*, and the central raphe endings are almost 3 μm apart.

No live structure or SEM information are available.

Distribution: Presumed mesotrophic to eutrophic freshwater. Hattenprice, England (Van Heurck slide); Loa, Chile (Hustedt); Patagonia (Rumrich *et al*.).

Navicula abiskoensis Hustedt

Hustedt (1942) described this species from Abisko (Lappland). The valves are linear or very slightly undulate, ending in subcapitate apices, with strongly radiate, areolate striae, the central ones shorter forming a broad central area. The raphe is slightly curved, like *P. rostrata*. However, it can be distinguished from *P. elginensis*, *P. paraelginensis* and *P. rostrata* by its size and shape, the angle of the striae and the clearly visible pores. Unfortunately, the illustration provided by Krammer & Lange-Bertalot (1986: fig. 48:1) does not represent this taxon, but *P. rostrata*. Simonsen (1987: pl. 456, figs 32,33) provides two micrographs of the taxon from Hustedt's original slide that clearly show that this is distinct from the taxa above. Metzeltin & Witkowski (1996: pl. 6, figs 1–6) illustrated *N. abiskoensis* from Bear Island, and published the new combination *Placoneis abiskoensis* (Hustedt) Lange-Bertalot & Metzeltin. This transfer is accepted. Specimens have also been found in Ehrenberg material from Iceland

Placoneis abiskoensis (Hustedt) Lange-Bertalot & Metzeltin (Metzeltin & Witkowski, 1996: 44) (Fig. 72)

Basionym: Navicula abiskoensis Hustedt, 1942: 118, fig. 36.
Holotype: Hustedt collection, N1/2 Abisko. 169. Abflußbach. A.
Other specimens: Ehrenberg, Iceland.

Description: Valves linear to slightly undulate, 37–46 µm long, 9–12 µm wide, with subcapitate apices. Striae strongly radiate, particularly near the raphe slits, then curving to become slightly less radiate, shorter opposite the transversely expanded central area, 10–11 in 10 µm, distinctly areolate, 20–23 pores in 10 µm.

Distribution: Seems to be a more northern species, in oligotrophic to mesotrophic lakes. Abisko, Sweden (Hustedt); Iceland (Ehrenberg material); Schöhsee, Germany (E. J. Cox); Bear Island, Arctic (Metzeltin & Witkowski); Julma Ölkky, Finland (Lange-Bertalot & Metzeltin).

Navicula semen Ehrenberg *sensu* Donkin

Ehrenberg (1875) used the epithet '*semen*' with two generic names. According to him (Ehrenberg, 1875: 56), *Navicula semen* (Ehrenberg, 1875: 192) was designated in 1841 (Ehrenberg, 1843: 419), and illustrated in *Mikrogeologie* from Degernfors (Sweden) (Ehrenberg, 1854: pl. 16, I, fig. 11) (Fig. 79). However, there are also records of *N. semen* from plant roots from Chile (Ehrenberg, 1843: 300, pl. 1, II, fig. 17a) (Fig. 73), and from a soil (sediment) sample around liverworts and *Hippuris vulgaris* from Okak, Laborador (Canada) (Ehrenberg, 1843: 360, pl. 4, II, fig. 8) (Fig. 74). Hustedt (1966) cited the Chile illustration (Fig. 73) as the first figure of this taxon.

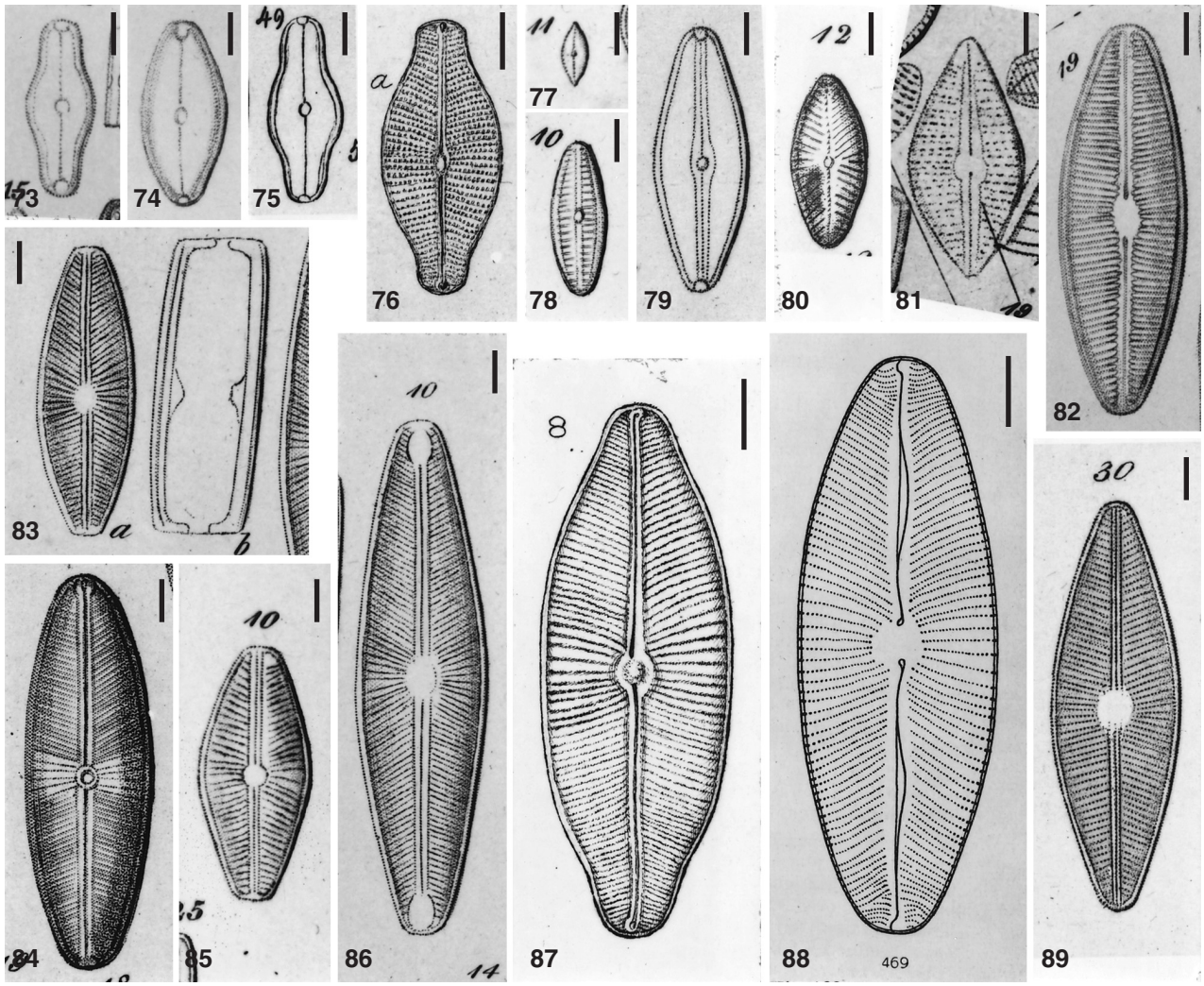
Pinnularia semen was designated and illustrated in the *Mikrogeologie* from Norwich, Connecticut (Ehrenberg, 1854: pl. 33, XIV, fig. 19) (Fig. 81). The Nachtrag (Ehrenberg, 1875: 198) indicates that *P. semen* was named and illustrated in another plate in the *Mikrogeologie* from Morea (Greece) (Ehrenberg, 1854: pl. 6, II, fig. 10) (Fig. 78), while Ehrenberg (1873: 276–7) gave yet another reference for *P. semen*, i.e. ' 1854: pl. 14, fig. 12 (Brakisches Erdlager unter Berlin)' (= brackish earth layer below Berlin, Germany) (Fig. 80). Careful reading of the figure legends for the *Mikrogeologie* (Ehrenberg, 1854) revealed that there were 14 illustrations of these taxa from different localities (Appendix 2) (Figs 73,74,77–81).

Ehrenberg (1854) seems to have been uncertain of the identity of some of the specimens he illustrated because the names are sometimes followed by a question mark (Appendix 2). However, it is apparent from the illustrations that Ehrenberg considered *N. semen* and *P. semen* to be different taxa; radiate striae are clearly shown for *P. semen* but stria detail is missing for *N. semen*. In the Index to the Ehrenberg collection (CD-ROM, Lazarus & Jahn, 1998) *N. semen* was from 'Isle de France' (Mauritius) (drawing sheets 858, 2247) and Laborador (Canada) (drawing sheets 873, 2078), while *P. semen* came from Berlin (drawing sheets 975, 2230).

Smith (1853: 50) applied the name *N. semen* Kützing (Kützing, 1844), ostensibly based on Ehrenberg (1843) pl. 4 II fig. 8, although Kützing's illustration (Fig. 75) is closer to Ehrenberg (1843) pl. I, II, Fig. 17a (compare Figs 73,74), a different diatom. Smith illustrated (1853: pl. 16, fig, 141) a *P. gastrum*-like specimen with radiate striae from the Peterhead (Scotland) deposit (Fig. 76). Subsequently, Donkin (1873) gave *P. semen* and *Amphiprora navicularis* Ehrenberg as synonyms of *N. semen*, stating explicitly that he had followed Smith's (1853) interpretation of *N. semen*, 'which is identical with *Amphiprora navicularis* Ehrenberg'. But Donkin also states that, 'It is difficult to say what species is meant by Ehrenberg as *Pinnularia semen*, as different species are figured under this name in the "Mikrogeologie," one of these only being striated (i.e. Ehrenberg, 1854: pl. 14, fig. 12 [Berlin], Fig. 80) and apparently identical with *Pin. Gastrum*' (i.e. Ehrenberg, 1854: pl. 15A, fig. 23 [Mourne], Fig. 2).

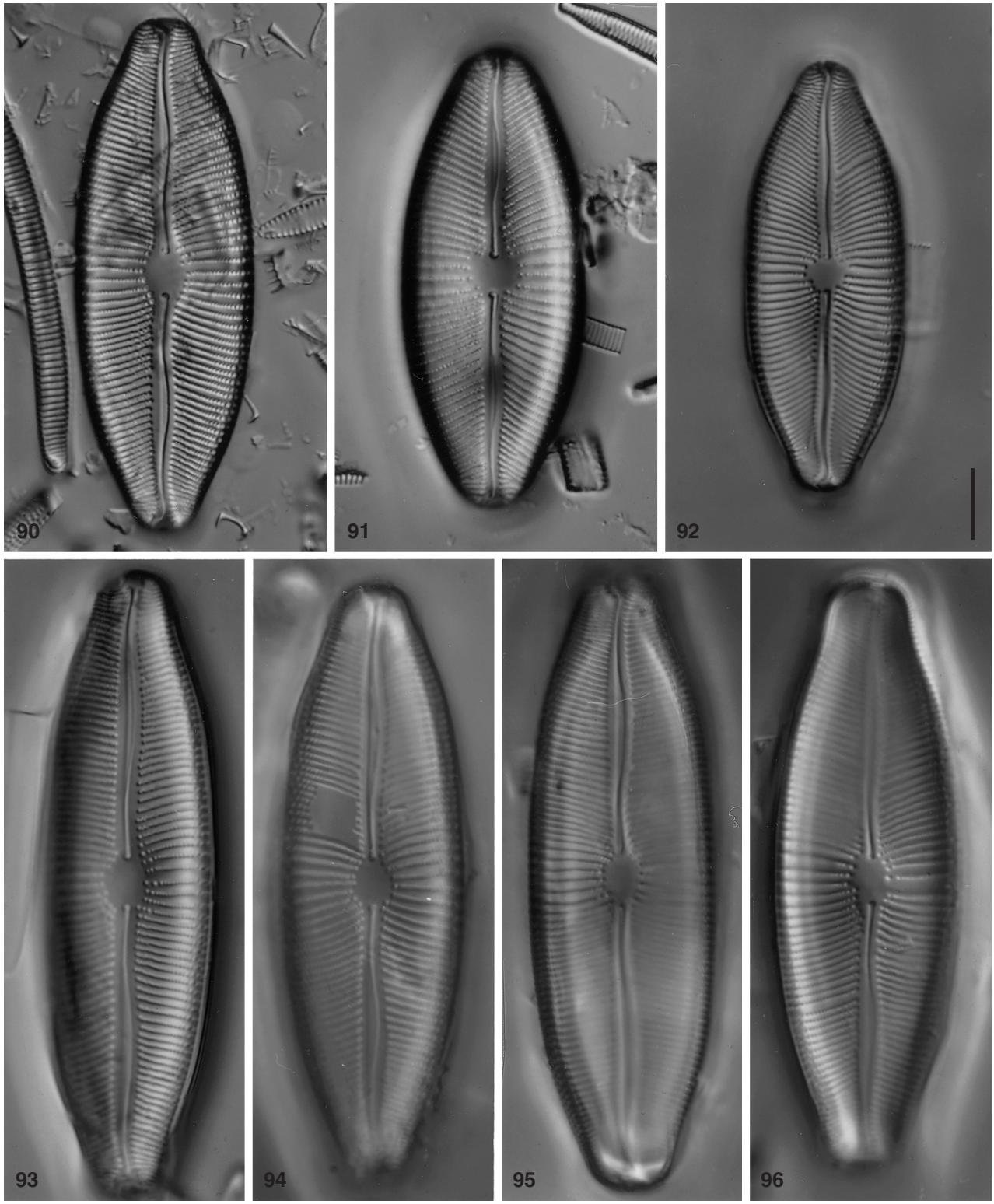
According to Ehrenberg (1875: 170), *A. navicularis* Ehrenberg was described in 1843 from West-Point, New York, Smithfield, Rhode Island, and Pelham, Massachusetts (USA) (Ehrenberg, 1843: 410), and illustrated from Loka (Sweden) (Ehrenberg, 1854: pl. 16, III, fig. 30). There are several other figures of the taxon from different localities in the *Mikrogeologie* (Ehrenberg, 1854) (Figs 82–86,89). Pelham and Westpoint are given as localities for *A. navicularis* in the Index to the Ehrenberg collection (Lazarus & Jahn, 1998), with reference to drawing sheets (98, 99, 2233).

The correspondence between specimens of *A. navicularis* Ehrenberg in material from Pelham (Figs 90,91), and those of *N. semen sensu* Donkin (1873) confirm that the modern concept of *N. semen* (Figs 90–96) is not derived from Ehrenberg's taxon of that name, but rather from A. *navicularis*. It is very probable that Ehrenberg's *P. semen* and *N. semen* represent quite different, smaller taxa with less distinct wall markings, although further work is required to confirm this. Whereas Donkin (1873) said that he was following W. Smith's (1853) concept of *N. semen*, closer examination of their illustrations (Figs 76,87) reveals discrepancies between their interpretations. Smith's illustration is much closer to *P. gastrum* than *N. semen* (*sensu* Donkin), and when BM 23481, which is labelled as containing *N. semen* from the Peterhead deposit, was examined the ringed specimen was found to be *P. gastrum*.



Figures 73–89. Illustrations of *Navicula semen*, *Pinnularia semen* and *Amphiprora navicularis* from 19th century publications and Hustedt (1930). Scale bars = 10 μm. Fig. 73. *Navicula semen*? Ehrenberg (1843): pl. 1, II, fig. 17a, Chile. Fig. 74. *Navicula semen*, Ehrenberg (1843): pl. 4, II, fig. 8, Okak, Labrador. Fig. 75. *Navicula semen*, Kützing (1844): pl. 28, fig. 49. Fig. 76. *Navicula semen*, W. Smith (1853): pl. 16, Fig. 141. Fig. 77. *Navicula semen*? Ehrenberg (1854): pl. 1, III, Fig. 11, 'Isle de France' (Mauritius). Fig. 78. *Pinnularia semen*, Ehrenberg (1854): pl. 6, II, fig. 10, Morea, Greece. Fig. 79. *Navicula semen*? Ehrenberg (1854): pl. 16, I, fig. 11, Degernfors, Sweden. Fig. 80. *Pinnularia semen*, Ehrenberg (1854): pl. 14, Fig. 12, Berlin. Fig. 81. *Pinnularia semen*? Ehrenberg (1854): pl. 33, XIV, fig. 19, Norwich, Connecticut, USA. Fig. 82. *Amphiprora navicularis,* Ehrenberg (1854): pl. 2, II, fig. 19. Fig. 83. *Amphiprora navicularis,* Ehrenberg (1854): pl. 3, I, fig. 11a,b. Fig. 84. *Amphiprora navicularis,* Ehrenberg (1854): pl. 2, II, fig. 16. Fig. 85. *Amphiprora navicularis,* Ehrenberg (1854): pl. 5, I, fig. 10. Fig. 86. *Amphiprora navicularis,* Ehrenberg (1854): pl. 3, III Fig. 10. Fig. 87. *Navicula semen*, Donkin (1873): pl. 3, fig. 8. Fig. 88. *Navicula semen*, Hustedt (1930): fig. 469. Fig. 89. *Amphiprora navicularis,* Ehrenberg (1854): pl. 16, III, fig. 30.

Although no Donkin material was available for SEM, specimens of *A. navicularis* in Pelham material were examined with SEM. This confirmed that the striae were areolate, the pores occupying far less space than the intervening virgae, like those in *P. gastrum*. Some striae were entirely uniseriate, but others were biseriate near the raphe slits, uniseriate towards the valve margin and over the apices (Figs 97–100). This can also be detected in the light micrographs (Figs 90–96). The curvature and unilateral apical deflection of the external raphe fissures are confirmed (Figs 97–99). As in other *Placoneis* spp. the external central raphe endings are slightly expanded (Figs 97,99) and the internal central raphe endings are unilaterally deflected (Fig. 101). A small helictoglossa is present at the internal polar raphe ending (Fig. 102). Girdle



Figures. 90–96. Light micrographs of *Placoneis navicularis* from Ehrenberg material and slides in the Natural History Museum, London. All figures to same magnification; scale bar = 10 μm. Fig. 90. Ehrenberg material from Pelham, USA. Fig. 91. Ehrenberg material from Iceland. Figs 92–96. *P. navicularis.* Figs 92,93. BM 26409, Van Heurck Types no. 98. *Navicula semen* W. Sm. England. Figs 94–96. BM 6989, '*Navicula semen* 1869 AS.D.'

bands have a single row of areolae (Fig. 98) and the valve mantle is deeper distal to the apices. Based on its ultrastructure it belongs in *Placoneis*.

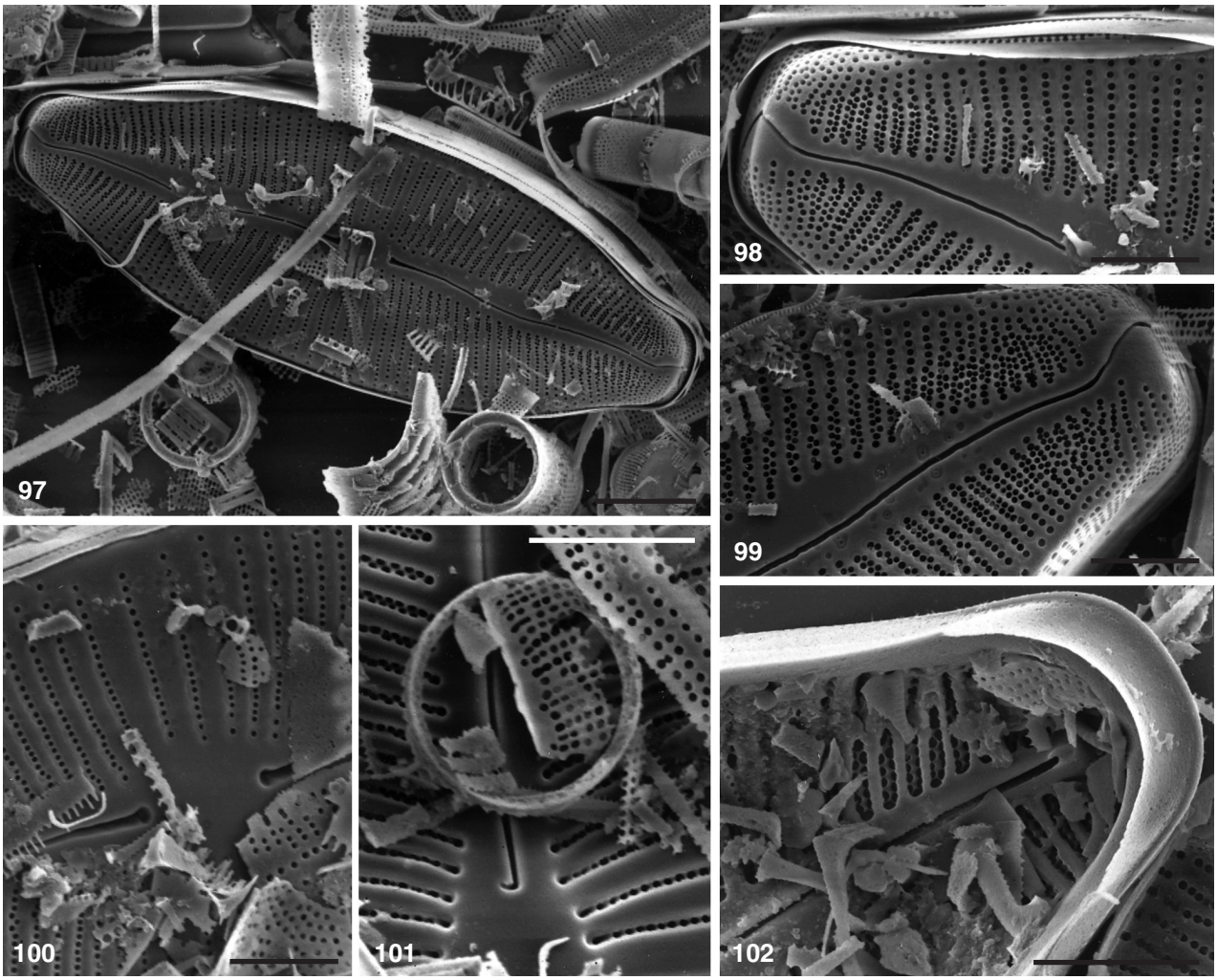
Since the taxon currently named *N. semen* is clearly conspecific with *A. navicularis* Ehrenberg, the epithet *navicularis* would be more appropriate. Whereas this combination would not have been favoured as long as the species was in *Navicula*, since it belongs in *Placoneis*, the combination is acceptable. Although the species has been recorded in the interim, it is not a common diatom and a name change will not introduce the type of confusion anticipated for *P. gastrum* or *P. placentula*. I therefore propose a new combination *Placoneis navicularis*, based on type material from Pelham. The slide from which the LMs were made will be deposited with the Ehrenberg collection in Berlin, and a duplicate lodged in The Natural History Museum, London.

Placoneis navicularis (Ehrenberg) E. J. Cox **comb. nov.** (Figs 90–96)

Basionym: Amphiprora navicularis Ehrenberg, 1843, Phys. Ahb. Akad. Wiss. Berlin 1841: 410; Ehrenberg (1854): pl. 16, III, fig. 30.

Synonym: Navicula semen sensu Donkin, 1873: 21, pl. 3, fig. 8; non *N. semen sensu* W. Smith (1853): 50, pl. 16, fig. 141.

Lectotype: Eco-006 Ehrenberg, Pelham Massachusetts (USA) (BHU)



Figures 97–102. SEMs of *Placoneis navicularis* from original material held in the Ehrenberg collection (BHU). Scale bar in Fig. 101 = 10 μm, all other scale bars = 5 μm. Figs 97–101. 102. *P. navicularis* from diatomite from Pelham, USA (Ehrenberg). Fig. 97. External view of whole frustule. Figs 98,99. External ends of valve showing polar raphe endings and biseriate striae near raphe slit. Fig. 100. Detail of external central raphe ending. Fig. 101. Internal view of central raphe ending. Fig. 102. Internal view of polar raphe ending.

Description: Valves bluntly lanceolate, sometimes with very slightly rostrate apices, 50–90 μm long, 20–27 μm wide. Raphe slit sinuate on the outer surface, slightly expanded at the centre, extending over the apical valve margin, and deflected to the same side at the apices. Striae slightly radiate throughout most of the valve, 8–10 in 10 μm, slightly wider at the centre, convergent at the apices, apparently (LM) with very short striae inserted at the changeover point. Striae composed of areolae, arranged in double rows near the raphe (SEM), but single in the central striae and towards the valve margins. Central area slightly expanded, oval.

Distribution: Northern species, abundant in interglacial fossil freshwater sediments avoiding strongly alkaline waters, but frequent in moss at about pH 7.0 (Hustedt, 1942, 1966). Pelham, Massachusetts, USA, & Iceland (Ehrenberg material); Lough Mourne & England (Donkin); England (Van Heurck slide); Poggenpohls Moor, Oldenburg, Germany (Hustedt).

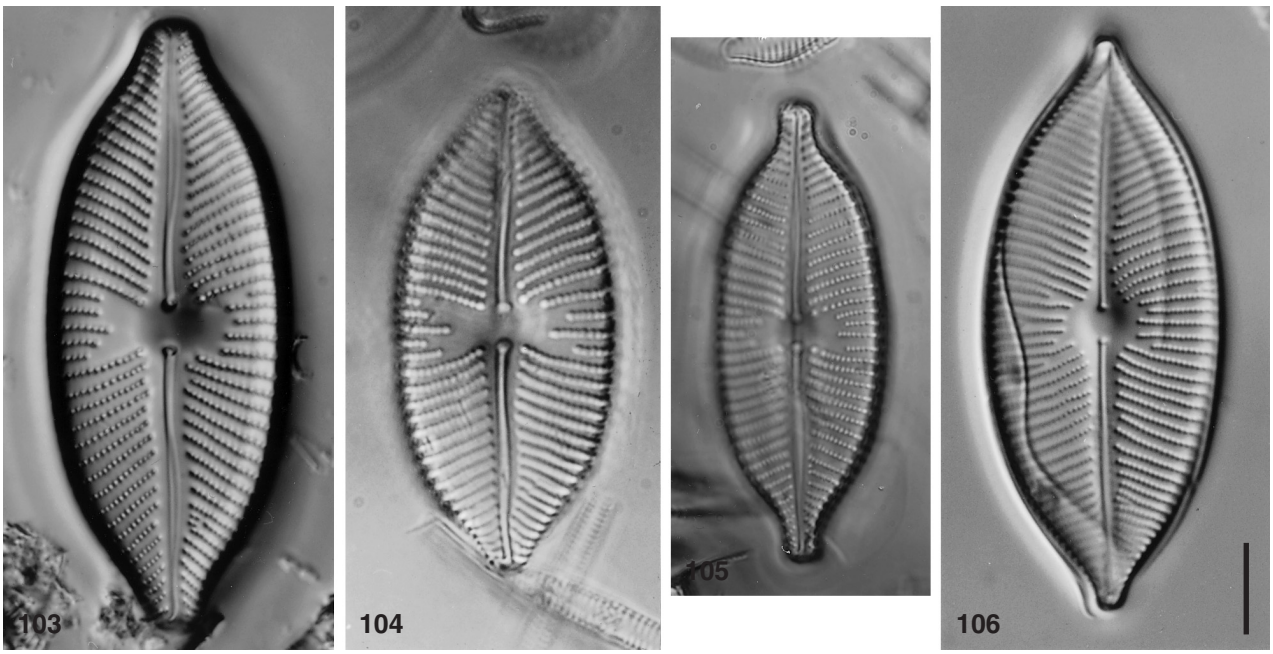
Navicula amphibola Cleve

Cleve (1891) recorded *N. amphibola* from Finland, giving *Navicula punctata* var. *asymmetrica* Lagst. and *N. gastrum* var? *styriaca* Grun. as synonyms. It was given a new name because, although Cleve (1891) would have liked to use the epithet *styriaca* at the specific level, that epithet was already occupied within *Navicula*. There is reasonable agreement between the illustrations shown by Lagerstedt (1873) and Grunow (1882) although they differ in dimensions. Lagerstedt (1873: pl. 2, fig. 7) shows a valve that is 62 μm long, 26 μm wide, whereas the Grunow (1882: pl. 30, fig. 50) specimen is smaller, 47 μm long and 18 μm wide. Cleve (1895) gives the dimensions of *N. amphibola* as 37–70 μm long, 20 μm wide. Hustedt (1944) commented that *N. amphibola* is closer to *N. gastrum* than to the *Naviculae punctatae*, where it was placed by Cleve (1891). However, Hustedt (1944) was perhaps imposing his 20th century concept of the *Naviculae punctatae*, whereas Cleve (1891) admitted to some uncertainty about his taxonomic arrangement. Cleve (1891) considered that the *punctatae* and *radiosae* (where *N. gastrum* was placed) were connected via *N. placentula*, and that *Cymbella* C.A. Ag. was closely connected to both of these groups.

Placoneis amphibola (Cleve) E. J. Cox **comb. nov.** (Figs 97,98)

Basionym: Navicula amphibola Cleve, 1891: 33.

Material: BM 12187, Lough Mourne; Ehrenberg, Iceland.



Figures 103–106. Light micrographs of *Placoneis amphibola* and some unidentified *Placoneis* species from Ehrenberg material and slides in the Natural History Museum, London. All figures to same magnification; scale bar = 10 μm. Figs 103,104. *P. amphibola*. Fig. 103. Ehrenberg, Iceland. Fig. 104. BM 12187 Lough Mourne. Figs 105,106. Unidentified *Placoneis* spp. Fig. 105. BM 68867, Bory (Hungary), freshwater fossil deposit. Fig. 106. BM 69051, Jastraba (Hungary), freshwater fossil deposit.

Description: Valves linear-elliptic to linear-lanceolate, 37–75 μm long, 22–27 μm wide, narrowing to subrostrate to broadly subapiculate apices. Striae coarsely areolate, radiate, 7–8 in 10 μm, shorter at the centre of the valve to form a bow-tie like transverse central area. Raphe slit with a straight outer fissure, undulate inner fissure. Central raphe endings expanded, terminal ones deflected towards one side.

Distribution: According to Krammer & Lange-Bertalot (1986) the species has a nordic-alpine distribution in Europe, and also occurs in freshwater fossil deposits. Lough Mourne, Ireland; Iceland (Ehrenberg material); N.W. Siberia (Lange-Bertalot & Genkal); Mackenzie Delta, Canada (Campeau *et al*.); Laptev Sea, Arctic (Cremer).

Navicula subplacentula Hustedt

This species was first published by an illustration in Schmidt's Atlas (1930), and later mentioned (Hustedt, 1944) in the context of a broader discussion of the morphology of *N. gastrum*, *N. placentula* and similar taxa. Hustedt (1944: 281–282) described *N. subplacentula* as having oppositely deflected polar raphe fissures, marked deflection of the inner raphe fissures near the valve apices, and striae comprising double rows of alternate areolae, but otherwise (im übrigen) looking very similar to *N. placentula*. The use of 'im übrigen' (i.e. otherwise) is slightly confusing because it seems to imply that *N. placentula* has single rows of areolae, whereas earlier Hustedt (1944: 278) explicitly stated that *N. placentula* has double rows of very fine areolae. In fact it is the path of the inner raphe fissure that is the best distinguishing character, together with the contrasting sizes of the taxa. Simonsen's illustrations (Simonsen, 1987: pl. 200, Figs 1,3) also show that the internal central raphe endings are hooked in opposite directions.

Placoneis subplacentula (Hustedt) E. J. Cox **comb. nov.**

Basionym: Navicula subplacentula Hustedt in Schmidt's Atlas, 1930: pl. 370, fig. 7.

Lectotype: Hustedt collection, N8/24. Tanganikasee (sic), 6. (Designated by Simonsen, 1987)

Description: Valves broadly lanceolate, 55–65 μm long, 23–28 μm wide, tapering to subapiculate apices. Striae radiate throughout, about 8–9 in 10 μm, comprised of double rows of areolae, with a single shortened stria inserted on either side opposite the central area, which is slightly transversely expanded. Raphe more or less straight throughout with oppositely deflected polar fissures; the internal fissures are markedly deflected near the apices with hooked central endings turning in opposite directions.

Distribution: Described from Africa (Lake Tanganyika). Skvortzov (1937) described a variety of this taxon from Lake Baikal although this lacks the internal raphe fissure deflection of the nominate variety. It is illustrated only by a drawing and further work is required to confirm its identity.

Placoneis ignorata (Schimanski) Lange-Bertalot and *Placoneis undulata* (Østrup) Lange-Bertalot

These taxa were first recognized as discrete species within *Placoneis* by Rumrich *et al*. (2000), having previously been included within *N. elginensis* (Krammer & Lange-Bertalot, 1986). Original material has not been examined during this study, but based on the published illustrations (Schimanski, 1978; Rumrich *et al*., 2000) there is no reason to doubt their position in *Placoneis*. It is clear from the comparison of LM features (Table 2) that they can be distinguished from *P. elginensis* and similar species.

Specimens from central Chile were illustrated by Rumrich *et al*. (2000: pl. 60, figs 11,12). It has been suggested that *P. ignorata* is holarctic and *P. undulata* has been illustrated from north Tirol, Austria (Lange-Bertalot & Metzeltin).

New combinations

The following new combinations are made, based on examination of Simonsen's (1987) figures of Hustedt's original material. In all cases valves are elliptical, bluntly lanceolate to elliptical or linear elliptical, usually with bluntly rounded, subrostrate to rostrate apices. Striae are areolate and clearly finer than the intervening virgae, radiate throughout the valves and often alternately longer and shorter around the central area. The central raphe endings are slightly expanded and the raphe fissures are slightly sinuate in *P. insignita*, *P. interglacialis* and *P. subgastriformis*. The polar raphe endings are usually deflected, but it is not always clear if they are deflected to one side or in opposite directions. It would clearly be preferable to obtain confirmatory live and SEM information, but visual comparisons with *P. gastrum* and other members of *Placoneis* indicate close relationships between all these taxa.

Placoneis constans (Hustedt) E. J. Cox **comb. nov.**

Basionym: Navicula constans Hustedt, 1944: 284, fig. 13.

Holotype: Hustedt collection, N14/33. Oberohe. 66.

Micrographs: Simonsen, 1987, plate 476, figs 1–5.

Other records: Julma Ölkky, Finland (Lange-Bertalot & Metzeltin); Lago Riñihue, Laguna Captrén, Chile (Rumrich *et al*.).

Placoneis insignita (Hustedt) E. J. Cox **comb. nov.**
Basionym: N. insignita Hustedt, 1942: 73, figs 126,139–141.
Lectotype: Hustedt collection, 163/27a. Laguna de Bay, Luzon. 184. (designated by Simonsen, 1987).
Micrographs: Simonsen, 1987: pl. 409, figs 7–11.

Placoneis interglacialis (Hustedt) E. J. Cox **comb. nov.**
Basionym: Navicula interglacialis Hustedt, 1944: 286, fig. 27.
Holotype: Hustedt collection, N10/17. Oberohe. 43.
Micrographs: Simonsen, 1987: pl. 477, figs 5–7.

Placoneis porifera (Hustedt) E. J. Cox **comb. nov.**
Basionym: Navicula porifera Hustedt, 1944: 284, fig. 25.
Holotype: Hustedt collection, N10/55, Breiter Lucin. 13m 16.viii.24.
Other specimens: Hustedt collection, N11/76, Breiter Lucin.
Micrographs: Simonsen, 1987: pl. 474, figs 15–18.

Placoneis subgastriformis (Hustedt) E. J. Cox **comb. nov.**
Basionym: *Navicula subgastriformis* Hustedt, 1945: 928, pl. 42, figs 13,14.
Lectotype: Hustedt collection, N1/33. Prespasee, Macedonien. (designated by Simonsen, 1987).
Micrographs: Simonsen, 1987: pl. 511, figs 1–4.

CIRCUMSCRIPTION OF *PLACONEIS*

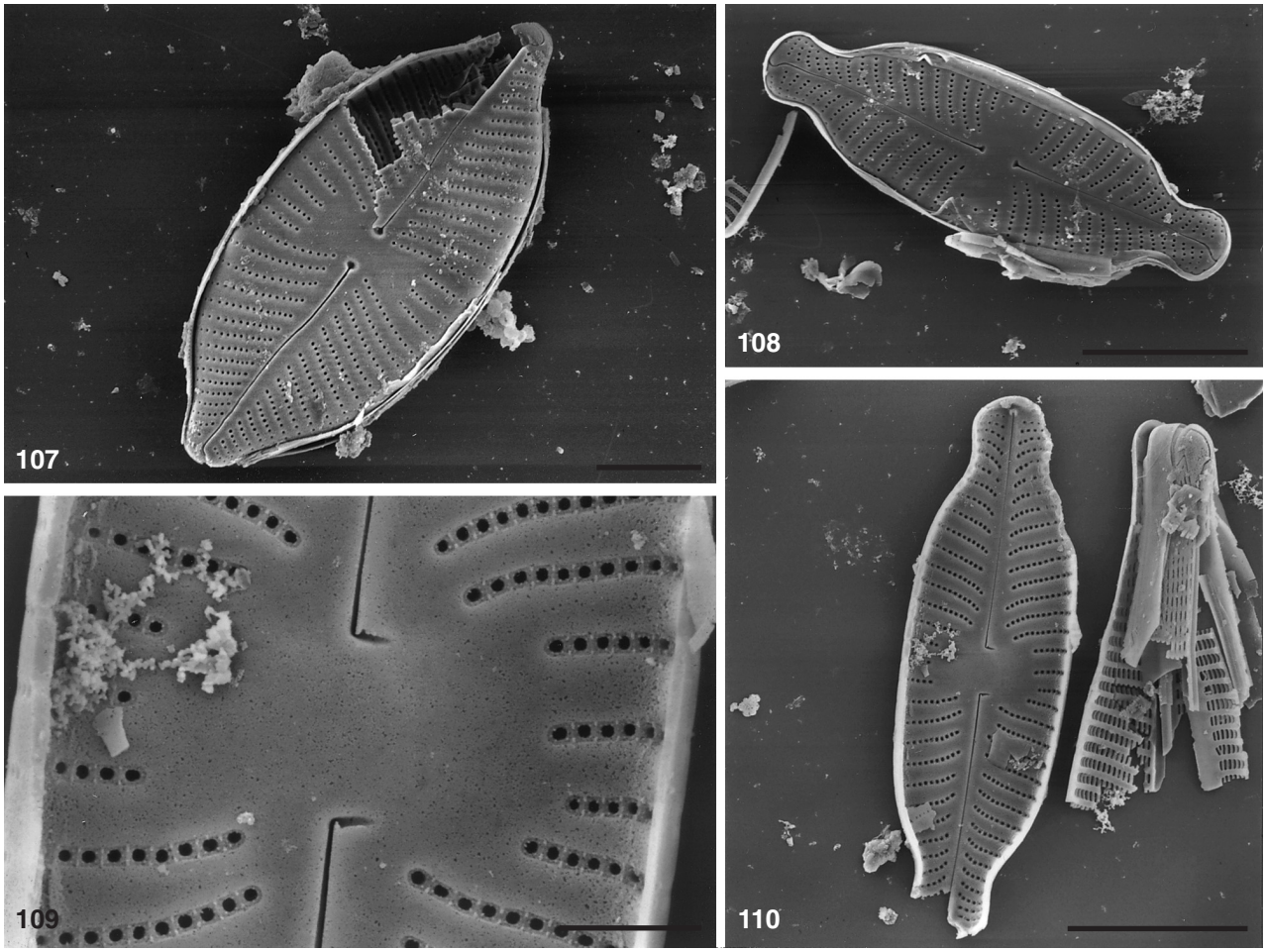
An emended description of *Placoneis* was given in Cox (1987) and SEMs in that paper show most of the ultrastructural features of the genus (Cox, 1987: figs 34–53). The inclusion of additional species in *Placoneis* (this paper) requires little modification of the generic circumscription (see below). Although it is clear that some species, e.g. *P. abiskoensis* (Fig. 72) and *P. amphibola* (Figs 103,104,107), are more coarsely areolate, the only significant additional variation is with respect to the raphe fissures. In a few taxa, e.g. *P. navicularis* (Figs 90–97), *P. amphibola* (Figs 103,104,107), *P. subplacentula* (Simonsen, 1987: pl. 200, figs 1,3), the raphe fissures are markedly sinuate rather than straight (Fig. 106). The central internal raphe fissures are also hooked in opposite directions in *P. subplacentula* (Simonsen, 1987: pl. 199, figs 3,4; pl. 200, figs 1,3) and *P. demeraroides* (Simonsen, 1987: pl. 766, fig. 5). In most species, the internal central raphe endings are deflected towards one side, but the deflection may vary from very slight (*P. placentula*) to moderate (*P. anglica*) to almost a right angle (*P. paraelginensis*), with or without a groove beyond the fissure (Figs 101,109).

In contrast to some other groups of naviculoid diatoms with markedly areolate striae, pore diameter in *Placoneis* is much less than the width of the virgae (Figs 100,101,107–110), so the striae form fine lines except in those species with biseriate striae, i.e. *P. placentula* and *P. subplacentula*. In these species the striae have a more diffuse appearance, but are still narrower than the virgae. By comparison, the virgae in most *Navicula* (*sensu stricto*) spp. are narrower than the striae, whilst pore size and shape along a stria are more regular in *Placoneis* than in *Cosmioneis* Mann & Stickle. *Placoneis navicularis* is an interesting intermediate between *P. placentula* and *P. gastrum*, with striae that are biseriate near the raphe slits (Figs 98,99), but uniseriate near the centre, margins and apices of the valve (Figs 97,100). Internally, short props of silica often extend from the virgae over the vimines (Fig. 109), as seen in some species of *Encyonema* Kütz. (Cox, 1976: figs 20,21,24) and *Cymbella* (Krammer, 1982: pls 1131, 1132, 1136, 1137, 1144).

Placoneis is probably a cosmopolitan genus, including taxa from North and South America, Africa, Europe and Asia, but although many species are apparently widely distributed they have rarely been recorded in large numbers. They are most often encountered as epipelic species in mesotrophic, circumneutral to slightly acidic, sometimes slightly brackish waters, in the shallow littoral of lakes and ponds rather than in flowing waters. The majority of species seem to occur predominantly in cooler areas, but some taxa have only been recorded from Central America (*P. demeraroides*, *P. jatobensis*, *P. molesta*, *P. santaremensis*, *P. surinamensis*).

DISCUSSION

Members of *Placoneis* are most easily recognized when alive, because of their distinctive chloroplast arrangement, and their affinities to other members of the Cymbellales are confirmed at the ultrastructural level. Interestingly, even without the availability of ultrastructural evidence and despite the contrast in symmetry, Cleve (1891) recognized the similarities between *Placoneis* (represented by *P. gastrum* and *P. placentula*) and *Cymbella*. But, although *Placoneis* valves are usually naviculoid in outline, some species are often slightly dorsi-ventral, and occasionally markedly dorsi-ventral specimens can be found. Other features of *Placoneis* shared with the Cymbellales are sinuous raphe fissures (some species), unilaterally deflected internal central raphe endings (in most cases), stepped valve margins (mantle is deeper along each side than around the apices), areolae not occluded by hymenes, and valvocopulae with a single row of pores. The occurrence of both uniseriate and



Figures 107–110. SEMs of *Placoneis* species from original material held in the Ehrenberg collection (BHU). Scale bars = 10 μm, except Fig. 109 in which scale bar = 2 μm. Fig. 107. External view of *Placoneis amphibola* from Iceland. Figs 108–110. *Placoneis paraelginensis* from Iceland. Fig. 108. External view of whole valve. Fig. 109. Detail of central raphe ending showing groove beyond deflected raphe fissure. Fig. 110. Internal view of partial valve.

biseriate striae in the same genus, and even in a single diatom, is also found in the Cymbellales, in *Gomphonema* C.A. Agardh (Cox, 1999b). However in *Gomphonema*, e.g. *G. acuminatum* Ehrenberg and *G. truncatum* Ehrenberg, the striae are usually uniseriate near the raphe slits and biseriate over the main part of the valve face (Cox, 1999b: figs 80,82,83), the opposite configuration to that in *P. navicularis*.

Mann & Stickle (1995) document a number of features of reproduction in *P. gastrum* that link *Placoneis* with other members of the Cymbellales. These include splitting of the chloroplast by the cleavage furrow and the type of auxosporulation. Each gametangium produces two gametes, one active and one passive. In addition, gametangia are closely associated during meiosis and plasmogamy, cells pair with girdles adjacent, and a robust mucilage capsule is produced.

A cladistic analysis of 50 raphid diatoms (including representatives of 5 genera from the Cymbellales), using a combination of valve and protoplast characters, also supports the inclusion of *Placoneis* in this order (E. J. Cox & D. M. Williams, unpubl.).

Other recent additions to the genus

In addition to taxa discussed above, Metzeltin & Lange-Bertalot (1998) and Rumrich *et al*. (2000) added 18 species to *Placoneis*: ten species were transferred from *Navicula* and eight new species (predominantly from South America) were described. However, none of the taxa were examined live, to confirm that they shared the same chloroplast morphology, and few supporting SEM data were presented. Of the 18 species, the inclusion (Metzeltin & Lange-Bertalot, 1998)

of two species, *P. jatobensis* (Krasske) Metzeltin & Lange-Bertalot and *P. surinamensis* (Cleve) Metzeltin & Lange-Bertalot, was supported by SEM data. Based on published light micrographs, *P. tersa* (Hustedt) Metzeltin & Lange-Bertalot, *P. demararoides* (Hustedt) Metzeltin & Lange-Bertalot and *P. explanata* (Hustedt) Lange-Bertalot should probably also be included in the genus, as should *P. molesta* Metzeltin & Lange-Bertalot and *P. santaremensis* Metzeltin & Lange-Bertalot, which appear to be very similar to *P. surinamensis*. Mayama & Kawashima (1998) also recognized *P. explanata* as a member of *Placoneis*, but their publication appeared in December 1998, after that by Metzeltin & Lange-Bertalot (1998), received by the NHM in October 1998. *Placoneis pellaifa* Lange-Bertalot & Rumrich and *P. scharfii* Lange-Bertalot & Rumrich have the widely spaced, finely areolate striae and rostrate to subapiculate apices typical of many *Placoneis* species and are probably correctly assigned to the genus (Rumrich *et al*., 2000).

However, the inclusion in *Placoneis* (Metzeltin & Lange-Bertalot, 1998) of *P. centropunctata* (Hustedt) Metzeltin & Lange-Bertalot, *P. conveniens* (Hustedt) Metzeltin & Lange-Bertalot, *P. dacostae* Metzeltin & Lange-Bertalot, *P. disparilis* (Hustedt) Metzeltin & Lange-Bertalot, *P. pseudodemerarae* (Hustedt) Metzeltin & Lange-Bertalot and *P. vicina* (Hustedt) Metzeltin & Lange-Bertalot is more questionable. *Placoneis dacostae* has rather lineate pores in SEM, and the relative proportions of stria to virga width in the others suggest that they may not belong in *Placoneis*. Similarly the rather lineate pores visible in *P. chilensis* Lange-Bertalot & Rumrich (Rumrich *et al*., 2000) argue against its position in the genus. *Placoneis disparilis* has more elongated, expanded external central raphe endings and elongated pores near the raphe system, and may belong nearer *Petroneis* Stickle & Mann. *Placoneis neotropica* Metzeltin & Lange-Bertalot and *P. zimmermannii* Metzeltin & Lange-Bertalot have very coarse pores and again may not be best placed in *Placoneis* (Metzeltin & Lange-Bertalot, 1998). Further investigation is needed to elucidate the affinities of all these taxa.

Elsewhere, Mayama & Kawashima (1998) raised a variety of *P. gastrum* to specific level, proposing the new combination *P. signata* (Hustedt) Mayama, and there is no reason to question this allocation to the genus.

CONCLUSIONS

Because of the confusion over the identity of the original material on which the names were based, it is proposed that the names *N. gastrum* Ehrenberg and *N. placentula* Ehrenberg be conserved with conserved types. Formal proposals are being prepared. After its transfer to *Placoneis*, the diatom formerly called *N. semen* should be re-named *P. navicularis*. It is also demonstrated that the name *N. elginensis* was applied too widely, subsuming several species under a single epithet. Five species are now recognized. A table summarizing their LM features, and three closely related species, is presented (Table 2) to facilitate their identification.

Based on their valve structure, *N. amphibola, A. navicularis* and *N. subplacentula* should be transferred to *Placoneis*, and the transfer of *N. abiskoensis* to *Placoneis* (Metzeltin & Witkowski, 1996) is supported. The transfer (Metzeltin & Lange-Bertalot, 1998) of five species to *Placoneis* is accepted (based on SEM data), but the inclusion (Metzeltin & Lange-Bertalot, 1998; Rumrich *et al*., 2000) of *P. centropunctata*, *P. chilensis*, *P. conveniens*, *P. dacostae*, *P. disparilis*, *P. neotropica*, *P. pseudodemerarae*, *P. vicina* and *P. zimmermannii* in this genus is contested. On the basis of published light micrographs of original material (Simonsen, 1987) my earlier suggestion (Cox, 1987) that *Navicula constans* Hustedt, *N. porifera* Hustedt and *N. interglacialis* Hustedt probably belong in *Placoneis* is supported. Light micrographs of *N. subgastriformis* Hustedt and *N. insignita* Hustedt (Simonsen, 1987) also support their inclusion in *Placoneis*. New combinations have therefore been made.

Placoneis Mereschkowsky

Description: Valves symmetrical, occasionally slightly dorsi-ventral, elliptical, lanceolate or broadly linear, with variously rounded, often rostrate to capitate apices. Girdle relatively shallow, more or less rectangular, the valve mantles stepped, being deeper in their mid regions than around the apices. Each cell contains a single chloroplast. The plastid has a central axial portion in which the pyrenoid lies, with lateral lobes extending under the valves. The nucleus lies to one side of the central bridge of the plastid. Two volutin droplets are usually visible, one towards each cell apex (on the same side of the cell as the nucleus). The striae are usually radiate near the centre of the valve, becoming more parallel, or very occasionally convergent, at the apices, composed of small rounded poroids. The striae are uniseriate in most species, markedly narrower than the virgae, but sometimes biseriate and then appearing more diffuse in LM. (In *P. navicularis*, striae are biseriate near the raphe and uniseriate towards the valve margins.) Internally, poroids are closed by volae and small props are visible over the vimines (SEM). Isolated pores (stigmata), with simple internal openings, may be present near the centre of the valve. The axial area is usually narrow while the central area is often somewhat

expanded, although the form and arrangement of the central striae vary with species. In the majority of species, the raphe slits are usually straight, but the external or internal fissures may be markedly sinuate in some species. The external polar raphe fissures form rounded hooks, opening towards the secondary side of the valve in most species, but occasionally the polar curvature is dissimilar. The external central raphe endings are straight and slightly expanded, the internal endings usually deflected towards the secondary side, occasionally hooked in opposite directions. Small helictoglossae are present at the polar ends of the internal fissures. Girdle bands are narrow, at least the advalvar band with a single row of poroids.

Type species: P. gastrum (Ehrenberg) Mereschkowsky

Other members of the genus: P. abiskoensis (Hustedt) Lange-Bertalot & Metzeltin, ***P. amphibola*** (Cleve) E. J. Cox **comb. nov.**, ***P. anglica*** (Ralfs) E. J. Cox **comb. nov.**, *P. clementioides* (Hustedt) E. J. Cox, *P. clementis* (Grunow) E. J. Cox, ***P. constans*** (Hustedt) E. J. Cox **comb. nov.**, *P. demeraroides* (Hustedt), *P. elginensis* (Gregory) E. J. Cox, *P. exigua* (Gregory) Mereschkowsky, *P. explanata* (Hustedt) Lange-Bertalot, *P. ignorata* (Schimanski) Lange-Bertalot, ***P. insignita*** (Hustedt) E. J. Cox **comb. nov.**, ***P. interglacialis*** (Hustedt) E. J. Cox **comb. nov.**, *P. jatobensis* (Krasske) Metzeltin & Lange-Bertalot, *P. molesta* Metzeltin & Lange-Bertalot, ***P. navicularis*** (Ehrenberg) E. J. Cox **comb. nov.**, *P. paraelginsis* Lange-Bertalot, *P. pellaifa* Lange-Bertalot & Rumrich, *P. placentula* (Ehrenberg) Heinzerling, ***P. porifera*** (Hustedt) E. J. Cox **comb. nov.**, *P. pseudanglica* (Lange-Bertalot) E. J. Cox, ***P. rostrata*** (A. Mayer) E. J. Cox **comb. nov.**, *P. santaremensis* Metzeltin & Lange-Bertalot, *P. scharfii* Lange-Bertalot & Rumrich, *P. signata* (Hustedt) Mayama, ***P. subgastriformis*** (Hustedt) E. J. Cox **comb. nov.**, ***P. subplacentula*** (Hustedt) E. J. Cox **comb. nov.**, *P. surinamensis* (Cleve) Metzeltin & Lange-Bertalot, *P. tersa* (Hustedt) Metzeltin & Lange-Bertalot, *P. undulata* (Østrup) Lange-Bertalot.

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APPENDIX 1

ORIGINAL DRAWINGS, SLIDES AND MATERIAL EXAMINED

Ehrenberg collection (Museum für Naturkunde, Berlin (BHU))

Number	Locality	Sample type
Drawing sheets		
2062	Vera Cruz, Mexico	
2063	Vera Cruz, Mexico	
2223	Iceland	
Original material		
1227	Mexico, near Vera Cruz	Marine sediment
1767	Pelham, Massachusetts	Diatomite
2297	Iceland	Peat
	Westpoint, New York	Diatomite

The Natural History Museum, London (BM(NH)), slides

Number	Collection	Locality	Other information on slide
BM 329	Greville	Peterhead Deposit	*Stauroneis punctata* WS[1] 184
BM 334	Greville	Peterhead Deposit	*Navicula semen* WS 141
BM 434	Greville	Mull deposit	Gregory (1854)
BM 631	Greville	Mull deposit	
BM 642	Greville	Elgin	Gregory 7.54
BM 657	Greville	Mull deposit	Gregory (1854)
BM 665	Greville	Elgin	*Gomphonema subtile* Ehr. Gregory
BM 677	Greville	Elgin	*Cymbella turgida* Greg. Gregory
BM 689	Greville	Elgin	*Stauroneis legumen* Gregory
BM 2485	Greville	Hull	Norman 1860
BM 2580	Greville	Hull	Norman Nov. 1862
BM 6989	Deby		*Navicula semen* 1869 ASD[2] Donkin Original Box 197
BM 11751	Deby	Elgin	Dr. Gregory
BM 11930	Deby	R. Coquet, Caistron	ASD, 4.v.1870
BM 11931	Deby	R. Coquet, Caistron	ASD, 4.v.1870
BM 11932	Deby	R. Coquet, Caistron	ASD, 4.v.1870
BM 12048	Deby	R. Coquet, Elyhaugh	ASD, 15.iv.1869
BM 12049	Deby	R. Coquet, Elyhaugh	ASD, 21.v.1869
BM 12050	Deby	R. Coquet, Elyhaugh	ASD, 15.iv.1869
BM 12051	Deby	R. Coquet, Elyhaugh	ASD, 15.iv.1869
BM 12052	Deby	R. Coquet, Elyhaugh	ASD, 21.v.1869
BM 12053	Deby	R. Coquet, Elyhaugh	ASD, 15.iv.1869
BM 12054	Deby	R. Coquet, Elyhaugh	ASD, 21.v.1869
BM 12055	Deby	R. Coquet, Elyhaugh	ASD, 21.v.1869
BM 12076	Deby	R. Coquet, Flotterton	ASD, 3.v.1870

APPENDIX 1
Continued

Number	Collection	Locality	Other information on slide
BM 12078	Deby	R. Coquet, Flotterton	ASD, 3.v.1870
BM 12079	Deby	R. Coquet, Flotterton	ASD, 3.v.1870
BM 12080	Deby	R. Coquet, Flotterton	ASD, 3.v.1870
BM 12081	Deby	R. Coquet, Flotterton	ASD, 3.v.1870
BM 12082	Deby	R. Coquet, Flotterton	ASD, 3.v.1870
BM 12083	Deby	R. Coquet, Elyhaugh	ASD, 15.iv.1869
BM 12084	Deby	R. Coquet, Flotterton	ASD, 3.v.1870
BM 12085	Deby	R. Coquet, Flotterton	ASD, 3.v.1870
BM 12086	Deby	R. Coquet, Flotterton	ASD, 3.v.1870
BM 12087	Deby	R. Coquet, Flotterton	ASD, 3.v.1870
BM 12090	Deby	R. Coquet, Elyhaugh	15.iv.1869, ASD
BM 12091	Deby	R. Coquet, Elyhaugh	15.iv.1869, ASD
BM 12092	Deby	R. Coquet, Elyhaugh	21.v.1869, ASD
BM 12093	Deby	R. Coquet, Elyhaugh	21.v.1869, ASD
BM 12094	Deby	R. Coquet, Elyhaugh	21.v.1869, ASD
BM 12095	Deby	R. Coquet, Elyhaugh	21.v.1869, ASD
BM 12096	Deby	R. Coquet, Elyhaugh	15.iv.1869, ASD
BM 12097	Deby	R. Coquet, Elyhaugh	21.v.1869, ASD
BM 12120	Deby	R. Coquet, Hepple	ASD, 7.v.1870
BM 12121	Deby	R. Coquet, Hepple	ASD, 7.v.1870
BM 12186	Deby	Loch Mourne Deposit	1870 AS.D.
BM 12187	Deby	Lough Mourne Deposit	1870 AS.D.
BM 12191	Deby	Louch Mourne Deposit	1870 AS.D.
BM 12195	Deby	Lough Mourne Deposit	1870 AS.D.
BM 12197	Deby	Mull Deposit	Prof. Gregory 1858 ASD
BM 12198	Deby	Mull Deposit	Prof. Gregory 1858 ASD
BM 12199	Deby	Mull Deposit	Prof. Gregory 1858 ASD
BM 12200	Deby	Mull Deposit	Prof. Gregory 1858 ASD
BM 12201	Deby	Mull Deposit	Prof. Gregory 1858 ASD
BM 12291	Deby	R. Coquet, Thropton	ASD, 6.v.1870
BM 12292	Deby	R. Coquet, Thropton	ASD, 6.v.1870
BM 12313	Deby	River Coquet, Thropton	29.vi.1870 AS.Don.
BM 12384	Deby	R. Coquet, Warkworth	1859
BM 14316	Deby	Ile de Malte, fossile	Tempère & Peragallo, no. 64
BM 18769	Kützing	Trouville 1573	*Navicula placentula* Kütz
BM 23481	Wm. Smith	Peterhead	*Navicula semen*
BM 23510	Wm. Smith	Guildford	*Navicula tumida* J.R. Capron Esq. misit Nov 4 1850
BM 23544	Wm. Smith	Peterhead deposit	*Pinnularia major* Dickie in Ann.^{ls} N. Hist. Aug^{t} 1848 WS.
BM 23620	Wm Smith	N. Guildford	G.H. Capron Esq., 5.xi.1852
BM 26326	Van Heurck	Types du Synopsis No. 15	*Cymbella ehrenbergii* Kütz. Belgique
BM 26336	Van Heurck	Types du Synopsis No. 25	*Cymbella cistula* var. *curta* Grun. Belgique
BM 26354	Van Heurck	Types du Synopsis No. 43	*Stauroneis anceps* Ehr. Angleterre
BM 26370	Van Heurck	Types du Synopsis No. 59	*Navicula brebissonii* var. *bicuneata* Grun. Angleterre
BM 26373	Van Heurck	Types du Synopsis No. 62	*Navicula borealis* Kütz. Belgique
BM 26374	Van Heurck	Types du Synopsis No. 63	*Navicula borealis* et formae intermediae Belgique
BM 26409	Van Heurck	Types du Synopsis No. 98	*Navicula semen* Wm. Sm. Angleterre
BM 26422	Van Heurck	Types du Synopsis No. 111	*Navicula tuscula* Ehr. Belgique
BM 26424	Van Heurck	Types du Synopsis No. 113	*Navicula mutica* Kütz. Belgique
BM 26435	Van Heurck	Types du Synopsis No. 124	*Navicula sphaerophora* Belgique

Number	Collection	Locality	Other information on slide
BM 31746	Comber	Badeschlamm, Loka, Sweden	
BM 33213	Comber	Carlin deposit, Nevada	A 1
BM 33214	Comber	Carlin deposit, Nevada	A 2
BM 35935	N. Polunin	Craig Harbour, Ellesmere Island	W.30; 5–6.ix.1936
BM 35936	N. Polunin	Craig Harbour, Ellesmere Island	W.30; 5–6.ix.1936
BM 68380	T & P 2ndEd. 34	Estuaire du Brivet S' Hajache	
BM 68480	T & P 2ndEd. 134	Auxillac, Cantal, France	
BM 68517	T & P 2ndEd. 171	Boxford, Mass. USA	
BM 68551	T & P 2ndEd. 205	Kopecz (Hongrie)	
BM 68552	T & P 2ndEd. 206	Ryssby Calmar (Suède)	*N. gastrum* Ehr.
BM 68558	T & P 2ndEd. 212	Tamarack Swamp, Conn. USA	
BM 68572	T & P 2ndEd. 226	St Saturnin (Puy-de-Dôme) France	*N. gastrum* Donk.
BM 68573	T & P 2ndEd. 227	St Saturnin (Puy-de-Dôme) France	*N. gastrum* Donk.
BM 68574	T & P 2ndEd. 228	St Saturnin (Puy-de-Dôme) France	*N. gastrum* Donk.
BM 68609	T & P 2ndEd. 263	Moissac Cantal	
BM 68610	T & P 2ndEd. 264	Moissac Cantal	
BM 68639	T & P 2ndEd. 293	Varennes (Puy-de- Dôme) France	*N. gastrum* f. *elliptica* M.P. et F.H.
BM 68711	T & P 2ndEd. 365	Swan Lake, Klamath cty, Oregon	*N. gastrum* f. *maxima* (long. 50µ)
BM 68712	T & P 2ndEd. 366	Swan Lake, Klamath cty, Oregon	*N. gastrum* f. *maxima* (long. 50µ)
BM 68865	T & P 2ndEd. 516	Lac des Escluses, Puy-de-Dôme (France)	
BM 68866	T & P 2ndEd. 517	Gijon Oviedo (Espagne)	*N. gastrum* & var. *major*
BM 68867	T & P 2ndEd. 518	Bory (Hongrie)	*N. gastrum* var. *boryana* Pant.
BM 68868	T & P 2ndEd. 519	Bory (Hongrie)	*N. gastrum* var. *boryana* Pant.
BM 68893	T & P 2ndEd. 544	Thrais (Hongrie)	*N. gastrum* & var. *maxima*
BM 68894	T & P 2ndEd. 545	Thrais (Hongrie)	*N. gastrum* & var. *maxima*
BM 68953	T & P 2ndEd. 604	Ile de Malte	*N. gastrum*, *N. placentula*
BM 68988	T & P 2ndEd. 639	Beatties pond, Conn, USA	*N. gastrum* f. *minor*
BM 68989	T & P 2ndEd. 640	Beatties pond, Conn, USA	*N. gastrum* f. *minor*
BM 69028	T & P 2ndEd. 678	Hopkinton, New Hampshire, USA	
BM 69051	T & P 2ndEd. 700	Jastraba Hongrie	N. gastrum Ehr.
BM 69127	T & P 2ndEd. 776	Phillips – Maine – Conn. (USA)	*N. semen* Ehr.
BM 69269	T & P 2ndEd. 918	Wangarei (Nouvelle-Zélande)	*N. placentula* Ktz.
BM 69297	T & P 2ndEd. 945	Lyons Farm New Jersey USA	*N. gastrum* Donk.
BM 93093	J.R. Carter 2278	Lilliesleaf pond	
BM 93177	J.R. Carter 2341	Wooden Loch	
BM 95758	J.R. Carter 4400	River Ane	August 1988

[1]WS = William Smith
[2]ASD = Donkin

APPENDIX 2

ILLUSTRATIONS OF *P. GASTRUM*, *P. PLACENTULA, N. SEMEN*, *P. SEMEN* AND *A. NAVICULARIS* IN EHRENBERG'S MIKROGEOLOGIE (1854).

Plate	Part	Figure	Species	Locality
5	I	12	*Pinnularia gastrum*	Brenn-Torf aus Island (fuel peat from Iceland)
5	II	12	*Pinnularia gastrum*	Brenn-Torf aus Newhaven, Connecticut (fuel peat, Newhaven, Connecticut, USA)
7	IIA	14	Pinnularia gastrum	Braunkohlen-Tripel von Geistingen im Siebengebirg (lignite, Geistingen, Siebengebirge,Germany)
15		23	*Pinnularia gastrum*	Kieselguhre von Down, Mourne Mountains Irland (diatomite, Mourne Mountains, Ireland)
37	III	10	*Pinnularia gastrum*	Bacillarien im Bernstein von Ost- Preussen. Europa (diatoms in amber, E. Prussia)
38	VIII	2	*P. gastrum*?	Gewöhnlich gebrannter, verglühter, Mauerstein aus Infusorien-Erde (common, baked bricks from infusorial earth)
8	II	6a,b	*Pinnularia placentula*	Dichtes Tripel-Gestein von Zamuto (dense, siliceous rock from Zamuto, Hungary)
8	III	5	*Pinnularia placentula*	Halb-Opal von Arca (chalcedony/opal, Arca, Hungary)
12		19a,b	*Pinnularia placentula*	Silbergrauer Polirschiefer zwischen Basalt-Tuff bei Cassel (silver-grey slate between basalt tuff, Kassel,Germany)
15		21	*Pinnularia placentula*	Kieselguhre von Down, Mourne Mountains, Ireland (diatomite, Mourne Mountains, Ireland)
1	III	11	*Navicula semen*?	Kieselguhr (Vulkanische Asche) von Isle de France der Mascarenen-Inseln (diatomite, volcanic ash, Mauritius)
16	I	11	*Navicula semen*?	Bergmehl von Degernfors ('mountain flour', Degenfors, Sweden)
16	III	26	*Navicula semen*	Badeschlamm von Bad Loka (mud, Bad Loka, Sweden)
34	VII	10	*N. semen*?	Lehmgelbe Blumen-cultur-Erde von Canton. China. Asien. (yellow-brown potting compost, Canton, China)
38	XVI I	2	*N. semen*	Hekla-Asche von Island, 2 September 1845. Nord-Amerika (volcanic ash from Hekla, Iceland)
38	XX	3	*N. semen*	Vulkanische Asche aus Quito – Moya von den Antillen. Süd-Amerika. (volcanic ash from Quito – Moya, Cuba)
39	I	37	*Navicula semen*	Passat-Staub des Atlantischen Dunkelmeeres (desert dust, Atlantic Ocean)
39	II	88,89	*Navicula semen*	Passat-Staub des Atlantischen Dunkelmeeres (desert dust, Atlantic Ocean)
6	II	10	*Pinnularia semen*	Süsswasser-Mergel von Morea (freshwater marl, Morea, Greece)
12		26	Pinnularia semen	Blätter-Tripel (Polirschiefer), Saugschiefer und Halbopal von Bilin (Böhmen) (slates, chalcedony/opal, Bilina, Czech Republic)

Plate	Part	Figure	Species	Locality
14		12	*Pinnularia semen*	Brakisches, strickweis lebendes Erdlagen unter Berlin (brackish, partly living earth layers, Berlin)
17	II	8	*Pinnularia semen*	Bergmehl von Kymmene Gård (mountain flour, Kymmene Gård, Finland)
33	X	23	*Pinnularia semen*	Weisser Kieselguhr von Neu-Hampshire. Nord-Amerika (white diatomite, New Hampshire, USA)
33	XIV	19	*Pinnularia semen*?	Schwarzer Brakischer Moorgrund bei Norwich Connecticut Nord-Amerika (black, brackish peat near Norwich, Connecticut, USA)
37	I	19	*Pinnularia semen*	Tripel und Polirschiefer von Moskau. Europa (slates, Moscow, Russia)
2	II	19	*Amphiprora navicularis*	Kieselguhr von Neu-York, Nord-Amerika (diatomite from New York, USA)
3	I	10,11a,b	*Amphiprora navicularis*	Kieselguhr von Pelham in Massachusetts (diatomite, Pelham, Massachusetts, USA)
3	III	8a,b,c	*Amphiprora navicularis*	Kieselguhr von Spencer in Massachusetts (diatomite, Spencer, Massachusetts, USA)
4	II	16	*Amphiprora navicularis*	Kieselguhr von Smithfield in Rhodes Island (diatomite, Smithfield, Rhode Island, USA)
5	I	10	*Amphiprora navicularis*	Brenn-Torf aus Island (fuel peat from Iceland)
16	III	30	*Amphiprora navicularis*	Badeschlamm von Bad Loka (mud, Bad Loka, Sweden)