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Studies on type material from Kützing's diatom collection VIII. Species assigned to the genera *Epithemia* Brébisson ex Kützing and *Rhopalodia* O. Müller

JOHN PATRICK KOCIOLEK[1]*, DAVID M. WILLIAMS[2], SARAH HAMSHER[3], SCOTT MILLER[4] & JINGCHUN LI[1]

[1]*Museum of Natural History and Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, CO, USA*
[2]*Department of Life Sciences, The Natural History Museum, London, UK*
[3]*Department of Biology and Annis Water Resources Institute, Grand Valley State University, Allendale and Muskegon, MI, USA*
[4]*Division of Biological Sciences, University of Montana, Missoula, MT, USA*

We detail the diatom taxa described by F.T. Kützing across three of his publications that have been referred to the diatom genera *Epithemia* and *Rhopalodia*. Taxa considered include *Frustulia adnata, F. picta, E. alpestris, E. musculus, E. porcellus, E. proboscidea, E. sorex, E. ventricosa, E. vertagus, E. ventricosa β. gregaria* and *E. reticulata*. For these 12 taxa, this represents the first time Kützing's specimens have been illustrated with light microscopy. Most of the material consulted here is from the Natural History Museum, London, though we also reviewed material from the Academy of Natural Sciences for *E. adnata*. We present light microscope images of the Kützing taxa and complement these observations with images of the type slides, material packets and both herbarium (unpublished) and published drawings. In some cases, modern concepts of Kützing species are supported, but in others it is likely that species concepts will be changed by the specimens in the type material. Lectotypes are designated for *Epithemia adnata* and *Epithemia reticulata*.

Keywords: *taxonomy, Rhopalodiales, light microscopy, type species, nomenclature*

Introduction

Friedrich Trautgott Kützing (1807–1893) was a pre-eminent phycologist, publishing a number of substantial works (e.g., Kützing 1844, 1845, 1849, for biographic details see Müller & Zaunick 1960). He was responsible for numerous nomenclatural acts related to a range of different algal taxa. While today, Kützing's larger taxonomic works are still frequently cited, he was also known to his colleagues for his thoughts (pre-Darwin) on the potential transformation of species published in works rarely cited today and some difficult to find (e.g., Kützing 1856, see Potonié 1881, pp. 354–6 specifically on Kützing). Kützing was an advocate of considering algae (including diatoms) as plants, bringing the condemnation of his peer Ehrenberg (1795–1876), who instead advocated diatoms as being animals (e.g., Ehrenberg 1837a; for a succinct account of the controversy see the anonymous review of Kützing (1844) in *Ann. Mag. nat. Hist.* 15: 185-188, 1845, or the English translation of the introductory pages from Kützing 1844 by H.L. Smith 1873 [1877]; a more recent account is in Ragan 2023). Kützing was also an advocate for the idea that morphologically simple 'algae' were progenitors of more complex forms suggesting (pre-Darwin) that 'algae' evolved into aquatic and higher plants. Kützing was joined by some of his contemporaries in this belief, including Perty (1848), Braun (1850 '1851') and Nägeli (1847, 1849).

Kützing described numerous species of diatoms (as well as many other algae, Kützing 1849) and was responsible for over 50 diatom genera (Fourtanier & Kociolek 1999, 2003), *Epithemia* Bréb. ex Kütz. (Kützing 1844, p. 33) being one. The purpose of this paper is to bring together the original descriptions, type locality information, original illustrations and the first published light microscope images of the species in *Epithemia* described by Kützing, with some subsequently being transferred to *Rhopalodia* O.Müll. (Müller 1895, p. 57). This study is based on specimens primarily held in the Natural History Museum, London (BM), although many Kützing specimens exist in other herbaria, for example ANSP, BR, L and PC all have specimens, some being type and original material; many of these are duplicates from Kützing's exsiccata *Algarum aquae dulcis Germanicarum* (Kützing 1831-36, details in Sayre 1969, p. 84).

Epithemia and *Rhopalodia* have been treated by Patrick & Reimer (1975), Sims (1983), Lange-Bertalot &

*Corresponding author. E-mail: Patrick.kociolek@colorado.edu
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Krammer (1987) and Krammer & Lange-Bertalot (1988). Patrick & Reimer (1975) designated types for some of Kutzing's taxa from BM specimens and in some cases provided line drawings of specimens observed from type material, but no light microscope images.

Methods and materials

Abbreviations: Herbarium acronyms follow *Index Herbariorum* (http://sweetgum.nybg.org/science/ih/); author names are abbreviated according to the *International Plant Name Index* (IPNI, https://www.ipni.org/); LM = light microscopy.

Material: As noted above, specimens illustrated herein are primarily from the BM, with others from ANSP and L. Specimens used are cited under each taxon name. The exclamation point (!) after a specimen citation means 'vidi' ('I have seen it'), that the specimen has been examined by us.

The Kützing samples numbered up to 825 would have been available to Kützing for the descriptions he proposed in his *Die kieselschäligen Bacillarien oder Diatomeen* (Kützing 1844) and some for his earlier studies (Kützing 1833). The higher numbers, being acquired later (Cox 1998, p. 168), may have been included in Kützing's later flora *Species Algarum* (Kützing 1849).

The BM packets of raw material in the Kützing herbarium are labelled in various hands, some from Kützing and may include his drawings. Annotations have been made later by additional persons. Some of the slides that bear a 'type' label were identified by R. Ross and P.A. Sims (both of the BM), sometimes with the help of other researchers or curators. In the case of Kützing's material, R. Patrick would have contributed to the identification of type material and slides.

Taxon Names:
Herein we include a brief note on the generic names used.

Epithema – Epithemia

Brébisson at first transferred two species from Kützing's *Cymbella* sub-group of *Frustulia* (Kützing 1833, p. 538) into his new genus *Epithema* Bréb. (Brébisson 1838a, p. 42, see Fig. 1–2), *Epithema pictum* (Kütz.) Bréb. (Brébisson 1838a, p. 42, basionym: *Frustulia picta* Kütz., the type of *Epithema* Bréb.) and *Epithema adnata* (Kütz.) Bréb. (Brébisson 1838a, p. 42 = *Frustulia adnata* Kütz.), and added one new species, *Epithema scutellum* Bréb. (Brébisson 1838a, p. 42). On inspection of Brébisson's specimens by Sims, *E. scutellum* turns out to be a species of *Cocconeis* and is excluded from further consideration (Sims 1983, p. 213). But in 1845, Brébisson abandoned his genus *Epithema*, writing in D'Orbigny's *Dictionnaire universel d'histoire naturelle*, 'Nous avions proposé ce nom dans un travail sur les Diatomées (Considérations sur la famille des Diatomées, 1838 [b]) pour des êtres ayant des frustules parasites, à dos convexe et planes en dessous et prenant la forme du corps qui les supporte. Le g. *Eunotia* de M. Ehrenberg, renfermant à peu près les mêmes espèces, devra lui être préféré' (Brébisson 1845, p. 369, and 'Le g. *Epithema*, que nous avions proposé il y a quelques années, est synonyme de celui-ci', Brébisson 1845, p. 498[1]).

In contrast to Brébisson, rather than adopt the name *Eunotia* for all species with lunate shaped valves ('à dos convexe et planes en dessous et prenant la forme du corps qui les supporte'), Kützing separated out a group of species previously assigned to the genus *Eunotia* by Ehrenberg (1837b, 1838, and numerous others during the period 1839–45) and placed them in his *Epithema*: 'Im Ganzen nahert sich seine Einteilung sehr derjenigen, welche ich in meiner *Synopsis Diatomearum* 1833 aufgestellt hatte. nur einenger Unterabteilugen meiner Gattungun erhob er zu selbstandigen Gattungen, wie z. B. *Cymbophora* (= *Cocconema* Ehrbg.), *Cyclotella* (= *Pyxidicula* Ehrbg.) und ausserdem noch *Epithema*, (welche der Gattung *Eunotia* Ehrg. entspricht) und *Surirella*' (Kützing 1844, p. 6; see Table 1).

In 1844, Kützing described a total of 29 species of *Epithemia* (with this different spelling), 8 as new species, the remaining 21 transferred primarily from *Eunotia*, species that were initially described by Ehrenberg (summarized in Table 1). Two additional species were included in Kützing's *Species algarum* both attributed to other authors: *Epithemia gregaria* Brébisson in Kützing (1849, p. 4) and *E. reticulata* Naegeli ex Kützing (1849, p. 889). *Epithemia gregaria* was added beneath the description of *Epithemia ventricosa* Kützing as 'β. *Epth. gregaria Bréb.* marina' (Kützing 1849, p. 4, type: BM 17815, Kützing 1342, Constantinople [Istanbul], Turkey, 'Ad Zonariam Pavoniam in freto Constantinopolitano. Specimina misit cl. De Brébisson') and *E. reticulata* was included in the 'Addenda et corrigenda' to be added as '18b' after *E. granulata* (Kützing 1849, p. 889, type BM 17821-2, Kützing 862, Zurich, Switzerland,' In aqua dulci Helvetiae: cl. Naegeli').

The lack of any precise description for both *Epithemia* and *Eunotia*, even though most kept the two genera apart but in the same higher taxon, led to some curious mix of names. Rabenhorst, for example, first placed nearly all species of *Epithemia* in *Eunotia*, but kept them separate in an unnamed sub-group still identified as *Epithemia*: '+ Mit ftareen Querstreifen (*Epithemia* De Bréb.) [With horizontal stripes]' (Rabenhorst 1847, p. 18, see Table 2, column 1). By 1853, Rabenhorst re-instated many as a separate genus under the name *Epithemia* but the plate legend for his illustrations included them all under the name *Eunotia* with *Epithemia* given in brackets after the relevant species (Table 2, column 2).

To square this particular circle, Brébisson reverted back to *Epithemia* in 1854 (Brébisson 1854, pp. 246, 250) where he at first provided William Smith with specimens

1

XV. EPITHEMA *Nob.* Frustules parasites, sans pédicelle, et attachés au corps qui les supporte par leur face inférieure.

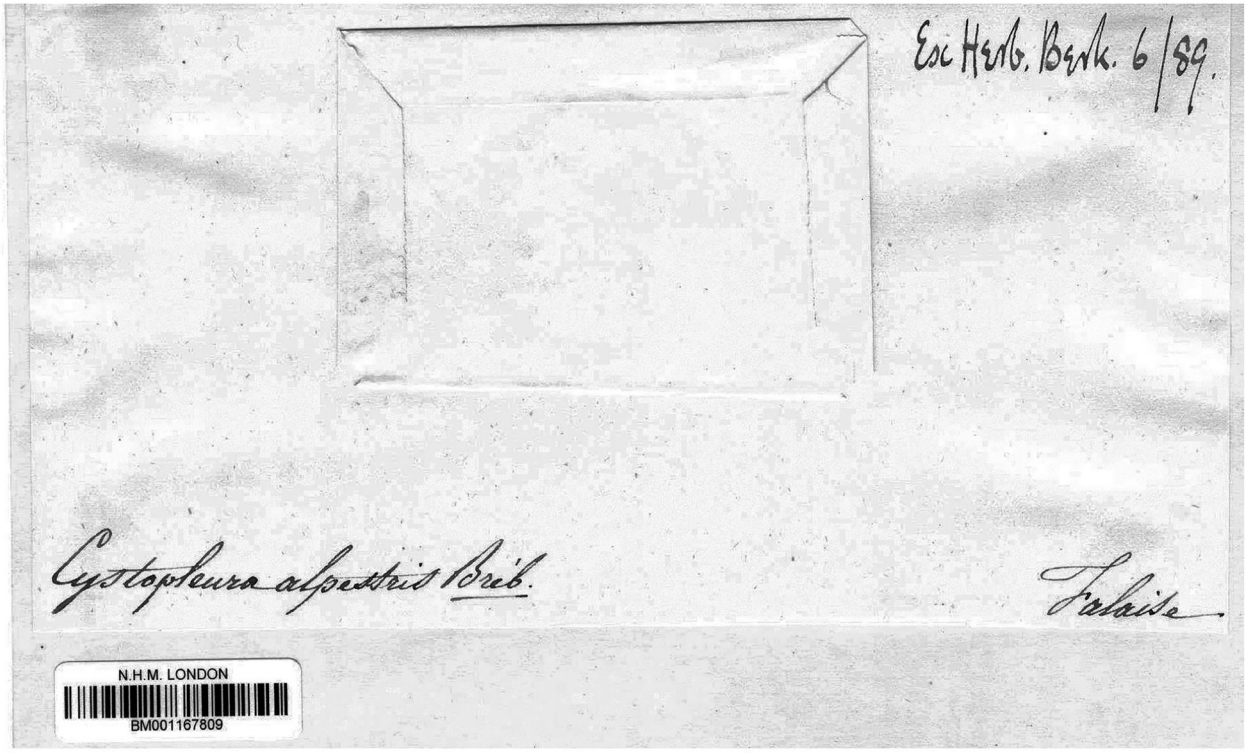
Les frustules sont un peu arqués comme dans les *Achnanthes*; ils vivent immédiatement attachés, par leur face inférieure un peu concave, aux confervées et aux brins d'herbe plongés dans l'eau. Ils semblent croître de préférence sur les *Conferva crispata* et *fracta*.

1. E. PICTUM *Nob. Frustulia picta* Kutz. Eaux douces. Allemagne, Normandie, Falaise.

2. E. ADNATUM *Nob. Frustulia adnata* Kutz. Allemagne, Italie, Normandie.

3. E. SCUTULUM *Nob.* Normandie, Rouen, Falaise; sur les *Conferva crispata* et *fracta* et sur quelques *Vaucheria*.

2



Figs 1–2. Reproduction of the original description of *Epithema* by Brébisson (1838a, p. 42, 1838b, p. 16). Fig. 2. Herbarium packet of Brébisson for '*Cystopleura alpestris*' at BM (BM 001167809).

subsequently named *Epithemia constricta* W. Sm. (Smith 1853, p. 14, pl. XXX, fig. 248, BM 23050, BM 23051, BM 23054; Smith did not use Brébisson's specimens but noted them in the protologue: '"Ep. constricta," cl. De Brebisson in litt. cum specim.') but later described them under the name *Epithemia succincta* Bréb. (Brébisson 1870, p. 42, pl. 1, fig. 7, BM 17823). Brébisson named, but did not publish, other species in *Epithemia*: '*Epithemia minutissima* Bréb.', *nom. herb.* (Type: – Germany, Heligoland BM 19294, Kützing 736, Brebisson) and '*Epithemia radula* Bréb.', *nom. herb.* (Type specimens: – France, Falaise, Type: – France, Falaise, BM 001222611) (https://data.nhm.ac.uk/object/f91c3b8a-52cf-425a-9e6e-94703cb67422); L4021433 (https://bioportal.naturalis.nl/en/specimen/L.4021433) – these specimens will be investigated in due course.

Table 1. Species of *Epithemia* included in various works by Kützing (1844, 1849, 29 species in total); left hand columns: species described by Kützing, with those in Kützing 1849 authored by others; right hand columns: species described by Ehrenberg and placed in *Epithemia* by Kützing; 1 = *E. zebra*, *E. vertagus*; 2 = *E. turgida*; ‡ = *Rhopalodia*

Kützing species		Ehrenberg species	
Epithemia	Basionym	*Epithemia*	Basionym
adnata[1]	1833 = *Frustulia adnata*		
picta[2]	1833 = *F. pictum*		
alpestris	1844	*argus*	1844 = *Eunotia argus*
musculus ‡	1844	*cingulata*	1844 = *Eunotia cingulata*
porcellus	1844	*faba*	1844 = *Eunotia faba*
proboscidea	1844	*gibba*	1844 = *Navicula gibba*
saxonica	1844	*gibberula*	1844 = *Eunotia gibberula*
sorex	1844	*granulata*	1844 = *Eunotia granulata*
ventricosa ‡	1844	*librile*	1844 = *Eunotia librile*
vertagus	1844	*ocellata*	1844 = *Eunotia ocellata*
		textricula	1844 = *Eunotia textricula*
		turgida	1844 = *Navicula turgida*
		westermannii	1844 = *Navicula westermannii*
		zebra	1844 = *Navicula zebra*
		zebrina	1844 = *Eunotia zebrina*
gregaria	1849		
reticulata	1849		

Rejection of the name *Cystopleura*

The name *Epithema* as used (and spelt) by Brébisson is a later homonym for a genus of flowering plants (*Epithema* Blume 1826, p. 737). Kützing (1844) used the name *Epithemia*, with this slightly different spelling, as a substitute name for Brébisson's *Epithema*. Kuntze (1891) had suggested *Cystopleura* Bréb. ex Kuntze (1891, p. 890) as a replacement name for this group of species, a name he attributed to Brébisson who never validly published it. Kuntze (1891) made numerous nomenclatural transfers from *Epithemia* to *Cystopleura*, those he missed were transferred by DeToni (1892) in his exhaustive catalogue of names. Fourtanier & Kociolek (1999, p. 51) discussed the name *Cystopleura* and the complications with it, joining Sims (1983) in recognizing this genus by the name of *Epithemia*.

Table 2. Species of *Epithemia* in Rabenhorst (1847 and 1853)

Rabenhorst	
1847	1853
turgida	*turgida*
westermannii	*westermannii*
sorex	*sorex*
musculus	
granulata	
depressa	*depressa*
vertagus	*vertagus*
gibba	*gibba*
ventricosa	*ventricosa*
contracta	
saxonica	*saxonica*
gibberula	*gibberula*
alpestris	*alpestris*
	nodosa
	zebra
	textricula
	angulosa
	lindigii
	ocellata
	otrantina
	librile
	quinquecostata

The name '*Cystopleura alpestris*' was used by Brébisson on some specimen labels (Fig. 2), which he distributed fairly widely. It is not clear from the BM specimens when they were donated to Kützing, although Kützing seems to have been the first to use the name in print, with '*Cystopleura alpestris*' as a synonym of *Epithemia alpestris* and '*Cystopleura ocellata*' as a synonym of *Epithemia ocellata* (Kützing 1849, p. 3). Both *Cystopleura* names attributed to Brébisson are invalidly published.

In short, *Epithemia* Brébisson ex Kützing is the legitimate replacement name for *Epithema* Brébisson; *Cystopleura* Brébisson ex Kuntze is an illegitimate substitute name for *Epithema* Brébisson.

Relationships

Ruck et al. (2016) studied the relationships of the orders Surirellales and Rhopalodiales; their results included a monophyletic *Epithemia* and a paraphyletic *Rhopalodia* (Ruck et al. 2016, fig. 1, the relevant parts of their cladogram have been reproduced in our Fig. 3). Moulin et al. (2023) have a similar cladogram (their figure 1E), as do Schvarcz et al. (2022, their figure 2a). In our Fig. 3a, the

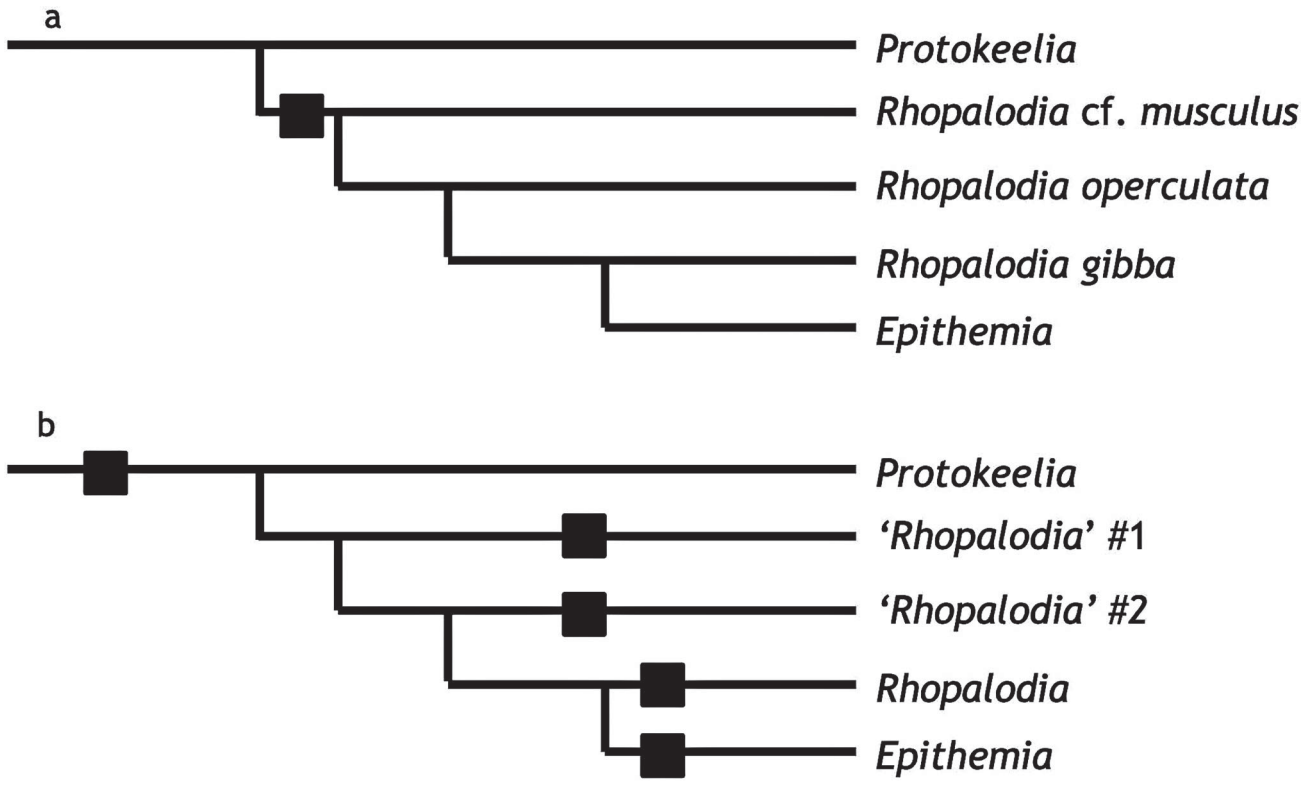


Fig. 3. a. Phylogenetic relationships of Rhopalodiales based on Ruck et al. (2016, fig. 1) simplified to show relationships between *Epithemia* and various species of a paraphyletic *Rhopalodia*; Fig. 3b. Phylogenetic relationships of Rhopalodiales with the various species of a paraphyletic *Rhopalodia* as monophyletic branches identified by the series of black boxes.

black box indicates the node that represents a natural group as 'defined' by Ruck et al. (2016). They suggested, 'One way to rectify this problem [of a paraphyletic *Rhopalodia*] is to subsume *Tetralunata* and *Rhopalodia* into *Epithemia*, creating a monophyletic genus defined by fibulae that extend beyond the canal raphe and into [the] valve face' (Ruck et al. 2016, p. 168). Ruck et al. (2016) offered the view that this option is best as there has been, among other things, such a 'slow rate of historical progress in establishing a natural classification of this group' (Ruck et al. 2016, p. 168). While the group of species included in the *Epithemia* plus *Rhopalodia* clade is monophyletic (by inclusion), an alternative naming system that preserves inclusive, but smaller (in numbers of species), monophyletic groups is possible (see Fig. 3b, with a series of monophyletic groups, the black boxes indicating the nodes that represents potential genera), a scheme touched on by Ruck et al. (2016, p. 168, 'Although in many ways we preferred to retain the name *Rhopalodia* for the freshwater clade sister to *Epithemia* and to relegate the remaining *Rhopalodia* to incertae sedis, allowing these to be resolved in future studies, decades may pass before such a solution is made'). As Vigneshwaran et al. (2021) wrote, 'If there was ever a way to impede taxonomic progress to ultimately develop a natural classification in a group, it is by masking evolutionary novelties and subsuming relationships within broad taxonomic units' (Vigneshwaran et al. 2021, p. 177).

Table 3. Specific epithets in *Epithemia* and their current generic assignments / names.

Species Epithet	Year described or treated by Kützing	Current genus assignment
adnata	1833	*Epithemia*
picta	1833	*Epithemia*
alpestris	1844	*Epithemia*
musculus	1844	*Rhopalodia*
porcellus	1844	*Epithemia*
proboscidea	1844	*Epithemia*
saxonica	1844	*Epithemia*
sorex	1844	*Epithemia*
ventricosa	1844	*Rhopalodia*
vertagus	1844	*Epithemia*
gregaria	1849	*Rhopalodia*
reticulata	1849	*Epithemia*

Results

The accounts below follow the sequence given in the first column of Table 1 ('Kützing species'), with the first two species from Kützing (1833), the remainder from Kützing (1844). These are presented in the sequence they appear in Kützing (1844). Table 3 lists their current generic name is provided after the accounts.

***Epithemia* Bréb. ex Kütz. 1844, p. 33**

Generitype: *Epithemia turgida* (Ehrenb.) Kütz. 1844, p. 34 (basionym *Navicula turgida* Ehrenb. 1830, pp. 84, 88, *invalid*, [Gairdner 1831, pp. 93, 94, 95], Ehrenb. 1832a ['1830'], pp. 69, 70, *invalid*, Ehrenberg 1832b, p. 80, designated by Boyer 1927, p. 488).

(a) Species in Kützing (1833)

***Frustulia adnata* Kütz. (Kützing 1833, p. 544, taf. XIII, fig. 15 = our Fig. 23–37); (Kützing 1833 [1834], p. 16, taf. I, fig. 15; Kützing 1833e: [3], no. 41, see Fig. 38–41) = *Epithemia* ('*adnatum*') *adnata* (Kützing) Bréb. (Brébisson 1838a, p. 42; Brébisson 1838b, p. 16)**

SYNONYMS (HOMOTYPIC):
Cymbella adnata (Kütz.) Bréb. (in Brébisson & Godey 1835, p. 50, pl. VII)
Cymbella adnata (Kütz.) Mont. (Montagne 1840, p. 194, *illegit.*)

TYPE: – GERMANY, Halle, 'Sie kommt an *Conferva fracta* vor, wo ich sie an verschiedenen Orten fand, aber nie an eintr andern Conferve' (Kützing 1833, p. 544); 'In *Conferva fracta* parastica, bei Halle' (Kützing 1833, [p. 3], no. 41; and *Flora* 16 (Nro, 44), p. 698, 1833 [Nov.]); ANSP GC 13705, GC 14174 = ' Kützing 1833, no. 41, '*Epithemia adata* ([Patrick & Reimer 1975] p. 179) A-Kütz. Dec. 5, #41, Germany, bei Halle' (Patrick & Reimer 1975, illustrated a specimen from the ANSP collection on pl. 24, fig. 4, but no slide number was referenced; see Mahoney & Reimer 1997, p. 147, Fig. 42–50 = ANSP GC 13705; **Fig. 6 = lectotype specimen designated here**; Fig. 38–41 = Kützing 1833e, no. 41 from ANSP).

OTHER MATERIAL

FRANCE, 'Auf *Cladophora fracta* in der Normandie: Lenormand in herb. Hering [Karl Hering (1796–1843)]. (*Frustulia adnata*)' (Kützing 1844, p. 36, noted under *Epithemia vertagus*, see below).

GERMANY, Merseburg BM 17797 (Kützing 11), BR; Bernstadt BM 17799 (Kützing 14, Braun 136 = *Frustulia adnata* var. *vaucheriae* Kützing *nom. herb., illegit.*)

DESCRIPTION: Valves distinctly asymmetrical to apical axis, with dorsal margin highly arched, ventral margin nearly straight to barely concave, with apices narrowly rounded, not protracted. Length 37 µm, breadth 8 µm. Raphe positioned about 1/2 way between dorsal and ventral margins at apices, running along ventral margin (even extending onto mantle), then curving onto valve face and extending a short distance, ca. 1/6-1/5 the distance towards dorsal margin. Raphe branches evident at centre. Costate fibulae 4–5 / 10 µm. Striae with 3–4 rows between adjacent fibulae, ca. 14–16 / 10 µm. Striae composed of rectangular to irregularly-shaped areolae.

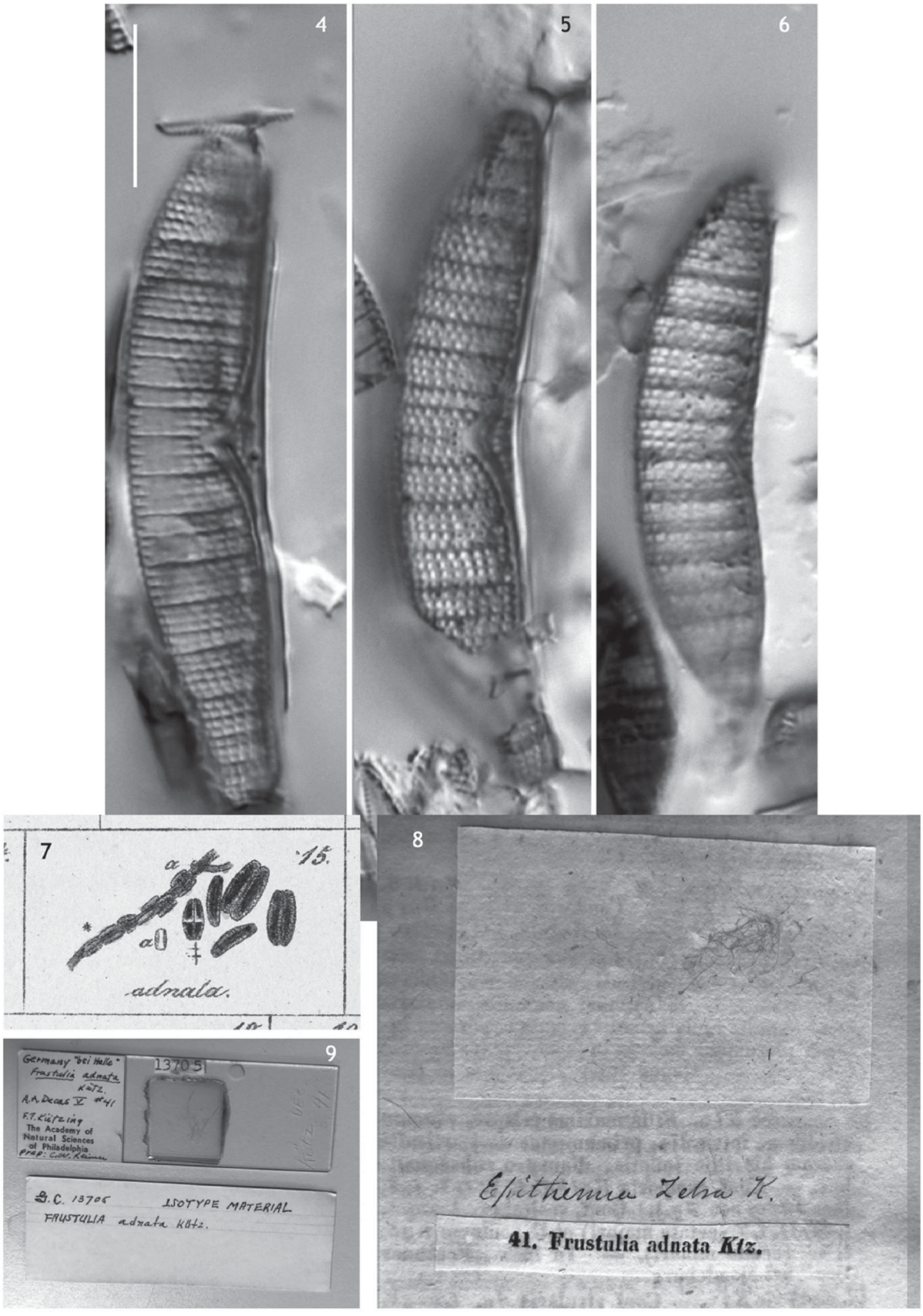
COMMENTS: In the slide from which we made our observations (ANSP GC 13705) there were 3 distinguishable groups, one easily assigned to *E. sorex*, the other two had valves with slightly protracted apices, which appear to be assignable to *E. porcellus* (see our Figs 4–9 and 10–18). Another was represented by a single specimen, which did not have protracted apices, but instead had apices narrowly rounded (see our Figs 19–22). We here designate the specimen on ANSP GC 13705 with narrow, not protracted apices, as the lectotype of *E. adnata*.

Jahn & Kusber (2006, p. 530) suggested that *Epithemia adnata* was a synonym of *Epithemia hellenica* (Ehrenb.) R.Jahn & Kusber (based on *Eunotia hellenica* Ehrenb. 1840, p. 210, 'Graeciae marga', 'subfossil limnic sediments, Greece'). They noted that 'The depicted lectotype is similar to the modern concept of *Epithemia adnata* (Kütz.) Bréb., based on *Frustulia adnata* Kütz. (e.g., Krammer & Lange-Bertalot 1988). Since Kützing's original material had not been studied and Kützing (1844) synonymized his *F. adnata* with *Epithemia zebra* (Ehrenb.) Kütz. [Kützing 1844, p. 34, Kützing 1845, p. 58, Kützing 1849, p. 2], the conspecifity of these taxa could not be proven' (Jahn & Kusber 2006, p. 530). Based on the poor image presented in Jahn & Kusber (2006, p. 531, figure 6), the specimen from Greece has a dorsal margin that is not as arched as in *E. adnata* and it has distinctly protracted apices, a feature not present in the designated lectotype of *E. adnata*.

The lectotype specimen of *Epithemia adnata* more closely resembles the specimens illustrated by Van Heurck (1896, pl. IX, fig. 357) and Krammer & Lange-Bertalot (1988, pl.107, figs 1-5). Krammer & Lange-Bertalot lumped several taxa (including *E. kurzeana* Rabenh. and *E. porcellus*) within their concept of *E. adnata*, as evidenced by differences in valve shape, the orientation of the costate fibulae, and presence/absence of protracted apices. *Epithemia kurzeana* should not be included in *E. adnata* (pers. obs.).

In 1844, Kützing cites '*Frustulia adnata Kg.* Alg. Dec. V. No. 41 (1838)… [and] *Epithemia adnatum Breb.* Considérations sur les Diat. p. 16' as synonyms of *Epithemia zebra* (Kützing 1844, p. 34; Kützing 1849, p. 2), but also has '*Epithemia adnatum Breb.* Considérations sur les Diat. p. 16' as a synonym of *Epithemia vertagus* (Kützing 1844, p. 36; Kützing 1849, p. 4). Under *Epithemia vertagus*, Kützing records the locality as 'Auf *Cladophora fracta* in der Normandie: Lenormand in herb. Hering. (*Frustulia adnata*)' (Kützing 1844, p. 36), which is (most probably) the same material that was used for *Frustulia adnata* (Kützing 1833, p. 544; see below for *Epithemia vertagus*).

'*Eunotia adnata* (Kützing) Rabenhorst' (1853, p. 18, pl. 1, fig. 24) is often cited as the source of this combination, but in 1853 Rabenhorst intended Kützing's species to be in *Epithemia*. For the section dealing with *Epithemia*, Rabenhorst noted that 'T.1 [plate 1] unter Eunotia!' (Rabenhorst 1853, p. 17) and the figure (his tab. I) is listed for the



Figs 4–9. *Frustulia adnata*. Figs 4–6, LM images all at same scale indicted by scale bar = 10 μm (Fig. 4–9). Specimens from Kützing 41, ANSP GC 13705. Figs 4, 5 possess protracted apices, Fig. 6 with narrowly rounded apices. Fig. 6 is the designated lectotype for *Epithemia adnata*. Fig. 7. Reproduction of the original drawing from Kützing (1833, pl. XIII, fig. 15) for *Frustulia adnata*. Fig. 8. Original material packet from Kützing at BM. Fig. 9. Image of lectotype slide, ANSP GC 13705.

genus *Eunotia* with some species having *Epithemia* as an additional name. *Epithemia adnata* is listed as a synonym of *Epithemia vertagus* in Rabenhorst (1847, p. 19), with the latter figure (Rabenhorst 1853, pl. 1, fig. 24) most probably derived from Kützing's *Epithemia vertagus* (Kützing 1844, pl. 30, fig. 2, see our Figures 96 and 104).

Ross made the combinations *Epithemia adnata* (Kütz.) Bréb. var. *genuina* (Grun.) Ross (1950, p. 464) and *E. adnata* (Kütz.) Bréb. var. *porcellus* (Kütz.) Ross (1950, p. 464) based on the fact that Lagerstedt (1884, p. 45) had examined specimens of Kützing's *Frustulia adnata* and noted they were the same as those of *Navicula zebra* Ehrenb., with Kützing's epithet having priority. VanLandingham included the combination '*Epithemia adnata* (Kütz.) Ross' (VanLandingham 1969, p. 1438) but this combination was not required nor made.[2]

This choice of lectotype may impact on whether Lagerstedt's conclusion that *E. adnata* and *E. zebra* are conspecific, potentially requiring review of the nomenclatural status of over 50 subspecific names included within both species.

***Frustulia picta* Kütz. (Kützing 1833, p. 544, taf. XIII, fig. 18; Kützing 1834 [1833], p. 16, taf. I, fig. 18 = our Fig. 106–113) = *Epithema pictum* (Kütz.) Bréb. (Brébisson 1838a, p. 42; Brébisson 1838b, p. 16)**

TYPE: – GERMANY, Halle, 'An *Vaucheria* in einem Teiche bei Halle' (Kützing 1833, p. 545; Kützing 1844, p. 34)
OTHER MATERIAL: – GERMANY, Bernstadt, BM 17799 (!) (Kützing 14, our Fig. 114–119)

SYNONYM (HOMOTYPIC):
Cymbella picta (Kütz.) Bréb. (in Brébisson & Godey 1835, p. 50, pl. VII)

DESCRIPTION: [BASED ON BM 17799]. Frustules planar. Valves asymmetrical to apical axis, dorsal margin weakly convex, nearly straight, tapering to distinctly protracted apices, ventral margin nearly straight. Length 33–102 µm, breadth 9–12 µm. Canal raphe near ventral margin at apices, along valve margin and mantle on ventral side of valve, deflected towards dorsal margin at centre of valve, reaching 20% of way towards dorsal margin. Proximal raphe ends distinct, dilated; portulae indistinct. Costate fibula distinct, radiate, 4–5 in 10 µm. Striae distinctly punctate, 3–5 striae between adjacent fibulae, 14–17 in 10 µm. Areolae rectangular in shape. Capitate costae present, small. Septa present at poles.

COMMENTS: *Frustulia picta* (the type of *Epithema* Bréb.) is cited as a synonym of *Epithemia turgida* by Kützing (and almost everyone else) along with *Frustulia juergensii* Agardh (1831, p. 44) as another potential synonym (Kützing 1844, p. 34). No specimens of *Frustulia picta* were prepared for Kützing's *Algarum aquae dulcis Germanicarum*.

Kützing, at first, doubtfully suggests *Frustulia juergensii* as a synonym, a name which, if so, would have priority. But Agardh, in turn, relates his species (*Frustulia juergensii*) to '*Echinella obtusa* Juergens', which itself is (apparently) *Echinella obtusa* Lyngbye (1819, p. 208, pl. 69, fig. F), a species of *Homeocladia* – at this time, we support Kützing's doubt over the identity of *Frustulia juergensii*.

Kützing includes these specimens under the name *Epithemia turgida* in Kützing (1844, pl. 5, fig. XIV, see our Fig. 96–105).

(b) Species in Kützing (1844)

***Epithemia alpestris* Kütz. (Kützing 1844, p. 34, pl. 5, fig. XVI:1-2 (see Fig. 34), pl. 7, fig. VII); see our Fig. 23–37.**
Cystopleura alpestris Bréb. (in Kützing 1849, p. 3), *nom.nud.*

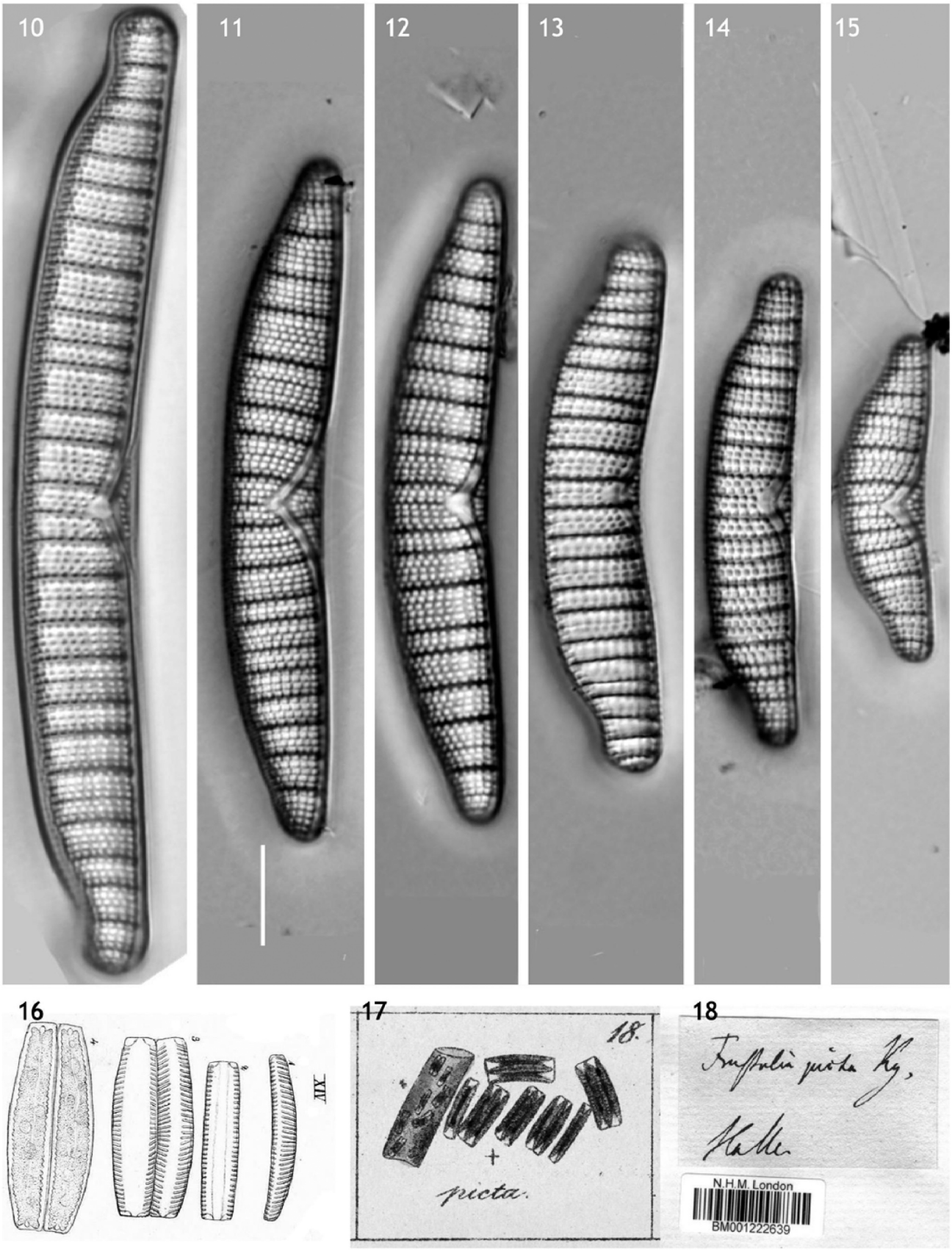
TYPE: – SWITZERLAND, Berner Oberlandes, near Thun: 'In stehendem Quellwasser des Berner Oberlandes, bei Thun' (Kützing 1844, p. 34), BM 17806 (!) (Kützing 23a, see Figure 30), Thun, BM 17829 (Kützing 13)

OTHER POSSIBLE TYPES: SWITZERLAND, BM 18205 (Kützing 192 ['In stehendem Wasser bei Thun und Hamburg'], Brébisson), BM 18517 (Kützing 324), BR, BM 18512 (Kützing 327, Brébisson), BM 18100 (Kützing 18, Braun)

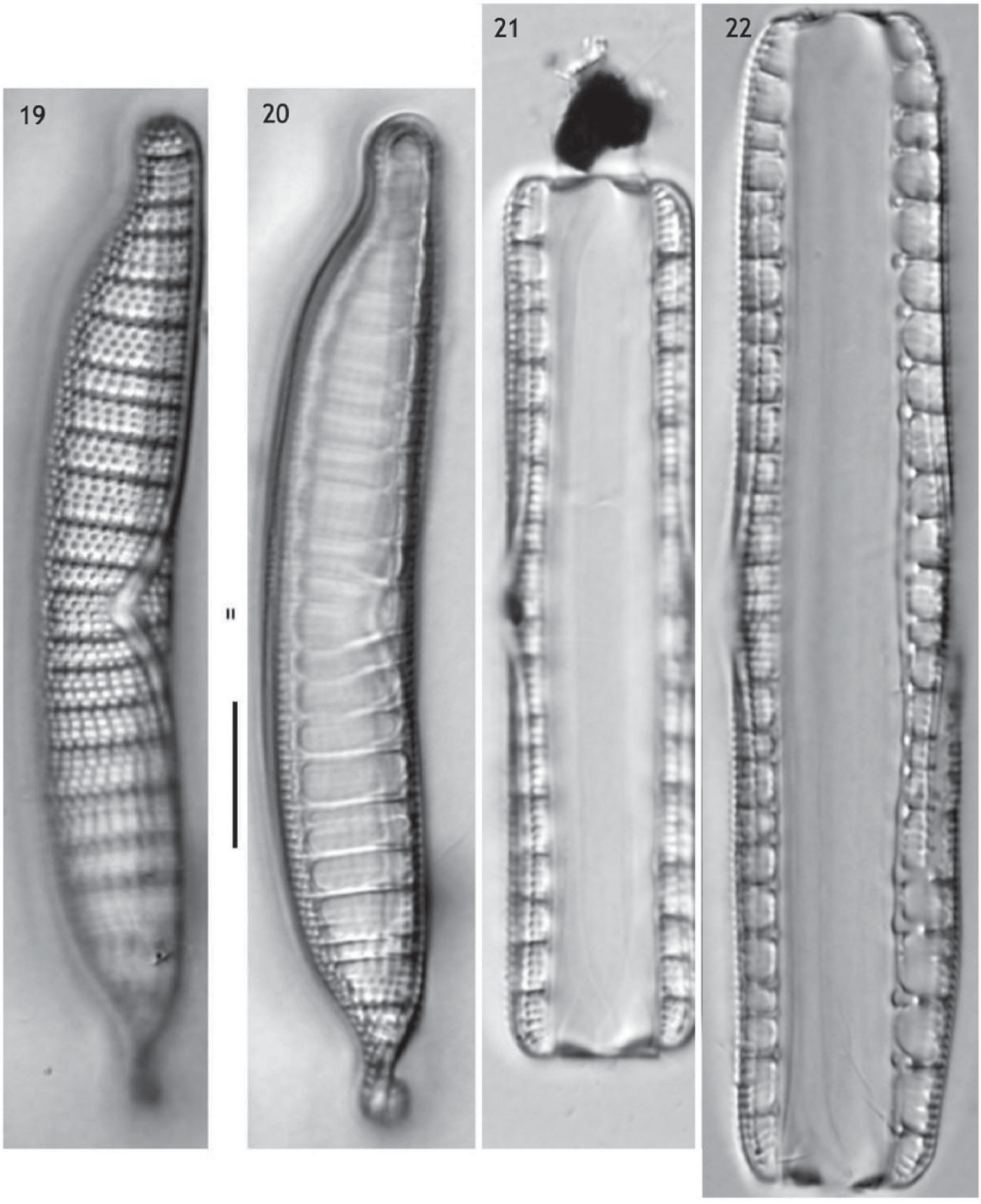
FRANCE, Falaise: BM 17804 (Kützing 1183, Brébisson, as '*Cystopleura alpetris* Bréb.'), BM 17805 (Kützing 1456, Brébisson), BM 17795 (Kützing 1182, Brébisson), BM 17867 (Kützing 1189, Brébisson), BM 17873, BM 18721 (Kützing 1283, Brébisson), BM 18777, BM 18805.

DESCRIPTION: Frustules planar. Valves asymmetrical to apical axis with dorsal margin convex, ventral margin weakly concave with apices only weakly protracted and broadly rounded; valve length 31–108 µm, breadth 9–15 µm. Canal raphe biarcuate, located ca. 1/2 way between dorsal and ventral margins at apices, extending along ventral margin then strongly deflected towards dorsal margin terminating 2/3 of the way towards dorsal margin. Canal distinct, portules small. Costate fibulae robust, 2 in 10 µm, with secondary costae also evident. Striae composed of rectangular areolae, 6–8 striae between adjacent fibulae, 12–16 in 10 µm. Septa present with robust ribs, interrupted towards ventral margin. Strongly capitate costae. Hautung valves produced.

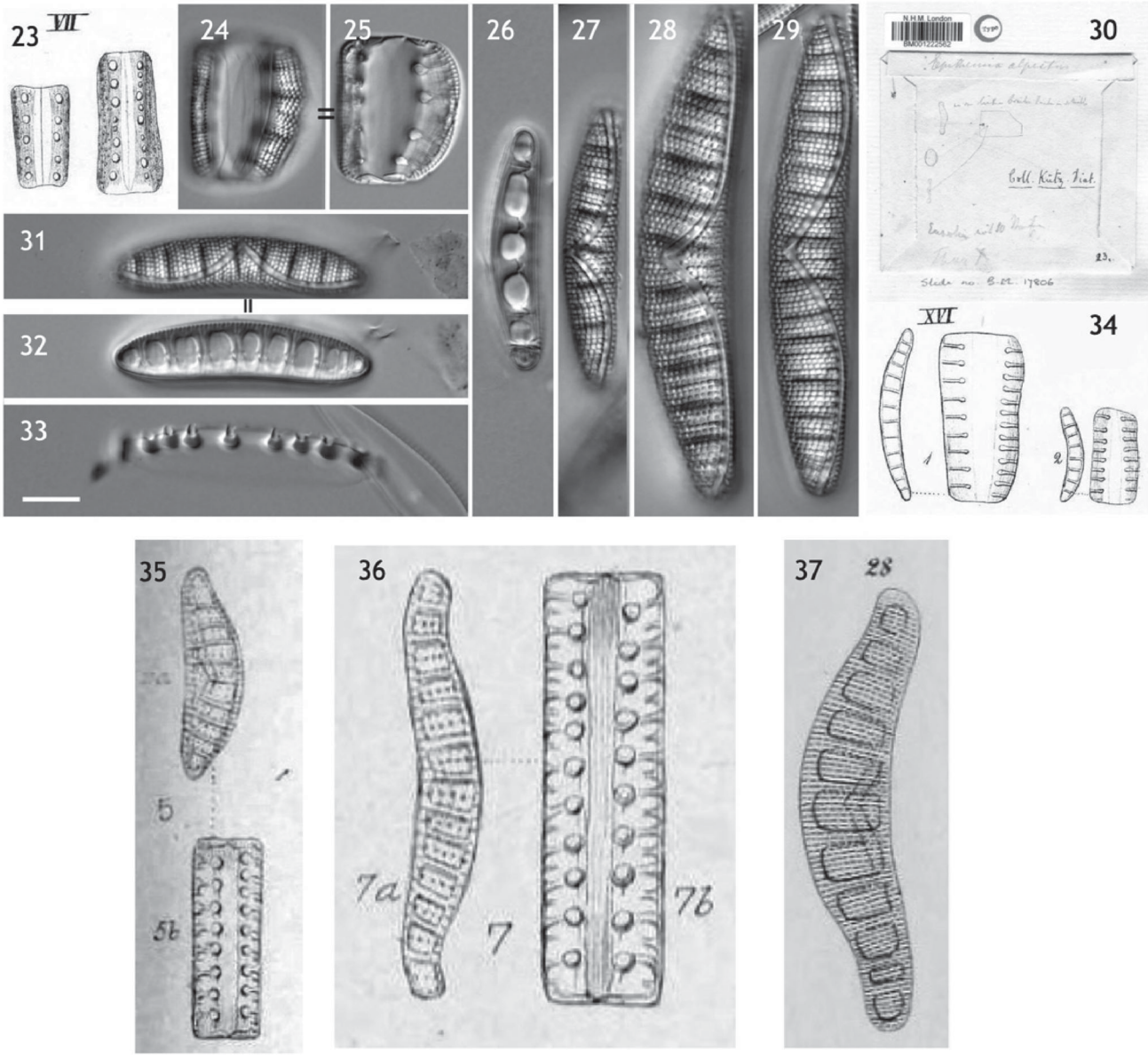
COMMENTS: '*Cystopleura alpestris* De Bréb.' was mentioned, but not accepted, by Kützing (1849, p. 2), who noted it only as a synonym of *Epithemia alpestris* (as did Rabenhorst 1853, p. 67). The name '*Cystopleura alpestris*' had been used by Brébisson on some of his specimen labels (Fig. 2); Kützing had examined some of these specimens as he notes 'Specimina gallica misit



Figs 10–18. *Frustulia picta*. Figs 10–15, LM images all at same scale indicted by scale bar = 10 μm (Fig. 11). Size diminution series of specimens from BM 17799, valve view. Fig. 17. Reproduction of the original drawing from Kützing (1833, pl. I, fig. 18) for *Frustulia* picta. Fig. 16. Reproduction of the original drawing from Kützing (1844, pl. 5, fig. XIV) for *Epithemia turgida*. Fig. 18. Original material packet from Kützing at BM.



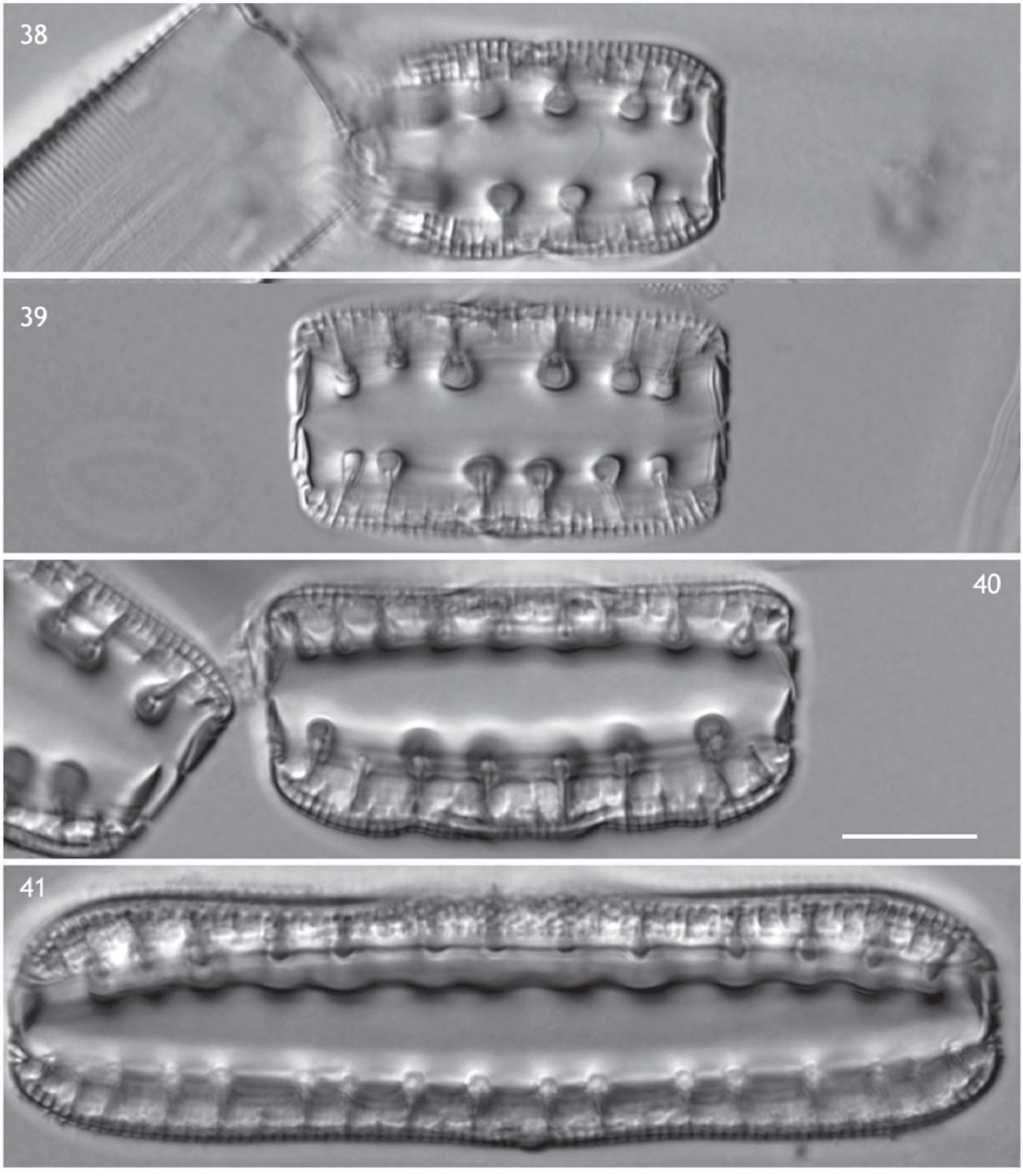
Figs 19–22. *Frustulia picta*. LM images all at same scale indicted by scale bar = 10 μm (Fig. 20). Specimens from BM 17799. Specimen in Figs 19 and 20 are of a teratological specimen, valve view. Figs 21, 22, in girdle view showing the lack of 'capitate costa' (Fig. 21) as well as under-developed (left valve) and well-developed capitate costa (right valve) (Fig. 22).



Figs 23–37. *Epithemia* alpestris. 23–37. Reproduction of the original drawing from Kützing (1844, pl. 7, fig. VII). Figs 24–29, 31–33, LM images all at same scale indicated by scale bar = 10 μm (Fig. 33) from BM 17806; ' = ' indicates images taken of the same specimen. Figs 24, 25. Girdle views of same specimen, with focus on valve exterior (Fig. 24, showing striae) and interior (Fig 25, showing 'capitate costae'). Fig. 26. Septum with separation towards ventral margin. Figs 27–29. Valve views. Figs 31, 32 Valve view of same species showing valve exterior (31) and septum (32). Fig. 33. Girdle band with extensions that fit over costate fibulae. Fig. 30. Packet of original material of Kützing collection #23. Fig. 34. Reproduction of the original drawing from Kützing (1844, pl. 5, fig. XVI:1-2). Fig. 35. Reproduction of the original drawing of *Epithemia argus* W.Sm. (Smith 1853, pl. I, fig. 5). Fig. 36, Reproduction of the original drawing of '*Epithemia alpestris* W.Sm.' (Smith 1853, pl. I, fig. 7). Fig. 37, reproduction of the original drawing of '*Eunotia alpestris* (Kützing) Rabenhorst' from Rabenhorst (1853, p. 18, pl. I, fig. 23)

amiciss. De Brébisson' (Kützing 1849, p. 2; these specimens are found on BM 17804-5, BM 17795, BM 17873, BM 18721, BM 18777, BM 18805, from 'Falaise, France').

'*Eunotia alpestris* (Kützing) Rabenhorst' (1853, p. 18, pl. 1, fig. 23, see our Fig. 37) is often cited as the source of this combination, but in 1853 Rabenhorst intended Kützing's species to be in *Epithemia*. For the section dealing with *Epithemia*, it is noted that 'T.1 [plate 1] unter Eunotia!' (Rabenhorst 1853, p. 17) and the figure (plate 1) is listed as *Eunotia* with some species having *Epithemia* as an additional name. Rabenhorst cites '*Cystopleura alpestris* De Bréb.' as a synonym in the index (Rabenhorst 1853, p. 67). The combination appears to have been made by Rabenhorst some years earlier (Rabenhorst 1847, p. 19).



Figs 38–41. *Epithemia alpestris*. LM images all at same scale indicted by scale bar = 10 μm (Fig. 40) from BM 17806. Girdle views, showing 'capitate costae'. Figs 39, 40 showing Hautung valves with undulate margin, interlocking edges of girdle bands at ends of the valve are evident.

The name *Epithemia alpestris* was used by William Smith (1853, p. 13, pl. I, fig. 7) but he did indicate the Kützing specimens as being possibly the same (Smith 1853, p. 13, 'Kütz. Bacill. v. 16?' [= Kützing 1844, pl. 5, fig. XVI:1-2]). Earlier, Smith suggests that *Epithemia alpestris* Kütz. is the same as his *Epithemia argus* W.Sm. (Smith 1853, p. 12, pl. I, fig. 5). Smith's specimens have not been investigated here, his drawings are reproduced as our Fig.

35 (*Epithemia argus*, Smith 1853, pl. I, fig. 5) and our Fig. 36 (Smith 1853, pl. I, fig. 7).

***Epithemia musculus* Kütz. (Kützing 1844, p. 33, pl. 30, fig. 6) = *Rhopalodia musculus* (Kütz.) O.Müll. (O. Müller 1900, pp. 278 [1899], 294 [1900])**

TYPE: – 'Im Brackwasser des baltischen Meeres bei Flensberg, an Lyngbya' (Kützing 1844, p. 33), BM 17792 (!) (Kützing 22), Baltic Sea [Flensburg], Biasoletto, isolectotype, HVH IX-63-C16, lectotype (Kützing 22 [Ostsee, Flensburg], now in BR; Krammer & Lange-Bertalot, 1988, p. 163, taf. 114, figs 2-5; Lange-Bertalot & Krammer 1997, p. 81)

SYNONYMS (HOMOTYPIC):
Eunotia westermanni var. *musculus* (Kütz.) Rabenh. (Rabenhorst 1847, p. 18)
Cystopleura musculus (Kütz.) Kuntze (1891, p. 891)
Rhopalodia gibberula var. musculus (Kütz.) Muschl. (Muschler 1908, p. 153)
Rhopalodia gibberula var. *musculus* (Kütz.) A.Cleve (Cleve-Euler 1952, p. 43, fig. 1415 o-r) (Invalid, latter homonym).

DESCRIPTION: Frustules segment-like. Valves strongly asymmetrical to apical axis. Asymmetry also about transverse axis, with one part of valve smaller in size with stronger angle than the other. Dorsal margin highly arched, convex, ventral margin concave, terminating as small, rounded apices that deflect ventrally. Length 23–50 µm, breadth 11.0–15.5 µm. Canal raphe extending from apices along dorsal margin to valve centre. Centre of dorsal margin indented to a small degree. Portules evident. Costate fibulae narrow, radiate. Secondary costae lacking. Fibulae 6–8 in 10 µm. Striae distinctly punctate, 1–4 rows of striae between adjacent fibulae. Areolae rectangular in shape. Striae 14–17 in 10 µm.

COMMENTS: *Epithemia musculus* is considered to be a species of *Rhopalodia*. Given the relationships in Ruck et al. (see above), the viewpoints expressed in Vigneshwaran et al. (2021) and the potential of the alternative naming of these relationships (Fig. 3b), '*Rhopalodia* #1' would constitute a new genus to include *Rhopalodia musculus*. As numerous varieties of *Rhopalodia musculus* have been recognized and formally named, the expectation is that this genus, should it receive a proper name, will include a number of species.

***Epithemia porcellus* Kütz. (Kützing 1844, p. 34, pl. 5, figs XVIII-XIX)**

TYPE: – ITALY, 'Im Bergmehl von San Fiore' (Kützing 1844, p. 34), BM 17802 (!); see Patrick and Reimer (1975, p. 181); BM 17803 (Kützing 911); additional slides (all from Kützing 911): BM 18066-7, 18508, 18685, 18717, 18746, 18757, 18768, 18808, 18816, 18820, 18926

SYNONYMS (HOMOTYPIC):
Epithemia zebra var. porcellus (Kütz.) Grun. (Grunow 1862, p. 328, pl. 3/6, fig. 3-4)

Cystopleura porcellus (Kütz.) Kuntze (1891, p. 891)

Cystopleura zebra var. *porcellus* (Kütz.) De Toni (1892, p. 785)

Cystopleura zebra var. *porcellus* (Kütz.) Gutw. (Gutwinski 1899, p. 683)

Epithemia adnata var. *porcellus* (Kütz.) R.Ross (Ross 1950, p. 464)

Epithemia zebra f. *porcellus* (Kütz.) Hust. (Hustedt 1957, p. 335)

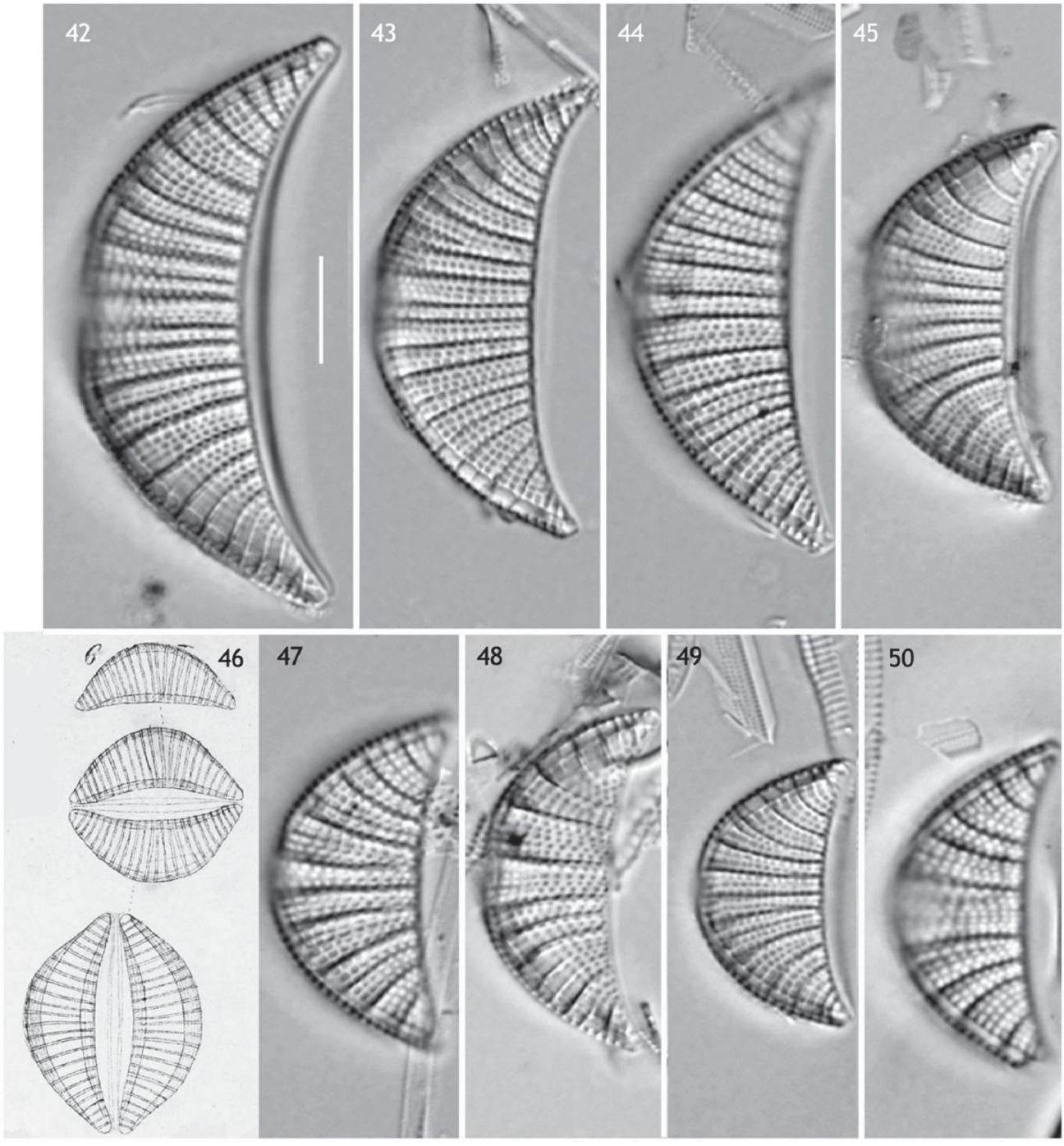
Epithemia adnata var. *porcellus* (Kütz.) R.M.Patrick (in Patrick & Reimer 1975, p. 180, pl. 24, fig. 6)

FIGURES: 51–58 (BM 17802)

DESCRIPTION: Frustules planar. Valves asymmetrical to apical axis, dorsal margin weakly convex, tapering to distinctly protracted, broadly rounded apices, ventral margin slightly concave. Length 31–75 µm, breadth 9–11 µm. Canal raphe near ventral margin at apices, along valve margin and mantle on ventral side of valve, deflected towards dorsal margin at centre of valve, reaching 20% of way towards dorsal margin. Proximal raphe ends distinct, dilated; portulae indistinct. Costate fibula distinct, barely radiate, 4–7 / 10 µm. Striae distinctly punctate, 2–4 striae between adjacent fibulae, 12–15 / 10 µm. Areolae rectangular in shape. Capitate costae present, small. Septa present at poles.

COMMENTS: *Epithemia porcellus* differs from *E. adnata* in possessing protracted apices and the barely radiate orientation of the costate fibulae. Many specimens of *E. porcellus* have been reported in the literature as *E. adnata*. It is distinct enough in the morphological differences it exhibits relative to *E. adnata*, that it warrants being recognized as a distinct species.

Patrick (in Patrick & Reimer 1975, p. 181) identified BM 17802 as the holotype for this species. It cannot be the holotype for two reasons: (1) such designations were not available at that time, nor was the slide that they designated as such; (2) there are numerous slides from 'San Fiore' (listed above) that would all be syntypes. The catalogues to Kützing's collection indicate only sample 911 as the type (original) material. In addition, specimens from BM 178702 are much smaller than the length indicated in Kützing's original description (1/20'''to 1/18''' which is about 112–125 µm). Kützing's illustrations are stylized and do not provide any useful information on this species. The illustration in Patrick and Reimer (1975, pl. 24, fig. 6) is of a specimen ca. 100 µm long (and thus outside the original size range of Kützing) and is not from original material but from a slide in the General Collection of ANSP (#5999),



Figs 42–50. *Epithemia musculus*. LM images all at same scale indicted by scale bar = 10 μm (42–50) from BM 17792. Fig. 48. Reproduction of the original drawing of *E. musculus* from Kützing (1844, pl. 30, fig. 6).

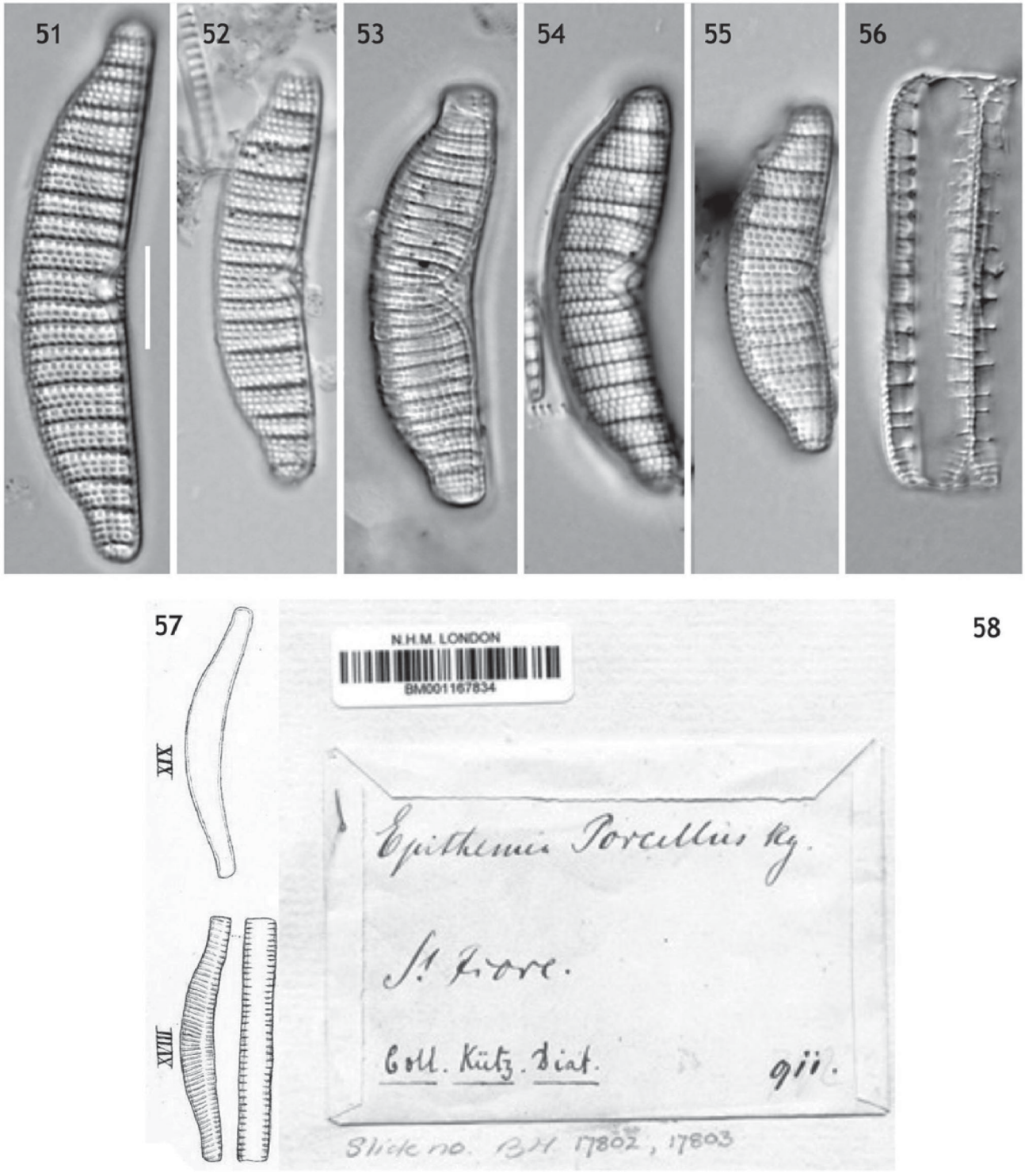
taken from a sample made in the state of Nebraska ('Hamilton Co., Platte River nr. Philipps, Floating in Sandpit Lake').

***Epithemia proboscidea* Kütz. (Kützing 1844, p. 35, pl. 5, fig. XIII)**

TYPE: – 'Im Bergmehl der Lüneburger Haide' (Kützing 1844, p. 35), BM 17810 (!) ('Kützing 906', Fig. 63); see Patrick & Reimer (1975, p. 181) who designated this slide as lectotype; BM 17995, BM 18054, BM 18510 (Kützing 906, Lüneburger Haide), isolectotypes as all are made from the same Kützing collection number (906).

SYNONYMS (HOMOTYPIC):

Epithemia zebra var. *proboscidea* (Kütz.) Grun. (Grunow 1862, p. 329, pl. 6, fig. 5)



Figs 51–58. *Epithemia porcellus*. Figs 51–56, LM images all at same scale indicted by scale bar = 10 μm (51–58) from BM 17802, Figs 51–55, valve views showing size diminution series. Fig. 56. Girdle view. Fig. 57. Reproduction of the original drawing of *E. porcellus* from Kützing (1844, pl. 5, figs XVIII-XIX). Fig. 58. Packet of original material from Kützing collection 911 at BM.

Cystopleura proboscidea (Kütz.) Kuntze (1891, p. 891)

Cystopleura zebra var. *proboscidea* (Kütz.) De Toni (1892, p. 784)

Epithemia adnata var. *proboscidea* (Kütz.) Hendey (1954, p. 577)

Epithemia adnata var. *proboscidea* (Kütz.) R.M. Patrick (in Patrick & Reimer 1975, p. 181, pl. 24, fig. 5)

DESCRIPTION: Valve asymmetrical to apical axis, dorsal margin weakly convex, ventral margin slightly concave, tapering to distinctly protracted, broadly rounded apices. Length 48.5 µm, breadth 10 µm. Canal raphe near ventral margin at apices, along valve margin and mantle on ventral side of valve, deflected towards dorsal margin at centre of valve, barely 20% of way towards dorsal margin. Proximal raphe ends distinct, dilated; portulae indistinct. Costate fibula distinct, radiate, 4–5 / 10 µm. Striae distinctly punctate, 2–4 striae between adjacent fibulae, 14–15 / 10 µm. Areolae elliptic to rectangular in shape. Capitate costae present, small (see fig. 59). Septa present at poles.

COMMENTS: A single *Epithemia* specimen is present and it has been circled on the slide marked 'Type' at BM. Comparing this specimen to Kützing's illustration (our Fig. 62), and the similarity of this specimen to some in the *Epithemia picta* size series (our Figs 10–15) and of the *E. porcellus* size series (our Figs 51–56), suggests that Kützing's *E. proboscidea* is not a separate taxon, but rather a synonym of (most likely) *E. picta*.

***Epithemia saxonica* Kütz. (Kützing 1844, p. 35, pl. 5, fig. XV)**

TYPE: – 'An Lemna trisulea bei Bruckforf und Dieskau zwischen Halle und Leipzig! Italien: Meneghini!' (Kützing 1844, p. 35), **BM 17807 (!) (Kützing 26), lectotype designated here**; BM 17808 (Kützing 15); BM 17809 (Kützing 25); BM 17820 (Kützing 17).

SYNONYMS (HOMOTYPIC):

Eunotia saxonica (Kütz.) Rabenh. (Rabenhorst 1847, p. 19)

Epithemia zebra var. *saxonica* (Kütz.) Grun. (Grunow 1862 p. 328, pl. III (6) fig. 6)

Cystopleura saxonica (Kütz.) Kuntze (1891, p. 891)

Cystopleura zebra var. *saxonica* (Kütz.) De Toni (1892, p.784)

Cystopleura zebra var. *saxonica* (Kütz.) Gutw. (Gutwinski 1899, p. 683)

Epithemia zebra f. *saxonica* (Kütz.) Hust. (Hustedt 1957, p. 335)

Epithemia adnata var. *saxonica* (Kütz.) R.M.Patrick (in Patrick & Reimer 1975, p. 182, pl. 24, fig. 9)

DESCRIPTION: Frustules planar. Valves asymmetrical about apical axis, dorsal margin distinctly convex, ventral margin barely concave with apices protracted in all but smallest specimens, rounded. Length 24–40 µm, breadth 7.5–9.0 µm. Canal raphe at ca. mid-valve at apices, extending along ventral margin, deflected towards dorsal margin at mid-valve, then extending to ca. $\frac{1}{4}$ to almost $\frac{1}{2}$ of the way towards dorsal margin. Costate fibulae distinct, 3–4 in 10 µm, radiate. Striae distinctly punctate, 3–5 rows of striae between adjacent fibulae, 13–17 in 10 µm. Areolae rectangular in appearance. Septa present. Capitate costae present, narrow.

COMMENTS: There are several taxa on slide BM 17807. The original figure and description by Kützing suggest that the specimens in our Figs 68 and 69 best fit Kützing's concept of this species. The specimen in Fig. 68 is designated as lectotype.

***Epithemia sorex* Kütz. (Kützing 1844, p. 33, pl. 5, fig. XII: 5 a-c)**

TYPE: – 'An Cladophora flavescens im salzigen See bei Rollsdorf (Eisleben)! An Cladophora fracta bei Schleusingen!' (Kützing 1844, p. 33), BM 17791 (!) (Kützing 10a, Schleusingen); see Patrick & Reimer (1975, p. 188).

SYNONYMS (HOMOTYPIC):

Cystopleura sorex (Kütz.) Kuntze (1891, p. 891)

Eunotia westermanni var. *sorex* (Kütz.) Rabenh. (Rabenhorst 1847, p. 18)

Eunotia sorex (Kütz.) Rabenh. (Rabenhorst 1853, p. 18, pl. I, fig. 7)

DESCRIPTION: Frustules segment-like. Valves distinctly asymmetrical to apical axis, with dorsal margin strongly arched, ventral margin weakly concave and apices protracted, and broadly rounded. Length 17–30 µm, breadth 7.5–9.0 µm. Canal raphe biarcuate, positioned at apices ca. mid-valve arched towards ventral margin then towards dorsal margin near centre of valve, terminating near dorsal margin. Costate fibulae narrow, radiate, 7–9 /10 µm along ventral margin. Striae distinctly punctate, radiate, 2–3 rows of striae between adjacent fibulae. Capitate costa absent. Septa present at apices.

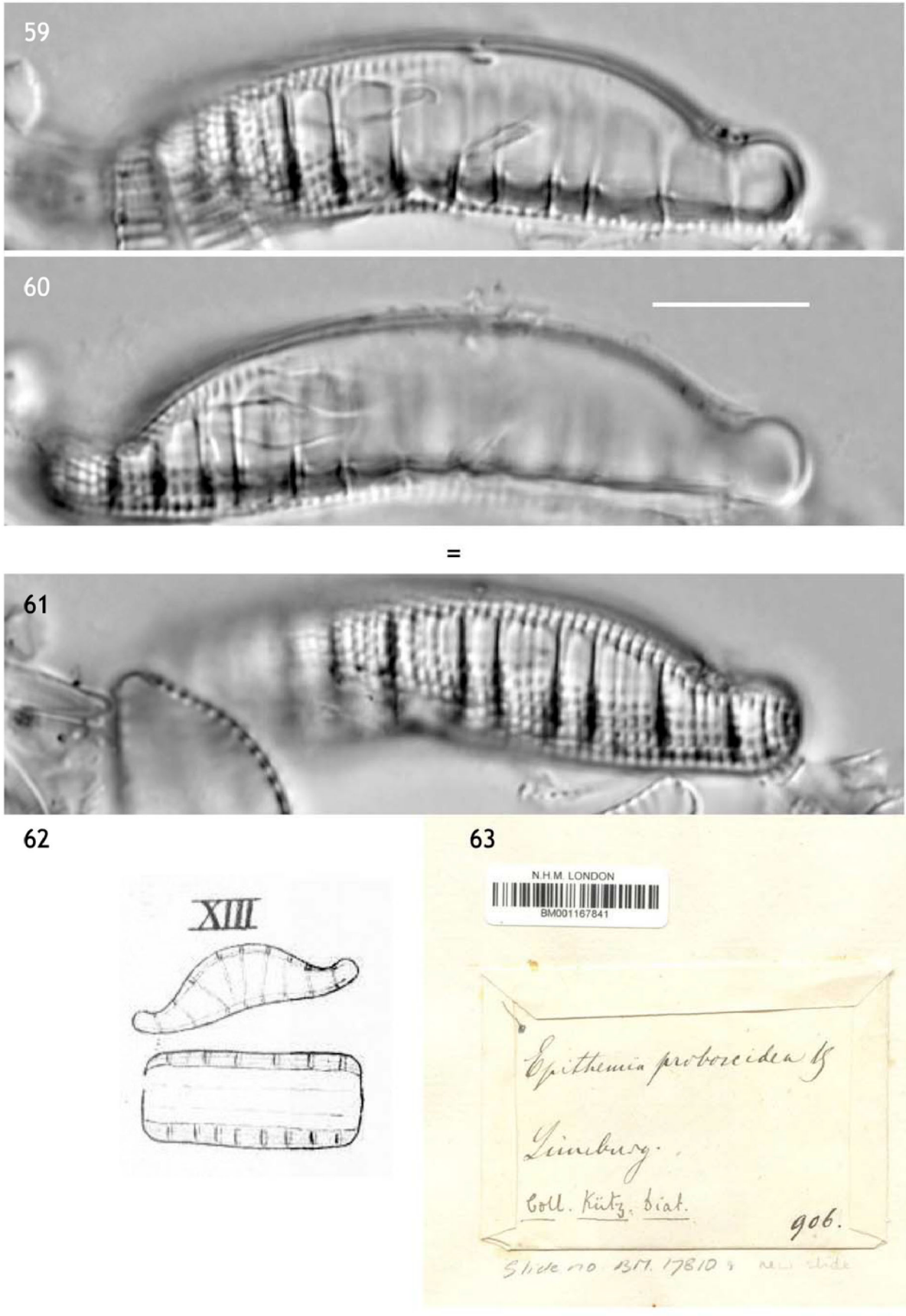
COMMENTS: As above, '*Eunotia sorex* (Kützing) Rabenhorst' (Rabenhorst 1853, p. 18, pl. I, fig. 7) is often cited as the source of this combination, but in 1853 Rabenhorst intended Kützing's species to be in *Epithemia* (see our Fig. 79).

***Epithemia ventricosa* Kütz. (Kützing 1844, p. 35, pl. 30, fig. 9 a, b)**

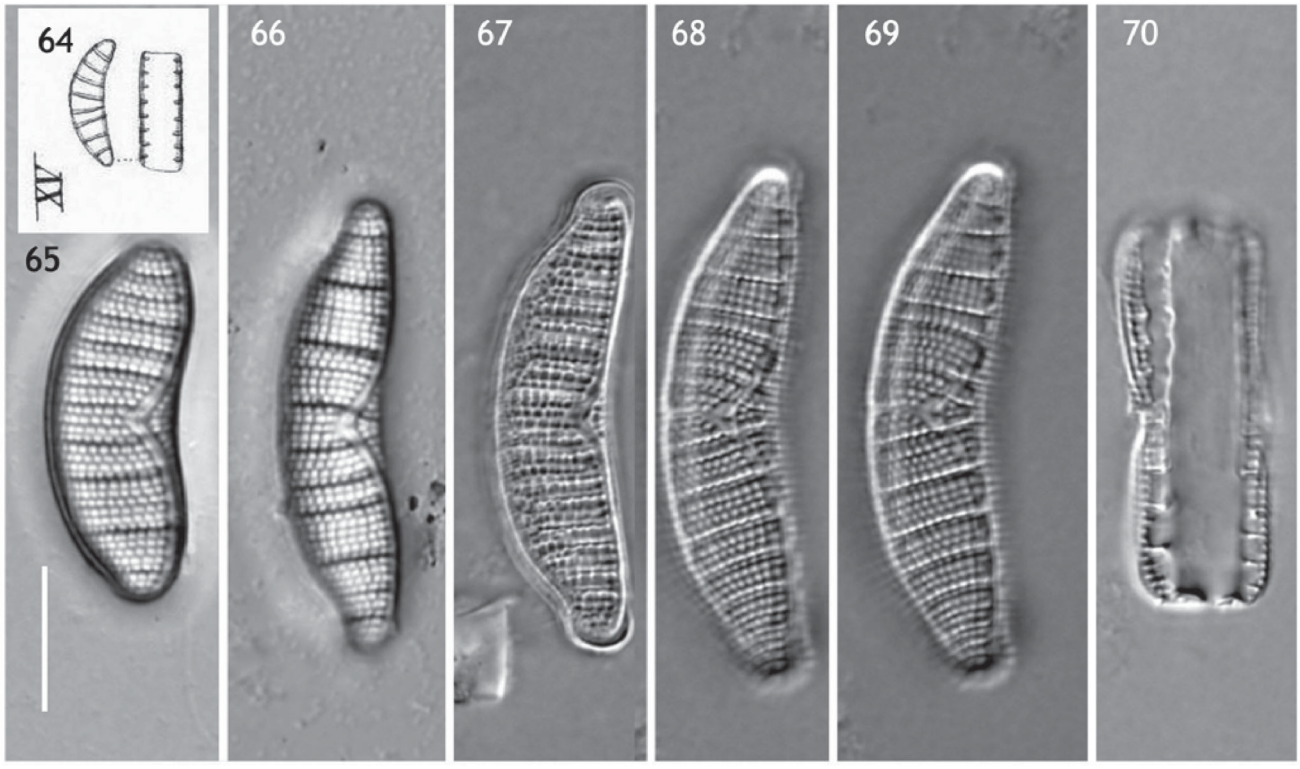
TYPE: – 'Bei Schleussingen, unter Conferven! 1830' (Kützing 1844, p. 35), BM 17814 (!) (Kützing 10), designated as lectotype by Patrick & Reimer (1975, p. 190).

SYNONYMS (HOMOTYPIC):

Eunotia gibba var. *ventricosa* (Kütz.) Rabenh. (Rabenhorst 1847, p. 19)



Figs 59–63. *Epithemia proboscidea*. Figs 59–61. LM images all at same scale indicted by scale bar = 10 μm (Fig. 60) from BM 17810; ' = ' indicates images taken of the same specimen. Fig. 62. Reproduction of the original drawing of *Epithemia proboscidea* from Kützing (1844, pl. 5, fig. XIII). Fig. 63. Packet of original Kützing material, collection # 906 at BM.



Figs 64–70. *Epithemia saxonica*. 64–70. Reproduction of the original drawing of *Epithemia saxonica* from Kützing (1844, pl. 5, fig. XV). Figs 65–70. LM images all at same scale indicted by scale bar = 10 μm (Fig. 65) from BM 17807. Figs 65–69 valve views, Fig. 66 girdle view.

Eunotia ventricosa (Kütz.) Rabenh. (Rabenhorst 1853, p. 17, pl. I, fig. 22[3])

Epithemia gibba var. *ventricosa* (Kütz.) Grun. (Grunow 1862, p. 327)

Cystopleura ventricosa (Kütz.) Kuntze (1891, p. 891)

Cystopleura gibba var. *ventricosa* (Kütz.) De Toni (1892, p. 781)

Rhopalodia ventricosa (Kütz.) O.Müll. (Müller 1895, p. 65, pl. 1, figs 20-21)

Rhopalodia gibba var. *ventricosa* (Kütz.) H. & M. Perag. (H. & M. Peragallo 1907, p. 302, pl. 77, figs 3-5)

Rhopalodia gibba var. *ventricosa* (Kütz.) Ad.Mayer (Mayer 1913, p. 279), *illegit*,

Cystopleura ventricosa (Kütz.) Elmore (1921, p. 128, pl. 17, figs 655-657), *illegit.*

Rhopalodia gibba f. *ventricosa* (Kütz.) Hust. (Hustedt 1957, p. 336)

DESCRIPTION: Frustules segment-like. Valves distinctly asymmetrical to apical axis, dorsal margin convex, undulate with peak at centre bearing slight apical notch, tapering to each apex, deflected ventrally, ventral margin straight except at apices. Length 42–88 µm, breadth 9–11 µm. Canal raphe positioned along dorsal margin. Costate fibulae distinct, parallel in centre, radiate at poles, 6–7 / 10 µm in middle of valve, 7–9 / 10 µm at poles. Striae without distinct areolae, 2–3 striae between adjacent fibulae, 15–17 /10 µm.

COMMENTS: This species belongs in the genus *Rhopalodia*, and has been treated as a separate species, as a variety of *R. gibba* (Patrick & Reimer 1975) and as a synonym of *R. gibba* (Krammer & Lange-Bertalot 1988).

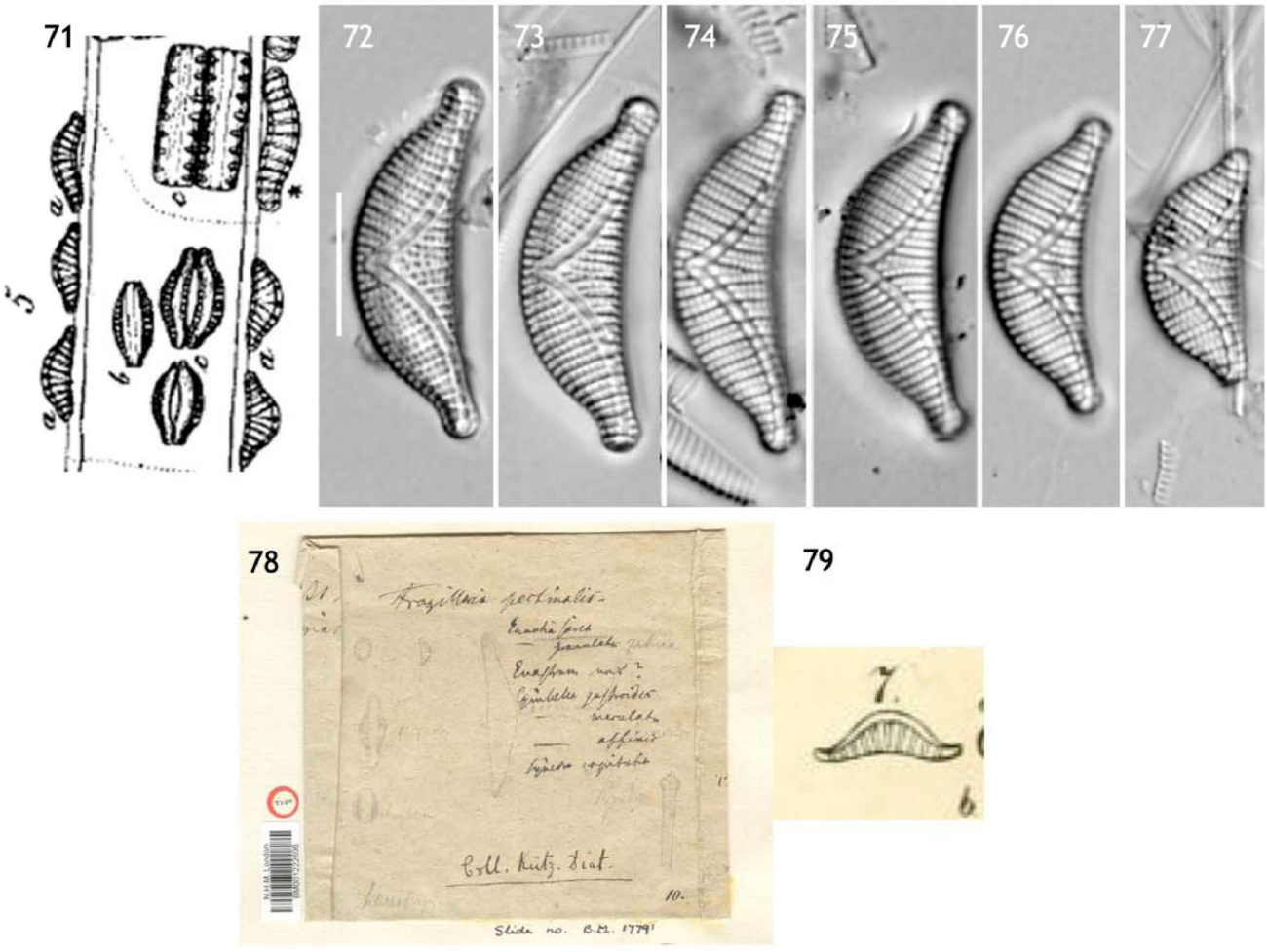
***Epithemia vertagus* Kütz. (Kützing 1844, p. 36, pl. 30, fig. 2)**

TYPE: – NORMANDY, 'Auf *Cladophora fracta* in der Normandie: Lenormand in herb. Hering. (*Frustulia adnata*)' (Kützing 1844, p. 36), 'Ad Cladophoram fractam, in Gallia' (Kützing 1849, p. 4), BM 17820 (!) (Kützing 17, Falaise), BM 17818-9 (Falaise, Brébisson), BM 18924 (Kützing 1748, Calvados), BM 19393 (Kützing 1180, Isles de Chausey, Normandy, Brébisson)

SYNONYMS (HOMOTYPIC):

Epithemia turgida var. *vertagus* (Kütz.) Grun. (Grunow 1862, p. 326)

Cystopleura vertagus (Kützing) Kuntze (1891, p. 891)



Figs 71–79. *Epithemia sorex*. Fig. 71. Reproduction of the original drawing of *Epithemia saxonica* from Kützing (1844, pl. 5, fig. XII: 5 a-c). Figs 72–77. LM images all at same scale indicted by scale bar = 10 μm (Fig. 72) from BM 17791. Fig. 78. Packet from Kützing's collection for BM 17791. Fig. 79. Reproduction of the original drawing of *Eunotia sorex* (Kütz.) Rabenh. (Rabenhorst 1853, pl. I, fig. 7).

Cystopleura turgidata var. *vertagus* (Kütz.) De Toni (1892, p. 778)

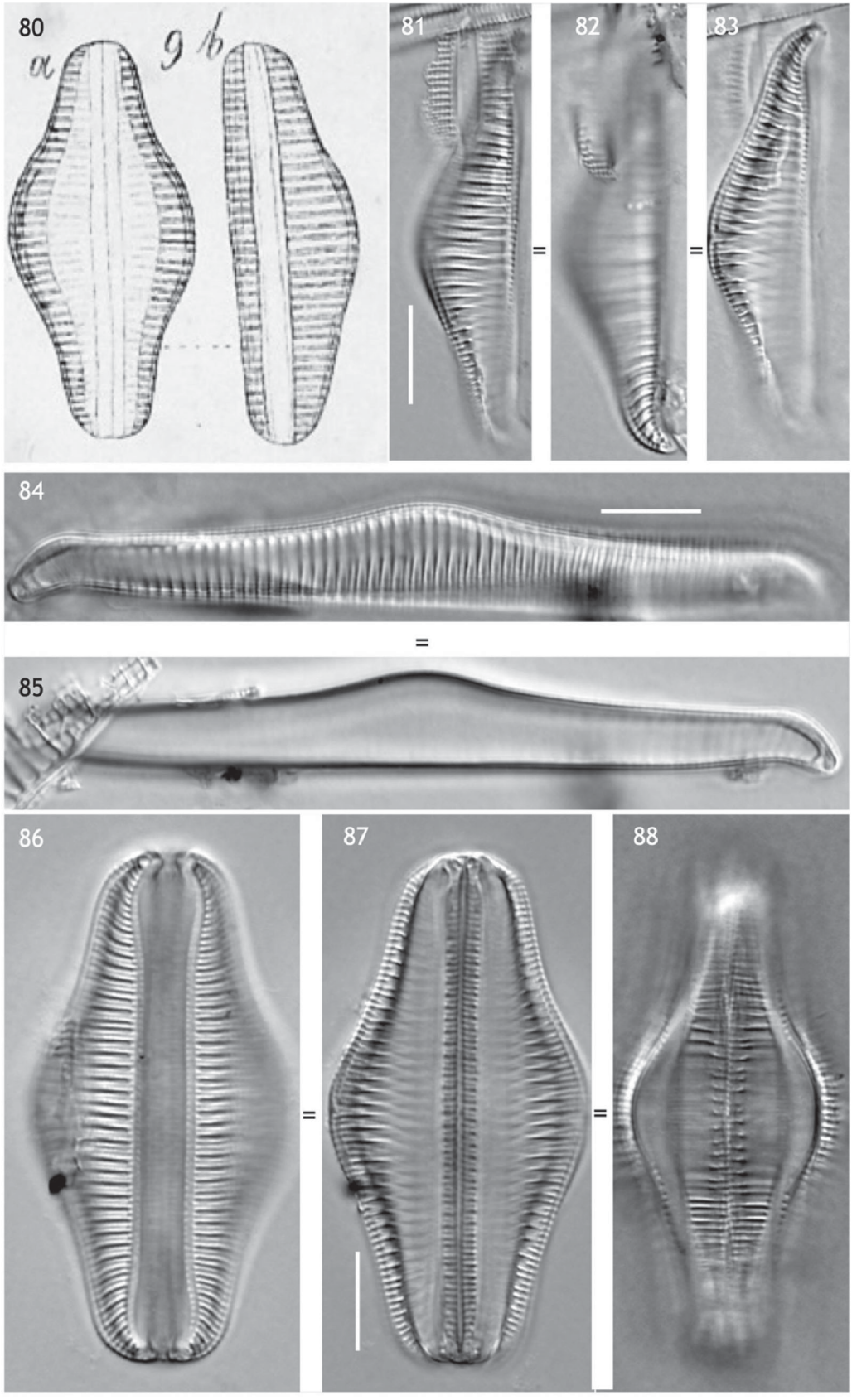
Epithemia granulata var. *vertagus* (Kütz.) Skvortzov & K.I.Mey. (Skvortzov & Meyer 1928, p. 38)
Epithemia turgida f. *vertagus* (Kütz.) Kisselev (in Proschkina-Lavrenko 1950, p. 306)

DESCRIPTION: Frustules planar. Valves asymmetrical to apical axis, dorsal margin convex, ventral margin concave with apices protracted; valve length 96–115 µm, breadth 13.5–15.0 µm. Canal raphe extending from middle of apices to ventral margin and mantle, then curving strongly near centre of valve towards dorsal margin, terminating ca. $\frac{1}{2}$ way towards dorsal margin. Costate fibulae distinct, radiate, 4–6 in 10 µm. Striae distinctly punctate, 2 striae between adjacent fibulae, 8–11 in 10 µm. Capitate costae small, septa present at apices.
COMMENTS: In the protologue for *Epithemia vertagus*, Kützing (1844, p. 36) notes that Brebisson's *Epithema adnatum* (Brébisson 1838a, p. 42) is from the same material (also noted in Kützing 1849, p. 4, and see above under *Epithemia adnata*). There are three slides in BM for *Epithemia vertagus*, all from Falaise, Normandy, Brébisson's material. As BM 17820 was made from 'Kützing 17', it is likely to be the specimens used for the protologue.

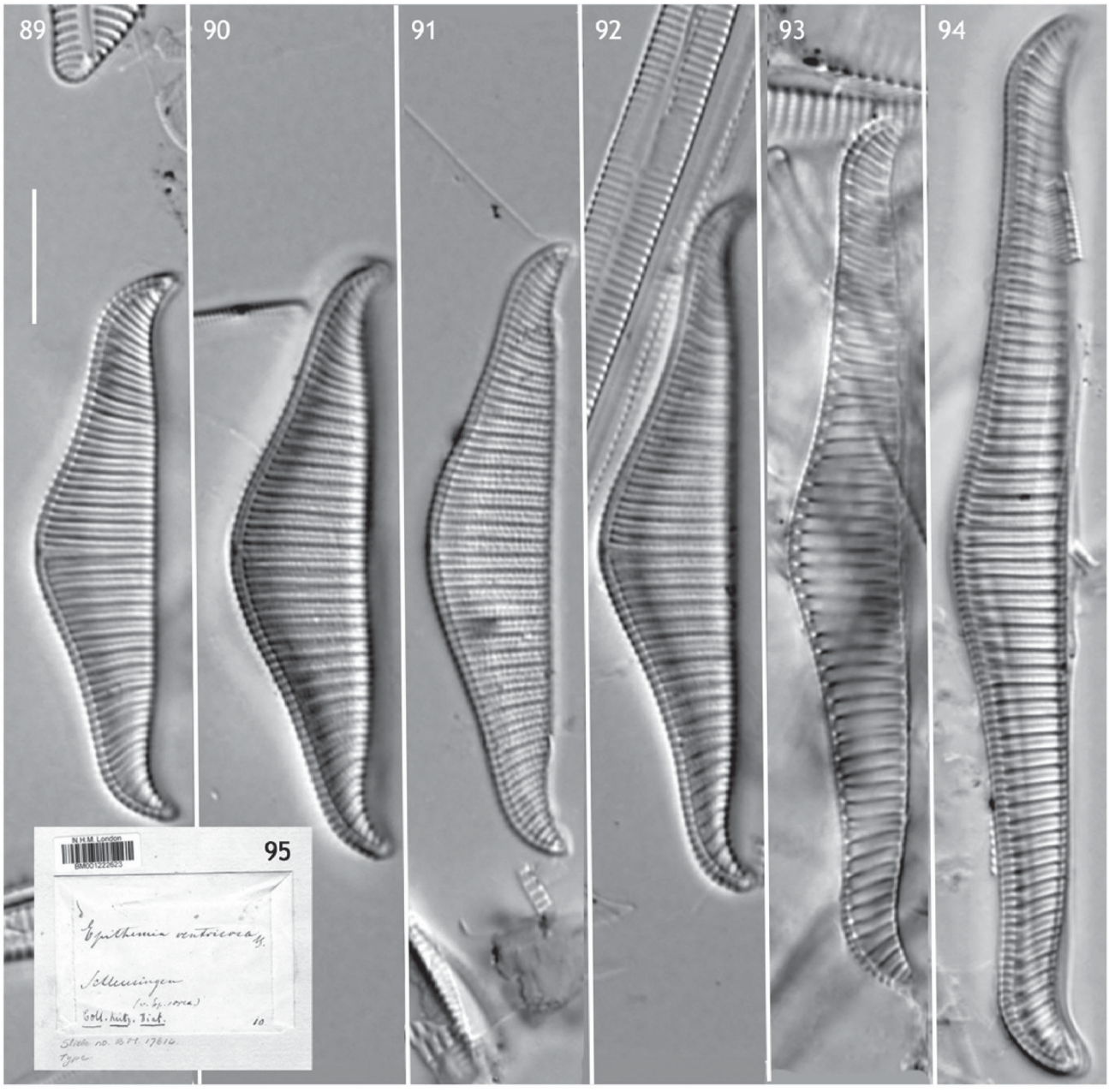
(c) Species in Kützing (1849)

***Epithemia ventricosa β*. [var.] *gregaria* Bréb. in Kütz. (Kützing 1849, p. 4)**
Type: – Turkey, Constantinople [Istanbul], 'Ad Zonariam Pavoniam in freto Constantinopolitano. Specimina misit cl. De Brébisson', **BM 17815 (!) (Kützing 1342), lectotype designated here**.

DESCRIPTION: Frustules segment-like. Valves distinctly asymmetrical to apical axis, dorsal margin convex, undulate with peak at centre bearing slight apical notch, tapering to each apex, deflected ventrally, ventral margin straight except at apices. Length 54–99 µm, breadth 7–11 µm.



Figs 80–88. *Epithemia ventricosa*. 80–88. Reproduction of the original drawing of *Epithemia ventricosa* from Kützing (1844, pl. 30, fig. 9 a, b). Figs 81–88. LM images all at same scale indicted by scale bar = 10 μm (Fig. 81) from BM 17814, ' = ' indicates images taken of the same specimen.



Figs 89–95. *Epithemia ventricosa*. LM images all at same scale indicted by scale bar = 10 μm (89–95) from BM 17814 showing size diminution series. Fig. 95. Image of the material packet for Kützing Collection #10 at BM.

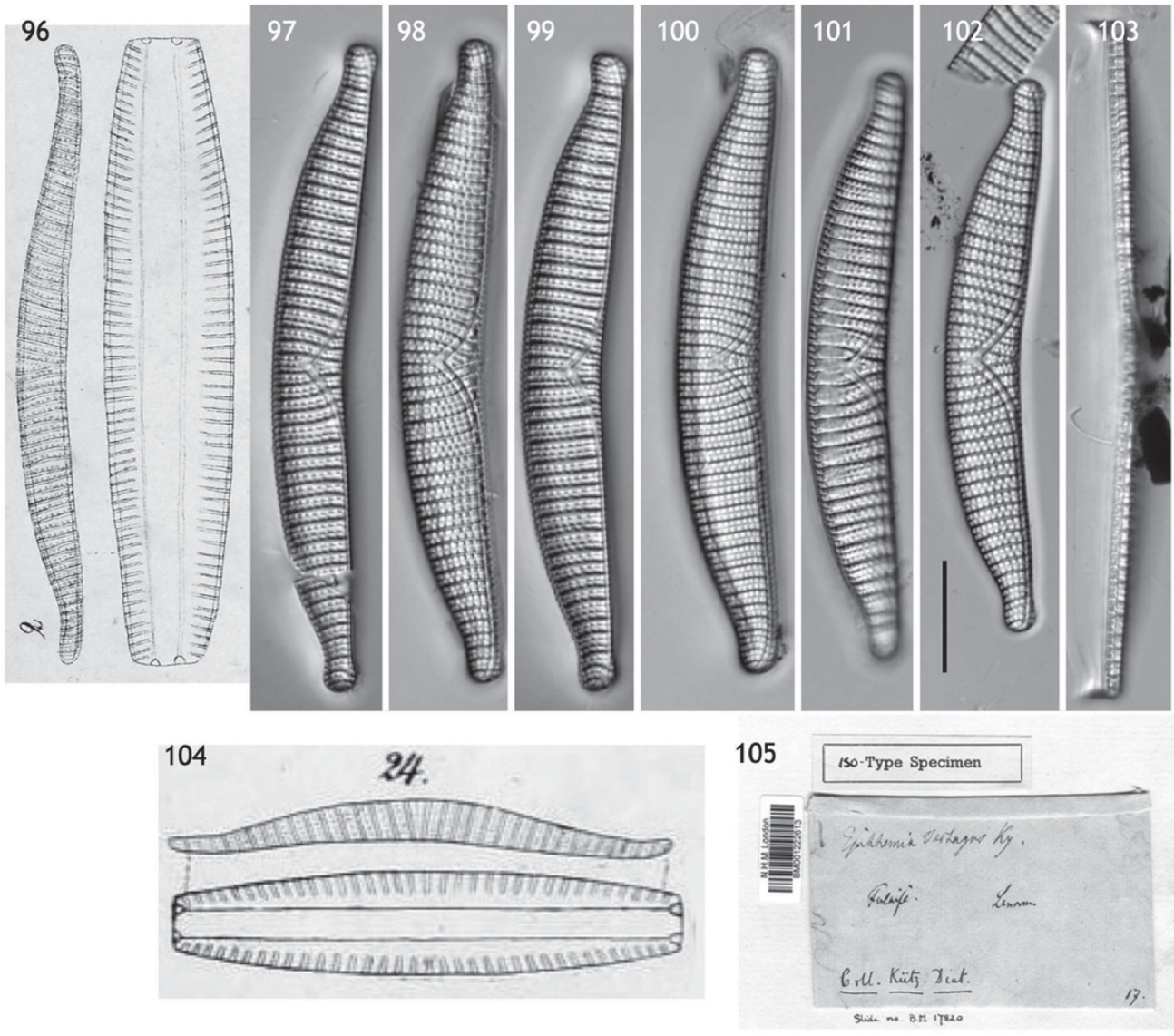
Canal raphe positioned along dorsal margin. Costate fibulae distinct, parallel in centre, radiate at poles, 6–7 / 10 µm in middle of valve, 7–9 / 10 µm at poles. Striae without distinct areolae, 2–3 striae between adjacent fibulae, 15–17 /10 µm.

COMMENTS: Specimens from this material represent a taxon in the genus *Rhopalodia*. There is no substantial difference in valve shape, metrics or description to separate this variety from the nominate, which was described by Kützing in 1844 (see above).

***Epithemia reticulata* Naegeli ex Kütz. (Kützing 1849, p. 889)**

TYPE: – Switzerland, Zurich, 'In aqua dulci Helvetiae: cl. Naegeli', **BM 17821 (!), lectotype designated here**, BM 17822, BM 78099 [single specimen, R.Ross] (from Kützing 862)

DESCRIPTION: Frustules planar. Valves weakly asymmetrical to the apical axis. Dorsal margin weakly convex, ventral margin slightly concave with apices rounded, not protracted. Length 24.5–52.0 µm, breadth 13 µm (only 1 valve measured for breadth). Raphe distinctly biarcuate, extended from ca. $\frac{1}{2}$ way between dorsal and ventral margins at apices, arched towards ventral margin, then strongly arched towards dorsal margin, extending to > $\frac{1}{2}$



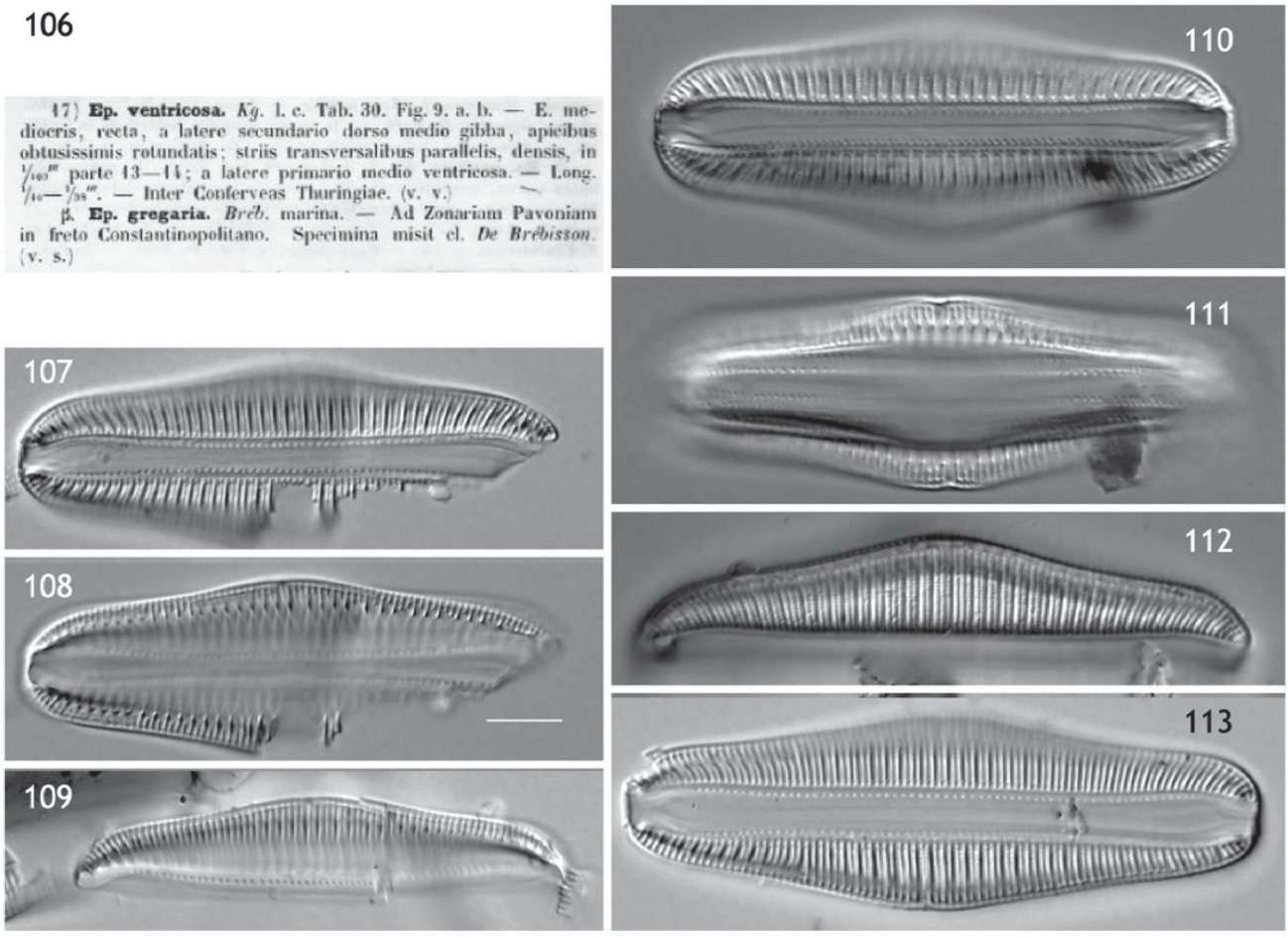
Figs 96–105. *Epithemia vertagus*. 96–105. Reproduction of the original drawing of *Epithemia vertagus* from Kützing (1844, pl. 30, fig. 2), valve (left), girdle (right). Figs 97–103. LM images all at same scale indicted by scale bar = 10 μm (Fig. 102) from BM 17820. Figs 97–102 valve views, Fig. 103, girdle view. Fig. 104. Reproduction of the original drawing of '*Eunotia adnata* (Kützing) Rabenhorst' from Rabenhorst (1853, pl. I, fig. 24), *Epithemia adnata* is listed as a synonym of *Epithemia vertagus* in Rabenhorst (1847, p. 19), the figure (Rabenhorst 1853, pl. I, fig. 24) probably derived from Kützing's *Epithemia vertagus* (Kützing 1844, pl. 30, fig. 2, see 96–105). Fig. 105. Herbarium packet Kützing 17.

way towards dorsal margin. Raphe branches distinct. Canal raphe evident, with small portulae. Capitate costae present, robust. Costate fibulae coarse, 2 / 10 µm. Striae composed of rectangular areolae, ca. 13 in 10 µm, with 5–9 present between two adjacent fibulae. Septum present at poles.

COMMENTS: Kobayasi & Kobayashi (1988) documented this species with LM and SEM from specimens in an unnamed lake in Finland. This species was not treated in Krammer and Lange-Bertalot's flora (1988) of Central Europe. The species resembles *E. frickei* Krammer (in Lange-Bertalot & Krammer 1987, p. 71) and *E. goeppertiana* Hilse (1860, p. 79, type specimens: BM 001222582, BM 001222584 = Rabenhorst 1021) in terms of shape and not having the apices being protracted. It differs from *E. goeppertiana* in the density of the striae (being coarser in *E. reticulata*) and from both *E. frickei* and *E. goeppertiana* in having the external proximal raphe ends extending more the notation of 1/2 the way towards the dorsal margin.

Discussion

This report represents the first published light micrographs of type specimens from Kützing for taxa assigned to the genera *Epithemia* and *Rhopalodia*. Given the availability

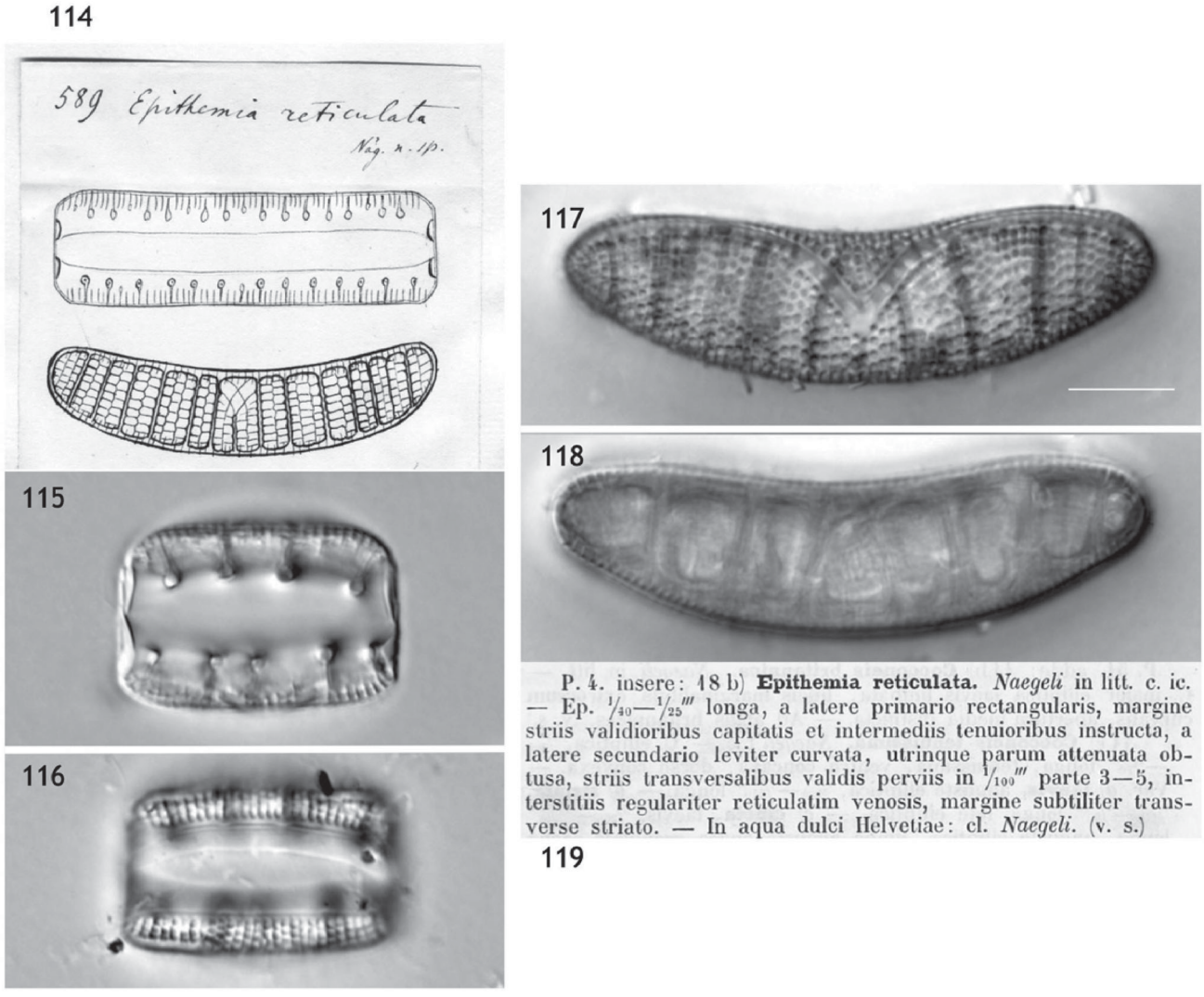


Figs 106–113. *Epithemia ventricosa β. gregaria*. Fig. 102. Original description from Kützing (1849, p. 4). Figs 103–109. LM images all at same scale indicted by scale bar = 10 μm (Fig. 108) from BM 17815.

of Kützing's exsiccatae (Sayre 1969), it is surprising that the most detailed treatment of these materials was done by Patrick & Reimer (1975) who illustrated them with only line drawings of individual specimens. We have tried here to illustrate every specimen on the type slides that could be obtained with light microscopy, hopefully documenting the range of variability as indicated in the population of a taxon on the holotype, lectotype or isotype slide.

Some taxa described by Kützing have been consistently treated in the literature since the time of their first description. An example is *Epithemia sorex*: Historical and recent literature, whether they be floristic or revisionary in nature, all seem to have consistently shown this species to possess a highly arched dorsal margin, with slightly capitate apices, and a canal raphe that nearly reaches the dorsal margin. We can see this consistent application of the concept of *E. sorex* in specimens treated from Australia (John 2018, 2020), Africa (Gasse 1980, Ehrlich 1995), Europe and Asia (e.g., Foged 1982, Kulikovskiy et al. 2016), North America (Patrick & Reimer 1975) and South America (Sala 1996; Guerrero & Gorriti 2001). There are some inconsistencies, however. For example, although no one has illustrated specimens over 60 µm in length, Hustedt (1930, then mimicked by Patrick & Reimer 1975, Krammer & Lange-Bertalot 1988, Lange-Bertalot et al. 2017) all include lengths up to 65 or 70 µm (see also Kociolek et al. Accepted). Also, *E. sorex* has been misidentified as *E. smithii* Carruthers, (e.g., Foged 1980) and *E. amphicephala* (Østrup) Kobayasi & Kobayshi (Foged 1981) and as an unknown taxon in Bateman & Rushforth (1984).

While there has been consistency in interpretations of taxa like *E. sorex*, there have been some taxa that have had conflicting interpretations. For example, '*Epithemia' ventricosa* and its relationship to *Rhopalodia gibba* have included recognition of *E. ventricosa* as a separate species (Kützing 1844), as a variety of *R. gibba* (Van Heurck 1896; Patrick & Reimer 1975) and as a synonym of *R. gibba* (Krammer & Lange-Bertalot 1988). In the case of *Epithemia proboscidea*, it has been treated as a separate species (as Kützing 1844 did) or a variety (of *E. adnata* or *E. zebra*, Grunow 1862, Van Heurck 1896). Likewise, *E.*



Figs 114–119. *Epithemia reticulata*. 114–119. Illustration of *E. reticulata* from herbarium packet Kützing 589 in BM, showing girdle view (top) and valve view (bottom). Figs 115–118, LM images all at same scale indicted by scale bar = 10 μm (Fig. 117) from BM 17821. Figs 115, 116. Girdle views of same specimen at different levels of focus. Fig. 115 shows 'capitate costae'. Fig. 116 shows striae on valve exterior, valve view of same specimen showing valve exterior and internal septum, respectively. Figs 117, 118. Valve views of same specimen. Fig. 117 shows valve exterior. Fig. 118 shows internal septum. Fig. 119. Reproduction of the original description for *E. reticulata* from Kützing (1849, p. 889).

vertagus, has been treated as a separate species (similar to Kützing's original treatment), as a variety (of *E. turgida*; Grunow 1862; Van Heurck 1896) or as a synonym of *E. turgida* (Krammer & Lange-Bertalot 1988). Many of these (re)considerations were made without the benefit of seeing the original Kützing material or based solely on drawings that interpret the taxa.

Our observations on the type specimens suggest that some of them may be synonyms of one another, or contain more than one species. For example, based on the size range found in the type material of *Epithemia picta* leads to the suggestion that it is the same as *E. proboscidea* (but this is only based on a single specimen in the type material) as well as *E. porcellus* (for which there were several specimens). If so, the correct name is *E. picta*. The suggestion by Lagerstedt (1884) that *E. adnata* is the correct name for *E. zebra* has been widely adopted, but the concept of *E. adnata*, as indicated by the type material here, is quite different from those of Patrick & Reimer (1975) and Krammer & Lange-Bertalot (1988). If these interpretations are supported by the review of other populations and material, or congruence between morphological and molecular data, this could have significant implications for the taxonomy and nomenclature of the group (there are 6 different described subspecific taxa of *E. adnata* and over 50 for *E. zebra*; Catalogue of Diatom Names 2011).

Identification of synonymies, as well as the need to tease out several taxa from a single name, can have implications for other information resources in addition to nomenclature. For example, when revisionary studies are done, there may be important implications for our understanding of biogeography, at least as summarized by tools such as AlgaeBase (Guiry & Guiry 2024). For example, it will require teasing out which of the records are assignable to which name and concept (e.g., *E. adnata* versus *E. porcellus*). This also includes misidentifications of any type, such as Foged's listing of *E. sorex* as records of *E. smithii* (Foged 1980) and *E. amphicephala* (Foged 1981).

Some of the taxa recognized as distinct species by Kützing were subsequently treated as varieties of another species. For example, Patrick (in Patrick & Reimer 1975) looked at the type specimens of Kützing and treated *E. saxonica* and *E. porcellus* as varieties of *E. adnata*. Van Heurck (1896, plate IX) recognized a total of 16 taxa in *Epithemia* and its sister taxon *Rhopalodia*, and only 7 of them were of the nominate variety. The use of the categories 'variety' and 'form' are almost without any context or justification, and the situation that Van Heurck described in 1896 may be just the same as the situation today. Van Heurck wrote, (1896, p. 99), '. . . it is almost impossible-in our present state of knowledge at least-to fix, with any certainty what forms should be as . . . species . . . [versus] varieties, etc.'

Notes

1. 'We proposed this name in a work on Diatoms [. . . 1838b] for beings having parasitic frustules, with a convex back and flat below and taking the shape of the body that supports them. The g. [genus] *Eunotia* by M. Ehrenberg, containing approximately the same species, should be preferred' (Brébisson 1845, p. 369, and 'The g. [genus] *Epithema*, which we proposed a few years ago, is synonymous with this one').
2. VanLandingham's citation is incorrect – Ross (1950) has no reference to a combination for *Epithemia adnata* on the given page.
3. Within *Eunotia* (designated as 'XI. *Eunotia*') Rabenhorst separated out taxa that had been put into *Epithemia* in this way: 'XI. *Epithemia* De. Bréb. (T.I under *Eunotia*!') and then abbreviates the genus and uses the authority of the name as if it was within *Epithemia* (e.g., '*E. ventricosa* Ktz.'). Thus, it is ambiguous if Rabenhorst is assigning these taxa to *Eunotia* (and thus making new combinations) or not (see also Table 2).

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