The diatom genus Ctenophora : a discussion on its morphology, relationships, and some species

The diatom genus *Ctenophora*: A discussion on its morphology, relationships, and some species

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Abstract

The diatom genus *Ctenophora* is examined for its morphological characters and its relationships. Some aspects of the nomenclature of the genus are clarified with respect to various specimens identified as *Ctenophora pulchella*, *Ctenophora saxonica* and *Ctenophora vertebrata*. The focus is on the structure of the valves and girdle rather than a complete account of the species-level diversity in *Ctenophora*. General conclusions are (1) *Ctenophora* is not a monotypic genus; (2) the relationships of *Ctenophora* will include '*Fragilaria*' *famelica*, *Catacombas* (= *Synedra*) and the various groups within the paraphyletic *Tabularia.*

Key-words: *Ctenophora*, morphology, relationships

Introduction

The diatom genus *Ctenophora* (Grunow) D.M.Williams & Round (1986: 330) was considered to be monotypic (e.g. Round *et al.* 1990, Spaulding & Edlund 2008) with *Ctenophora pulchella* (Kütz.) D.M.Williams & Round (1986: 330, figs 53–61) its only species. A number of other species had been transferred to *Ctenophora* at one time or another (see below) but none remain, nor were the names used very frequently. One new species, *Ctenophora sinensis* Lui & D.M.Williams (in Lui *et al.* 2020: 119, 'China, Lake Quinhai'), found in China, has been formally described.

Williams & Round (1986: 385) adopted the name for the genus from Grunow (1862) who used it as a 'Gruppe' in his subdivision of *Synedra* Ehrenberg (1830: 60).

Ctenophora is primarily (i.e. traditionally) distinguished by the valves' relatively unique central area, a robust structure, a buttressed system of coalesced 'striae' (sensu Bixby *et al.* 2005, see below) usually occupying the entire width of the valve face and mantle (Lui & Williams 2020) rather than just an area lacking any structure (such as found, for instance, in *Fragilaria rinoi* S.F.P.Almeida & Delg. in Delgado *et al*. 2016: 5). Other taxa have a similar structure to this kind of central area; similar in the sense that the central area is enclosed with buttressed 'ribs' (e.g. *Hannaea*, Bixby *et al.,* 2005, Liu *et al.* 2020). The relevance of the structure to higher level classification remains to be established but will be briefly discussed below.

Ctenophora pulchella, the generitype, is based on *Synedra pulchella* Kütz.(1844: 68, pl. 29, fig. 87 [based on Ralfs' proposed '*Exilaria pulchella* (ex. specim.)' in the description notes]; Kützing 1849: 46) but many of its nomenclatural details have been overlooked. In this contribution we clarify some of the nomenclatural peculiarities with respect to various specimens identified as *Ctenophora pulchella* and describe a few of the other purported species previously named as such – others await formal description.

Abbreviations, terminology and material

Abbreviations: LM = light microscope, SEM = scanning electron microscope; for parts of the valve and girdle: the individual bands are abbreviated as valvocopula (VC), copula (C), and the parts of the bands as pars interior (*pi*) and pars exterior (*pe*); herbarium acronyms follow *Index Herbariorum* (http://sweetgum.nybg.org/science/ih/). Authors are abbreviated according to the *International Plant Name Index* (IPNI, https://www.ipni.org/).

Terminology: For the most part, the three standard terminology papers have been followed (Anonymous 1975, the updated version of Ross *et al.* 1979, and the recent Russian/English language version of Gogorev *et al.*, 2018) with supplemental terms adopted from Cox & Ross (1981) and Mann (1981). Further additions to valve structure are presented in Bixby *et al.* (2005: 234, detailed in their fig. 11) for the valve 'central area', and von Stosch (1975), Ross *et al.* (1979), Williams (1985) and Gogorev *et al.* (2018) for details on the cingulum. The term *cingulum* is understood here as the set of bands associated with a single valve (see Ross *et al.* 1979: 525, "Cingulum: portion of girdle associated with a single valve"); a slightly different version, but essentially meaning the same, is given in Gogorev *et al.* (2018: 290): "part of the cincture [= Latin for 'girdle'], the series of siliceous bands (copulae) associated with a valve". Ross *et al.* state that the "Girdle: part of the frustule between epivalve and hypovalve, composed of epicingulum + hypocingulum", Ross *et al.* 1979: 524, outlines a distinction between an epi- and hypocingulum according to which valve in the complete frustule is examined). In general, for an interpretation of valve structure the older term 'striae' = virgae + vimines (cf., Cox & Ross 1981) + closing plate (cf., Mann 1981); virgae integrate (sometimes seamlessly) with the sternum; as noted above, the 'central area' can be understood as a buttressed system of coalesced 'striae' (Bixby *et al.* 2005), rather than a simple clear or hyaline space, which may or may not have 'ghost striae'. Sims & Ross used the word 'buttress' "[…] for the structure at the base of the external tube of the labiate

processes in the species with which we deal [species in the genus *Trinacria* Heiberg]. These are flanges of silica attached to the tube of the labiate process which face upwards […] In some species they are extended over the valve face and unite to form external costae" (Sims & Ross 1988: 278). Their use is entirely different to that of Bixby *et al.* (2005), but they cannot be confused. Most of the terms used here are expanded on in the Discussion.

Additional sources for valve and girdle terminology can be found in the glossaries for the *Diatoms of North America* (see Spaulding *et al.* 2022) and the *Diatom Flora of Britain and Ireland* (Jüttner *et al.* 2022). Suffice to say, these sources do not always have the same, or even similar, definitions.

Material: All material examined is appended to each species description; each species protologue includes all relevant material, whether examined or not. Specimens examined in this study are appended with an exclamation mark (!, representing the term *vidi*, 'I have seen it', http://www.mobot.org/mobot/latindict/keyDetail.aspx?keyWord=exclamation). The purpose of listing unexamined material is to draw it to others' attention for future collection-based research.

Online digital resources are indicated with their hyperlinks. For example, BM material is documented via the NHM data portal (https://data.nhm.ac.uk/), which provides a link to individual species records as well as species-group records, and material in L is available at the Naturalis Bioportal (https://bioportal.naturalis.nl/).

Taxonomic treatment

***Ctenophora* (Grunow) D.M.Williams & Round 1986**

***Ctenophora pulchella* (Kütz.) D.M.Williams & Round (Figs 1–31)**

Basionym: *Synedra pulchella* Kütz. 1844: 68, pl. 29, fig. 87 (see Figs 1, 2)

Synonyms: *Exilaria pulchella* Ralfs ex Kütz. 1844: 68, *nom. nud.*
Ctenophora pulchella Bréb. ex Kütz. 1849: *nom. nud.*
Ctenophora pulchella (Kütz.) H.Schönf. 1907: 104, 248
Fragilaria pulchella (Kütz.) Lange-Bertalot 1980: 749

Registration: http://phycobank.org/104119 (type)

Valves lanceolate, gently tapering towards sub-capitate poles; length ca. 48–59µm, width ca. 2–4µm (Figs 4–11). Sternum very narrow, but linear, regular, slightly narrowing towards poles (Figs 17–19). Sternum meets at roughly square to broadly circular-oblong shaped 'central area', buttressed either side of valve (Figs 4–11, 19, 27, 30, arrow); buttressing composed of modified virgae enclosing clear hyaline area (= 'central area'), 'ghost striae' barely visible (Figs 4–11, 19, 27, 30). Sternum meeting and coalescing with virgae, both ca. same size, vimines reduced in size relative to virgae (Figs 17–19, 25, 26), appearing as mesh-work with ca. 4–8 strutted closing plates. Striae (= virgae+vimines) 13–14 (?) in 10µm, areolae ca. 20 (?) in 10µm, regularly spaced, parallel (Figs 25, 26), extending onto mantle, in 2–4 'rows' (Figs 17–19, 29). Apical pore field as ocellulimbus (sunken pore field), composed of 6 x 8 rows/columns of pores, situated entirely on valve mantle (Figs 16, 24, 25). Marginal spines absent, but faint thickenings overhanging ocellulimbus (Figs 16, 25). Rimoportulae simple, composed of (internally) paired lips situated on or adjacent to virga, externally occurring between virgae, one at each pole (Figs 16, 18, 22–25). Irregularly spaced, uneven silica plaques situated on mantle edge (Figs 16, 27, dashed arrow, 29). Girdle composed of two (?) open bands, VC plus one C (Figs 14, 20, 21, 28, 29, 31); VC plain, *pi* with crenulated edge to fit virgae, central smooth area to fit 'central area' (Fig. 31); *pe* separated with ridge, ca. four times larger than pars interior (*pi*) (Figs 29, 31). Open portions of VC meet at pole, aligned horizontally (Figs 14, 20, 21, 28).

TYPE:—ENGLAND, Penzance, [John] Ralfs (**BM 18310! [Kützing 193], lectotype designated here, https://data.nhm.ac.uk/object/9545df61-a24c-4fa8-a796-e11279a9e9f4**; BM

18644! (Kützing 360 [March 1844]; BM s.n.! and BM Adams Eul. 38! = Eulenstein, *Diatomacearum species typicae* no. 38, "b) Penzance, Angl. *In aqua dulci*" […] b) Spec. originale. Ktz. Bac. tab. 29. fig. 87 = Fig. 12]; "*Exilaria pulchella* n. sp., on aquatic plants, Penzance, Feb., 1840, J. Ralfs", BM herb. Diat. 2536!; "Exilaria pulchella. *Kutz. Kies. Bacil. t.* 29. *f.* 87, Penzance" [*British Algae, dried specimens of marine and freshwater algae, including the Desmidieae and Diatomaceae*, volume 1, no. 34, 1850, see *Ann. Mag. Nat. Hist.* 2 (7), 412, 1850–1?, for date see *Ann. Mag. Nat. Hist.* 2 (7): 412, 1851 and Sayre 1969: 97[1], "*Exilaria pulchellum*"]; "Penzance, M^r. Ralfs", Diat. Herb. diat. 2534!, W. Smith, BM 23735–6!; L4020117!, Penzance, Herb. Lenormand https://data.biodiversitydata.nl/naturalis/specimen/L.4020117, FH: J. W. Bailey coll. E337 (http://www2.huh.harvard.edu/diatom/baileycat.htm), and ANSP: Febiger 3049, *'Exilaria pulchella* Ralfs ex Kutzing' (I = isotype).

ADDITIONAL MATERIAL:—

ENGLAND, Ilfracombe, Ralfs (BM 18575! [Kützing 947])

WALES, Bangor, Aug. 1841, J.R.[alfs], herb. Diat. 2536!

FRANCE, Falaise (BM 18308! [Kützing 1731]); BM 18309!, BM 18913!, Mortain, "*Ctenophora pulchella* Breb. *Synedra* Kg." (Kützing 1571 [Brébisson 407] [=*Ctenophora pulchella* Bréb. *in litt.*]; BM 2533! "*Ctenophora pulchella* Bréb. | *Exilaria* Ralfs. Mortain", J. W. Bailey Coll. E338 (http://www2.huh.harvard.edu/diatom/baileycat.htm).

The protologue for *Synedra pulchella* notes for the locality that only "Originalexemplare wurden mir von dem Hrn. Berkeley mitgeteilt [Original specimens were given to me by Mr. Berkeley]" (Kützing 1844: 68) and adds the name "*Exilaria pulchella* Ralfs! (ex specimen)". Further details were provided in Kützing (1849: 46): "*Ad Conferveas in aqua dulci Angliae et Galliae. — Specimina communicaverunt cl. Ralfs et De Brebisson. (v. s.)*".

In BM, four slides are listed as having specimens of *Synedra pulchella* (there are no species catalogued under the name *Ctenophora*) in Kützing's collection: BM 18308–18311 (there are a number of other Ralfs' slides in BM other than in Kützing's collection). BM 18310 ('Kützing 193') is described in the unpublished notebook to the collection as '*Exil. pulchella* Ralfs Penzance (Ralfs hand)'. There are no notes for BM 18308**,** 18309 or 18311 ('Kützing 1340', 'Kützing 1571' or 'Kützing 1731', respectively) but all three were acquired from de Brébisson: two from Falaise, the third from Vire, both localities in Normandy, France (summarised in Table 1).

[Table 1 here]

In addition, the notebooks list Kützing's collection numbers 943–954 as being from 'Berkeley', presumably meaning Miles Joseph Berkeley (1803–1889), the donator of the 'Originalexemplare' noted in the protologue for *Synedra pulchella*. There are no specific comments in the notebook for 'Kützing 948' (BM 17938, the slide label indicates the presence of *Diatoma vitreum* Kütz.) or 'Kützing 949' (BM 19285, the slide label indicates the presence of *Striatella unipunctata* (Lyngb.) C.Agardh). For 'Kützing 946' (of which there is no prepared BM slide), '*Gomphonema dichotomum*, Penzance, J. Ralfs' is recorded and for Kützing 947 (BM 18575) '*Encyonema prostratum*, Berkeley Kg. ms (?) Ilfracombe Ralfs' is recorded. The latter series of specimens and names is included here to demonstrate that collection numbers 'Kützing 943–954' were actually from Berkeley. 'Kützing 948' and 'Kützing 949' are marine samples, neither having any specimens of *Synedra pulchella*; 'Kützing 946' and 'Kützing 947' are freshwater samples, but neither of those have any

[1] *The History of the Collections contained in the Natural history departments of the British museum* [...], cited by Sayre (1969), notes "c. 1850" (p. 175).

specimens of *Synedra pulchella* either (summarised in Table 2). Further material from Penzance in the BM is summarised in Table 3.

[Tables 2 & 3 here]

With respect to the two names '*Exilaria pulchella*' and '*Ctenophora pulchella*', the following are relevant to their status:

'*Exilaria pulchella* Ralfs', *invalid* (herbarium name): As noted above, several slides in BM (and elsewhere) can probably be considered part of Ralfs' original material. These are all from Penzance, Cornwall, with Ralfs acknowledged as collector; some were acquired from Joseph Berkeley, others from de Brébisson. A packet of material in BM has the following on its herbarium label: "*Exilaria pulchella* n. sp., on aquatic plants, Penzance, Feb., 1840, J. Ralfs". There is also material from Ralfs' *British Algae, dried specimens of marine and freshwater algae, including the Desmidieae and Diatomaceae* (Ralfs 1850) for "*Exilaria pulchella*" (no. 34; see Sayre 1969: 97).

The name "*Exilaria pulchella* (Ralfs)" appears in Pritchard (1852: 482), but in spite of numerous references to '*Exilaria pulchella* Ralfs ex Kützing' in much of the subsequent literature, most citations of this name are to the unpublished basionym for *Ctenophora pulchella*. As far as can be established, the name *Exilaria pulchella* has never been validly published by Ralfs or anyone else.

'*Ctenophora pulchella* Brébisson' *invalid* (herbarium name): Kützing referred to '*Ctenophora pulchella* Brébisson *in litt.*', based on specimens received from de Brébisson (Kützing 1849: 46, as does Smith 1853: 70). As noted above, in BM there are several possible sources for these specimens. The most likely 'type' (original, or more appropriately, 'intended type') specimens are those from Mortain, Normandy, France, labelled as "*Ctenophora pulchella* Breb." ('Kützing 1571') (BM 18309, BM 18913, raw material in a packet on herbarium sheet 'diat. 2533', 'Mortain') [= '*Ctenophora pulchella* Brébisson *in litt.*'].

There is also material from Vire ('Kützing 1340') (BM 18311), labelled "*Exilaria licmoidea* Breb., *Exilaria pulchella* Ralfs ? ! 160" (herb. Diat. 2542!), which is most likely the 'intended type' specimens of *Exilaria licmoidea* Bréb.

'*Exilaria licmoidea*' Brébisson 1838: 41, *invalid* (no description, no illustration): *Exilaria licmoidea* first appeared in print as just a name and locality ("EXILARIA LICMOÏDEA Nob. Vire" Brébisson 1838: 41, see Fig. 3). It was noted again, just with its name, in Brébisson (1839: 275) and Kützing (1844: 69) but has never been validly published. Material exists in BM (FRANCE: Vire, "160 *Synedra* | *Exilaria licmoidea* Breb., *Exilaria pulchella* Ralfs ? !", 'Kützing 1340', BM 18311, see https://data.nhm.ac.uk/object/e2293b3c-8eee-423d-8815-ef57b85e2f12), which are specimens intended as types for *Exilaria licmoidea*. Inspection of this material yielded three different species, including what would be referred to as *Ctenophora pulchella*. Without a description or illustration, there is no rational way of deciding which of these three de Brébisson was referring to with his name *Exilaria licmoidea*.

***Ctenophora saxonica* (Kütz.) D.M.Williams & Van de Vijver, *comb. nov.* (Figs 32–51)**

Basionym: *Synedra saxonica* Kütz. 1844, *Die kieselschaligen Bacillarien oder Diatomeen*: 68, pl. 15, fig. XIV (see Figs 32–34)

Synonym: *Synedra pulchella* var. *saxonica* (Kütz.) Grunow in Van Heurck 1881, pl. 41, fig. 3 (see Figs 38, 39)

Ctenophora pulchella var. *saxonica* (Kütz.) H.Schönf. 1907: 104, 248, *invalid*

Registration: http://phycobank.org/104111 (name); http://phycobank.org/104119 (type)

TYPE: —GERMANY, "[…] in süssen und salzigen Gewässern an Conferven […]" (Kützing 1833: 561, 1834a: 33); "In lacu salso ad Confervam flavescentenem [*Cladophora flavescens*] prope Rollsdorf, fl. Halens" (Kützing 1834b [1833], Dec. VIII, no. 74),

see https://data.nhm.ac.uk/object/44e566fe-37b5-45b6-8e47-9da9a9e79d08; "An *C. flavescens* im Salzsee bei Rollsdorf" (in *Flora* 17(45): 716, 1834); "Im salzigen See [Salzsee] bei Eisleben an *Cladophora flavescens*! im Flensburger Meerbusen an *Ectocarpus*: Binder!" (Kützing 1844: 68), **BM 18344!, https://data.nhm.ac.uk/object/44e566fe-37b5-45b6-8e47-9da9a9e79d08, "Salzsee" ('Kützing 166', see Fig. 34, specimens Figs 35–7), "Salzee | Kützing", see https://data.nhm.ac.uk/object/24051470-3546-4bb4-b01d-c5262e934f85, lectotype designated here**.

Valves lanceolate, gradually tapering towards sub-capitate poles; length ca. 51–97µm, width ca. 4–6µm (Figs 35–38, 40, measurements based on type specimens only). Sternum narrow, but linear, regular, slightly narrowing towards poles (Figs 35–37, 40–43). Meeting square to broadly circular-oblong shaped 'central area', not buttressed, simply series of infilled virgae and vimines, not extending on mantle (Fig. 41, 46, arrows); 'ghost striae' present, faint (Fig. 41). Sternum meeting and integrated with virgae, both same size; vimines reduced in size relative to virgae (Figs 44, 46, 48), appearing as mesh-work with ca. 6–8 strutted closing plate, circular with smaller pores at centre (Figs 44, 46, 48). Striae (= virgae+vimines) 13–14 (?) in 10µm, areolae ca. 20 (?) in 10µm, regularly spaced, parallel, extending onto mantle, in ca. 4 'rows' (Figs 44, 46, 48). Apical pore field as ocellulimbus (sunken pore field), composed of 5 x 7 rows/columns of pores, situated entirely on valve mantle (Figs 44, 45, 48). Spines absent. Rimoportulae simple, composed of (internally) paired lips situated on or adjacent to virga, externally occur between virgae, one at each pole, externally centred (Figs 42–5, arrow in Fig. 44). Girdle composed of two (?) open bands, VC plus one C (Fig. 48); VC plain, *pi* with crenulated edge to fit virgae, central smooth area to fit 'central area'; *pe* separated with ridge, ca. four times larger than *pi* (Fig. 48, arrows). Open portions of VC meet at pole, aligned horizontally (Fig. 48).

In the protologue for *Synedra saxonica*, Kützing (1844: 68) refers to specimens he had previously named *Exilaria fasciculata* (Kützing 1833: 561, taf. 15, fig. 40, Kützing 1834a: 33, taf. III, fig. 40; Kützing 1834b [1833]: Dec. VIII, no. 74, see Figs 49–51). In this earlier account, Kützing attributed the name *Exilaria fasciculata* to Greville and provided a list of synonyms (Kützing 1833: 561, and Kützing 1834a: 32; in Kützing 1834b [1833]: no. 74, he cites just the two Greville publications; all of these synonyms are summarised in Table 4). In addition, he offered an additional sub-taxon (without no specified rank) with the name "β *Frustulis longioribus*" itself with two synonyms (Table 4). Inspection of all the specimens related to these names is beyond the scope of this paper but potential synonym to one side, the name *Synedra saxonica* can be interpreted as the given valid name for *Exilaria fasciculata* sensu Kützing (1834b [1833]: Dec. VIII, no. 74). The locality details given for *Synedra saxonica* in Kützing (1844) and *Exilaria fasciculata* sensu Kützing are (almost) identical and one might conclude they are based on the same material.

[Table 4 here]

Kützing wrote "Diese Art ist sehr häufig verbreitet, in süssen und salzigen Gewässern an Conferven, auch fand ich sie an *Melosira varians* und *orichalcea* und sogar an den Frustulen der *Exilaria crystallina* in der Soole bei Artern, aus der Ostsee erhielt ich sie von Herrn Lieutenant v. Suhr und Herrn Pastor Frölich" (Kützing 1833: 561, Kützing 1834a: 33). The reference to Lieutenant v. Suhr (Johannes Nicolaus von Suhr, 1792–1847) implies that Kützing may have been referring to the specimens later named *'Exilaria notata'* Suhr (in Kützing 1849: 47, *nom. nud.*). This name ('designation') was invalidly published as it was placed directly into synonymy with *Synedra fasciculata* (C.Agardh) Kütz. by Kützing (1849: 47, "Exilaria notata *Suhr* Herb."; In Prep.; Baltic Sea ['mer Baltique'], BM 18319, 'Kützing

1166'). The name '*Exilaria notata*' occurs only rarely in synonymy lists and is most likely derived from the entry in de Toni (1892: 662, e.g. Hustedt 1931: 218). It is unlikely anyone has studied Kützing's "Exilaria notata *Suhr*": the specimens are actually of a species of *Tabularia* (Kütz.) D.M.Williams & Round see Williams pers. obs.).

No material has yet been identified as original specimens of '*Exilaria fasciculata* β *Frustulis longioribus*'.

Synedra pulchella var. *saxonica* (Kütz.) Grunow (in Van Heurck 1881: pl. 41, fig. 3) is based on material from "Salzsee" ('Kützing 166').

***Ctenophora vertebra* (W.Greg.) D.M.Williams & Van de Vijver, *comb. nov.* (Figs 52–6)**

Basionym: *Synedra vertebra* (*vertebrata*) W.Greg. 1855 *Quarterly Journal of Microscopical Science* 3: 41, pl. IV, fig. 22 (= our Fig. 52)

Synonym: *Synedra pulchella* var. *vertebra* (W.Greg.) Van Heurck 1896: 309 (see Smith, 1856: 104, "Synedra Vertebra, Greg. Mic. Journ. vol. 3. pi. iv. 22 = *S. pulchella*, Synop. xi. 84?")

TYPE:—SCOTLAND, lacustrine sands, Glenshira, near Inverary (BM 24988!, isotype?, https://data.nhm.ac.uk/object/57f0e08a-1cdb-4262-99e6-a64d88c254ec)

Registration: http://phycobank.org/104112

Valves lanceolate, tapering towards capitate poles; length ca. 44–104µm, width 2–4µm (Figs 53–6). Sternum very narrow, regular, meeting distinctive ovoid central area, buttressed either sides of valve (Figs 53–6). 'Ghost striae' present. Sternum meeting virgae, sternum larger than virgae, vimines reduced in size relative to virgae (Figs 53–6). No data on apical pore fields, rimoportulae or girdle.

Only preserved LM specimens of Gregory's *Synedra vertebra* have been available for examination and these are limited to one slide from Dickie's collection in BM (BM 24988). There are no doubt other specimens. Gregory's own collection is poorly catalogued in BM and hence difficult currently to use, but it is well-known that the Glenshira material was widely circulated.

Gregory noted of *Synedra vertebra* that "This form, which is very frequent in the deposit, belongs to the same division as *S. pulchella* and *S. acicularis*" (Gregory 1855: 41); Grunow (1862: 385) included it in his '2 Gruppe *Ctenophora*'; Van Heurck gave a very brief description including it as a variety of *Synedra pulchella* (Van Heurck 1896: 309).

***Ctenophora pulchella* var. *smithii* (Ralfs in A.Pritch.) H.Schönf. 1907: 104, 248, *invalid* = ??**

Basionym: *Synedra smithii* Ralfs in A.Pritch. 1861: 786 non *S. smithii* O'Meara 1875: 313, pl. 28, fig. 42

A brief description, attributed to Ralfs, was given in Pritchard, which included vague locality details and the opinion that it is *Synedra acicularis* W. Sm. (1853: 70, pl. 11, fig. 86, see Figure 57): 'Frustules irregularly affixed; valves lanceolate, acute, with 36 very faint striae in ·001." = *Synedra acicularis*, SBD. i. p. 70, pl. 11. f. 86. Brackish water. England' (Pritchard 1861: 786). Smith's *Synedra acicularis* (non *Synedra acicularis* Kütz. 1844: 63, which is a species of *Nitzschia* Hassall) is very likely another species of *Ctenophora* as has been previously recognised by O'Meara (1876: 304, as *Synedra pulchella* var. *acicularis*) and West & West 1901: 196, also as *Synedra pulchella* var. *acicularis*) (Van de Vijver pers. obs). A few slides in BM may be of original Ralfs' material.

Excluded or (as yet) unknown

Excluded

Ctenophora pulchella* var. *longissima* (W. Sm.) H.Schönf. 1907: 104, 248, *invalid* = *Ulnaria longissima (W.Sm.) Van de Vijver & D.M.Williams 2022: 2.

Ulnaria longissima (W.Sm.) Van de Vijver & D.M.Williams 2022: 2
Basionym: *Synedra longissima* W.Sm. 1853: 72, pl. 12, fig. 95
Synonyms: *Synedra ulna* var. *longissima* (W.Sm.) Grunow 1862: 395
Syndera ulna var. *longissima* (W.Sm.) Brun 1880: 126
Synedra pulchella var. *longissima* (W.Sm.) H.Schönf. 1907: 104
Ctenophora pulchella var. *longissima* (W.Sm.) H.Schönf. 1907: 104, 248
Type:—England, "Pond in Botanic Garden, Belfast, 1850, *Dr. Dickie*" **BR** VI-46-B11, lectotype; BM 23758–60, BM 25314, BM 51036, isolectotypes.

***Ctenophora pulchella* var. *socialis* (Rabenh.) H.Schönf. 1907: 104, 248, *invalid* = ??**
Basionym: *Synedra socialis* Rabenh.1853: 56, pl. 4, fig. 22, see Figure 58
A brief description was given by Rabenhorst, with one figure and the vague locality details of 'Italien, auf *Cladophora* glomerata in Gräben' (Rabenhorst 1853: 56). Later, Rabenhorst revised *Synedra pulchella* and included two varieties, *socialis* and *fasciculata* (Rabenhorst 1864: 131) and Schönfeldt included it in *Ctenophora*. Nevertheless, from the figure in Rabenhorst it looks unlike a species of *Ctenophora*, as it lacks any central area demarcation. Original material requires investigation.

Ctenophora pulchella* var. *subaequalis* (Grunow in Van Heurck) H.Schönf. 1907: 104, 248, *invalid* = *Ulnaria subaequalis* (Grunow in Van Heurck) D.M.Williams & Van de Vijver *stat. nov.
Basionym: *Synedra subaequalis* Grunow in Van Heurck 1881: pl. 38, fig. 13
Synonyms: *Synedra ulna* var. *subaequalis* (Grunow) Van Heurck 1885: 151
Ulnaria ulna var. *subaequalis* (Grunow in Van Heurck) Aboal in Aboal, Alv,-Cobelas, Cambra & Ector 2003: 114
Registration: http://phycobank.org/104113

***Ctenophora vaucheriae* (Kütz.) H.Schönf. 1907: 105, 249, *invalid* = *Fragilaria vaucheriae* (Kütz.) J.B.Petersen 1938: 167, fig. 1 a–g**
Basionym: *Exilaria vaucheriae* Kütz.1833: 560, taf. XV, fig. 38, Kützing 1834a: 32, taf. 3, fig. 38; 1834b [1833], [3]: no. 24)
Synonyms: *Ceratoneis vaucheriae* (Kütz.) H.Kobayasi 1965: 126
In their study, Tuji & Williams used specimens to illustrate *Fragilaria vaucheriae* from three sources: (1) Kützing's packet 185 from AWH (now BR see Wetzel & Ector, 2015: 273; Tuji & Williams 2013: figs 1–7); (2) from *Algarum Aquae Dulcis Germanicarum* (*Alg. Aqu. Dulc.*): Dec. III. No. 24, located in C (Tuji & Williams 2013: figs 8–16); and from (3) BM 78023 (made from the BM copy of *Alg. Aqu. Dulc.* Dec. III no. 24; there are two slides, BM 78023–4, see Delgado *et al.* 2016). The locality of *Fragilaria vaucheriae* is: "Sie camm an *Vaucheria clavata* in einer Quelle bei Weissenfels […] [*im Quellen bei Leisling*[2]]".
***Ctenophora vaucheriae* var. *parvula* (Kütz.) H.Schönf.1907: 105, 249, *invalid* = *Fragilaria* ??**
Basionym: *Frustulia parvula* Kütz.1833: 551, taf. XIII, fig. 20, Kützing 1834a: 23, pl. 1, fig. 20
Inspection of Kützing's illustrations and specimens (BM 18394) suggest that this is not a species of *Ctenophora*, but quite probably, of a species in *Fragilaria*,

[2] See Wetzel and Ector for an explanation of this locality and others.

***Ctenophora pulchella* var. *fasciculata* (C.Agardh) H.Schönf. 1907: 104, 248, *invalid* =**
Tabularia fasciculata (C.Agardh) D.M.Williams & Round 1986: 326, figs 46–52
Basionym: *Diatoma fasciculata* C.Agardh 1812: 35.

Unknown
Synedra pulchella* var. *flexella* C.S.Boyer 1916: 49, pl. 12, fig. 2, not *Ctenophora
***Synedra pulchella* var. *genuina* f. *apicibus curvatis* A.Cleve 1932: 37, fig. 44b**
***Synedra pulchella* var. *capitata* Pant. 1912: 31, pl. 2, fig. 111**
***Synedra pulchella* var. *kitaibelii* Istv. 1891: 4**

Discussion

Our primary focus is on the structure of the valves and girdle in species of *Ctenophora* rather than a complete account of its species-level diversity, the latter to be documented in detail elsewhere. Here we comment on the structures found and the relationships implied for the genus *Ctenophora*. A more complete (and formal) analysis will appear elsewhere which will include documentation for the various groups within *Tabularia* – it is difficult, almost impossible, to deal with the relationships of *Ctenophora* without considering those in *Tabularia*.

Structure

Valve: As noted above, structurally the 'striae' of the valves are formed from a series of integrated virgae and vimines (as defined by Cox & Ross 1981) with a closing plate (as defined in Mann 1981) of finer siliceous structures linking (or uniting) both virgae and vimines. The virgae extend from, or meet, the sternum (= 'axial area', see below); the central area of the valves can be variously understood (see separate discussion below).

For the 'axial area', Ross *et al.* (1979) defined it as "a hyaline field along the apical axis" noting that the "use of 'pseudoraphe' for this structure in araphid diatoms is discouraged" (Ross *et al.* 1979: 518; 'pseudoraphe' is a much older term than 'axial area' and has now largely disappeared from use). Since then, 'axial area' is often, though not always, thought of as equivalent to the sternum (cf., Mann 1978). Gogorev *et al.* (2018: 288) defined the 'axial area' as Ross *et al.* (1979) did, "a hyaline field along the apical axis", but included the sternum as a separate entry: "a longitudinal element of the valve of pennate diatoms, usually thickened and hyaline" (Gogorev *et al.* 2018: 301). They offer some speculations on the origin and evolution of the sternum with respect to the raphe, which are largely irrelevant.

In the species of *Ctenophora* studied herein, the regularity of and integration of, virgae, vimines and sternum is relatively uniform with both virgae and sternum being roughly equal in size (their width) relative to one another, the vimines being (relatively) much smaller. Distinguishing aspect for individual species is the structure of the closing plate, usually composed of an external 'sheet' of silica attached to, or spanning across, both vimines and virgae by a series of struts that attach in an irregular fashion. These features occur beyond the genus *Ctenophora* (e.g. in species of *Tabularia*, see Kuriyama *et al.* 2010) so provide no diagnostic or defining value for this genus alone.

'The central area': In the revised and more detailed diatom valve terminology paper, the central area of pennate valves was defined simply as "an expanded or otherwise distinct portion of the axial area [= sternum] midway along its length" (Ross *et al.* 1979: 518). This definition was discussed further only in the context of raphid diatoms, with two structures,

the *fascia* and the *stauros*, being briefly outlined[3]. According to Cox (2012), Cleve had earlier defined the *stauros* as "a dilatation of the central nodule" and a *fascia* as "a transverse extension of the central area" (Cleve 1894, after Cox 2012: 18). Although some have understood *fascia* and *stauros* to be the same structure, they have since been considered distinct from a 'developmental-morphogenetic' point of view (for further details see Cox 2001, 2012). In contrast, Gogorev *et al.* (2018: 289) defined the valve 'central area' simply as "more or less well pronounced central hyaline part of valve in centric diatoms". Thus, little attention has been paid to the various kinds of 'central area' found in 'araphid' diatoms.

More recent descriptions of the central area in freshwater 'araphid' diatoms have used varying descriptive terms. For example, in *Fragilaria capucina* Desm., Tuji & Williams (2006: 196) simply added a descriptive phrase to the term 'central area', yielding 'unilateral central area', and for other specimens, 'rectangular to rhombic central area', the latter kind extending across the face of the valve. *Fragilaria rinoi*, which has a very simple, plain central area with the spaces (areolae) between the virgae and vimines filled in with 'ghost striae' (see below), also used the phrase 'unilateral central area' (but only in their Abstract, not in the formal description of the species, Delgado *et al.* 2016: 1). Overall, with the exception of variation in shape, one kind of central area in *Fragilaria* is captured by the combination of two descriptors: 'unilateral central area' and 'ghost striae' (see summary in Almeida *et al.* 2016: 178, table 4, and Wetzel & Ector 2015: 286, table 1), and another kind of central area has been described that is 'inflated on both sides', 'bilaterally gibbous' (e.g. *Fragilaria fusa* (R.M.Patrick) Wengrat, C.E.Wetzel et E.Morales and *Fragilaria billingsii* Wengrat, C.E.Wetzel et E.Morales, in Wengrat *et al.* 2016: 198) or 'unilaterally or bilaterally gibbous' (as in *Fragilaria rumpens* (Kütz.) G.W.F.Carlson, in Wengrat *et al.* 2016: 198). All of these descriptors refer almost exclusively to the shape and orientation (on just one side or both) rather than the structural components (see examples in our Figs 59, 60, 64).

A departure from these kinds of descriptions was made for species of *Hannaea* R.Patrick. The central area (the "unornamented tumid area" of Liu *et al.* 2019: 42; the "unilateral inflation" of Bixby *et al.* 2005: 225, 231, and other descriptions elsewhere) can also be of the two kinds noted above (just to note: it is unlikely that the genus *Hannaea*, in its present form, is monophyletic). Bixby *et al.* (2005), in their study of the genus *Hannaea*, took a structural approach and offered some useful additional terms that help describe more accurately the actual structure of the central area rather than just its shape and orientation. In valves of *Hannaea superiorensis* Bixby & Edlund (in Bixby *et al.* 2005: 231), internal views shows that the 'central area' is actually a central swollen portion of the valve with that area demarcated by *buttressing* (the "buttressed central inflation" of Bixby *et al.* 2005: 234 –5, fig. 11). In *Hannaea superiorensis*, the "buttressed central inflation" extends to the sternum. The buttresses are effectively a pair of heavily silicified virgae situated on either side of the demarcated central area enclosing a series of "ghost striae", the latter being a more heavily silicified set of virgae and vimines but each being visible (Bixby *et al.* 2005: 234, fig. 11, see our Figs 62, 63 for an example from *Hannaea baicalensis* Genkal, Popovskaya et Kulikovsky 2008: 322). Most species of *Hannaea* have this kind of central area construction, but not all – see *Hannaea tibetiana* Q.Liu *et al.*, for an example, which has a simple plain area demarcated by the virgae and vimines being more silicified in this area (Liu *et al.* 2019: 46, fig. 3; their figure 3B is of the 'plain' internal view). The buttressing is less obvious in species such as *Hannaea arcus* (Ehrenb.) R.M.Patrick and *H. inaequidentata* (Lagerst.) Genkal & Kharitonov. This has been shown as due to the developmental sequence of silicification

[3] The online *Diatom flora of Britain and Northern Ireland* defines the central area solely with reference to the structure that occurs in raphid diatoms: "Area at centre of valve, between the central raphe endings and the central striae" (Barber & Haworth 1981 is referenced).

(outlined in detail in Liu & Williams 2020). For comparison, a completely different kind of central area is found in *Tabulariopsis australis* (Perag.) D.M.Williams (1988: 249, a monotypic genus, but probably belonging to a sub-group of *Tabularia*, with this central area an autapomorphy, see Fig. 61).

The 'central area' in species of *Ctenophora* is usually of the buttressed type (the "buttressed central inflation") but with the buttressing occurring on both sides of the demarcated area, unlike species in *Hannaea*, which have a 'central area' on just one side of the valve but very heavily buttressed (Fig. 63). Thus, it seems acceptable to consider the *Ctenophora* central area a (putative) synapomorphy of the genus.

'Ghost striae': The term 'ghost striae' appears to have first been used by Hohn & Hellerman (1963) in their description of the species *Synedra netronoides* M.H.Hohn & Hellerman (1963: 328, "The central area of this species often shows 'ghost-striae' rather than well-defined structures"). The term has remained in common use with respect to a range of freshwater 'araphid' diatoms (e.g. Round *et al.* 1990: 366 for *Hannaea*, p. 367 for *Ctenophora*; Kociolek *et al.* 2015: 682 for *Ctenophora*, p. 683 for *Hannaea* and *Ulnaria*). It is not clear to what genus *Synedra netronoides* would be placed today, nor quite what was being referring to as 'ghost-striae' as only one line-drawing was included (Hohn & Hellerman 1963: pl. I, fig. 20). Hendey also used the term 'ghost' in relation to valve striae, 'markings', puncta and costae, in the descriptions of a few raphid pennate diatoms (Hendey 1964: 205, 214, 'ghost striae', p. 182, 'ghost markings', pp, 214, 223, 'ghost puncta', p. 276, 'ghost costae'), as did others later (e.g. Reimer 1970: 245, Kreis & Stoermer 1979: 286). For *Synedra*, Cunningham & Whitson (1978) used 'ghost striae' in the description of the central area in *Synedra cyclopum* var. *incisa* Cunningham & Whitson (1978: 526) and Schwarzwalder & Postek, when describing the central area of *Synedra goulardii*, wrote "Normarski differential interference contrast optics resolve these faint striations which have been previously termed 'ghost striae'" (Schwarzwalder & Postek 1981: 412). Using SEM images they were able to provide a more nuanced description: "These 'ghost striae' are due to internal costae [virgae] which are visible along the entire length of the valve but are less distinct in the central area. An examination of the interior of the valve […] reveals that the costae [virgae] in the central area are partially occluded with silica thus accounting for their faint appearance in that region" (Schwarzwalder & Postek 1981: 414). 'Ghost striae' have since been defined as "striae filled in with silica during valve morphogenesis, but, nevertheless, distinguishable in mature valve[s]" (Gogorev *et al.* 2018: 292). Close inspection of the valves in various species of *Ctenophora* do appear to have what might be called 'Ghost striae' (e.g. Fig. 41) but elsewhere there are only vague signs of this (e.g. Fig. 30; similar situations occur in many species of the genus *Ulnaria*). Of course, this might be due to the stage at which the valve is inspected and whether the silicification process does indeed fill in all the gaps when the virgae and vimines form (e.g. in *Hannaea* see Liu & Williams 2020). It remains to be seen if this is a defining character for any taxon within *Ctenophora*, or its relevance to higher level classification.

Pore-fields: Ross *et al.* is not that useful, noting that "apical and marginal fields" are "areas set off from the pattern of the rest of the valve" (Ross *et al.* 1979: 520). They discuss three types, all, more or less, features of 'centric' diatoms: "Pseudocellus […] areolae decreasing in size from those on the main part of the valve; the "Ocellus […] [a] plate of silica, normally with a thickened structureless rim […]" and the "Pseudonodulus […](Ross *et al.* 1979: 521). While it would be possible to apply the terms pseudocellus and ocellus to 'araphid' diatoms, neither are exact and the term *ocellulimbus* was proposed to cover some apical pore fields seen only in some 'araphid' diatoms: "[…] *Ocellulimbus* (from ocellus meaning pores, and

limbus meaning mantle) to differentiate it from the ocellus of the Eupodiscaeae (Ross & Sims 1973), the ocellulus of the Cymatosiraceae (Hasle *et al.* 1983) and the alternative pore field in other araphid (some of these are illustrated in Williams 1985) and raphid genera (e.g. Kociolek & Rosen 1984)" (Williams 1986: 146). Gogorev *et al.* reproduce the definitions from Ross *et al.* but add "We consider necessary to include in this group also *apical pore field* of pennate diatoms including *ocellulimbus* and *multiscissura* (Gogorev *et al.* 2018: 288) and write of the *ocellulimbus* that it is a "type of apical pore field characteristic for some araphid diatoms representing pore plate of densely packed porelli in linear rows lying in depression on the external surface of valve mantle. It is completely [sic] differentiated from the valvar structure (Gogorev *et al.* 2018: 296). While there is potentially room for re-defining the 'pore field' structures further in 'araphid' diatoms, species of *Ctenophora* share the ocellulimbus with a few other genera (see relationships section below).

Girdle: Ross *et al.* defined the girdle as "consisting of epicingulum and hypocingulum" (Ross *et al.* 1979: 517 and 524: "[…] part of the frustule between epivalve and hypovalve […]", also in Gogorev *et al.* 2018: 292), the *cingulum* being the "portion of girdle associated with a single valve" and the *band* or segment as "a single element of the girdle" (Ross *et al.* 1979: 525, also von Stosch 1975: 20 and later Gogorev *et al.* 2018: 290). Von Stosch refined the terminology clarifying the names of various bands encountered in each cingulum, basing his terms on earlier, pioneering studies (e.g. Müller 1886, 1895). Of relevance here is the valvocopula, copulae, and pleurae. Von Stosch also provided names for the various parts of each band, of relevance here is the *pi*, *pe* and ligula ("a silica projection on the advalvar margin of copula directed towards the valve that cover gap caused by the split in the older band next to it", Gogorev *et al.* 2018: 295).

For the elements of the girdle the conventional terms are: valvocopula ("an element adjacent to the valve", Ross *et al.* (1979: 525); "First formed (advalvar) band of a cingulum (von Stosch 1975: 21), copulae ("element of cingulum proximal to valve, different in structure or form from distal elements" (Ross *et al.* 1979: 525, as in von Stosch 1975: 22), and pleurae ("element of cingulum distal to copula(e), or any element when no intercalary bands [= copulae] are present", Ross *et al.* 1979: 525). Gogorev *et al.* use the same terminology (Gogorev *et al.* 2018: 290), but offer an additional term: "Hyaline band […] element of girdle with no perforations" (Gogorev *et al.*, 2018: 293), with Hemidiscaceae as an example but this might apply elsewhere).

It is the two terms copulae and pleurae that require some discussion in the light of the simple girdle structure found (so far) in *Ctenophora*. While examination of the girdle in species of *Ctenophora* is limited, the conclusion reached at this time is the cingulum is composed of just 2–4 bands. *Ctenophora pulchella* appears to have only two bands. The first band, conventionally, is the VC, as it is the "element adjacent to the valve". The second band differs from the VC but as there is just one band no comparisons can be made to others in the complete cingulum. Thus, either copula or pleura could be used – copula, as it bears some similarity to the VC and is an "element of cingulum proximal to valve", but in this sense, one might equally suggest the term pleura. It seems prudent to opt for copula in this case. *Ctenophora saxonica* appears to have three bands, a VC and two more or less identical bands, copulae and *C. sinensis* has a maximum of four (Liu *et al.* 2020). Obviously, further observations on the girdle for other species in *Ctenophora* will yield data that either confirms or disconfirms the status of the 2–4 band arrangement with VC and C only.

Relationships

A first attempt to understand the relationships of *Ctenophora* concluded that it was simply a unique example of a *Tabularia* (it was not stated as such then, but that was clear from the results: see our Fig. 65a, the white box at the node uniting *Tabularia*[2], *Tabularia*[3] and

Ctenophora) – but *Tabularia* was clearly paraphyletic (*Tabularia*[1] + *Tabularia*[2] + *Tabularia*[3] together are not monophyletic) and *Ctenophora* was, at that time, monotypic. These conclusions would require further study (see figures in Williams & Round 1988: 311 –2; the figure on p. 312 is that summarised in our Fig. 65a and can be compared to Cao *et al.* 2018, where *Ctenophora* was not included in their analysis, but species in *Tabularia* were distributed in many different places on the cladogram, see Cao *et al.* 2018: 180, fig. 40). One obvious item missing from both Williams & Round (1988) and Cao *et al.* (2018) was consideration of '*Fragilaria*' *famelica*. Almost all studies utilising molecular data, so far, have found that *Ctenophora* is most closely related to '*Fragilaria*' *famelica* (= '*Fragilaria*' in Fig. 65b, c) than it is to any other taxon.

The general conclusions, from this paper, coupled with previous morphological and molecular analysis, are:

(1) *Ctenophora* is not a monotypic genus – there are (probably) numerous species that possess the complex, buttressed central area, a putative synapomorphy supporting the monophyly of the genus;

(2) *Ctenophora* and '*Fragilaria*' *famelica* are more closely related to each other than they are to any other taxon (Sabir *et al.* 2018, Ma Dolores Belando *et al.* 2018, Gómez *et al.* 2018);

(3) *Ctenophora* and '*Fragilaria*' *famelica* together are more closely related to *Tabularia* plus *Catacombas* (= *Synedra*, see Williams 2011: Fig. 65b, c) than to any other taxon (Sabir *et al.* 2018 and Ma Dolores Belando *et al.* 2018), and many of the characters discussed above relate to this larger group;

(4) '*Fragilaria*' *famelica* is not a species of *Fragilaria* s.s. and probably belongs to an as yet to be described genus;

(5) *Tabularia* is non-monophyletic, differences of interpretation rest with how its non-monophyly can be better understood, i.e. how many groups are within the currently defined genus (Fig. 65c, modified from Ma Dolores Belando *et al.* 2018; see also Cao *et al.* 2018 and Williams & Round 1988), something noted in the first morphological descriptions (Williams & Round 1986) and the first analysis of those data (Williams & Round 1988, also Cao *et al.* 2018).

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Plate Legends

FIGURES 1–31: *Ctenophora pulchella*

FIGURES 1–12: *Ctenophora pulchella*

Fig. 1, reproduction of the original drawing of *Synedra pulchella* from Kützing (1844 : pl. 29, fig. 87); Fig. 2, reproduction of the original description of *Synedra pulchella* from Kützing (1844: 68); Fig. 3, reproduction of de Brébisson's note on '*Exilaria licmoidea*' from (Brébisson 1838 : 41); Figs 4–11, LM micrographs of type specimens of *Synedra pulchella* (Figs 4–7, BM 18310, Figs 8–10, BM 18309, Fig. 12, colony from BM Adams Eul. 38. Scale bars = 10µm.

FIGURES 13–16: *Ctenophora pulchella* (Ralfs, BM herb.)

SEM micrographs, Fig. 13, external view of whole valve; Fig. 14, external view of portion of valve, to the right a portion of the VC with undulating *pi* and plain 'space' for the attachment at 'central area'; Fig. 15, details of striae structure showing shape of areolae, virgae and portion of sternum; Fig. 16, external view of pole, with ocellulimbus and rimoportula. Scale bars = 1µm (Figs 15, 16), = 2µm (Fig. 14), = 10µm (Fig. 13).

FIGURES 17–21: *Ctenophora pulchella* (Ralfs, BM herb.)

SEM micrographs, Fig. 17, internal view of entire valve with VC at one side; Fig. 18, detail of pole, internal view showing rimoportula, virgae, vimines and sternum; Fig. 19, detail of central with enlarged (or modified) and (in this specimen) a vague appearance of 'ghost striae'; Fig. 20, entire VC; Fig. 21, detail of 2nd (?) band (copula) with 'areola'–like ornamentation along its length. Scale bars = 2µm (Figs 18, 19, 21), 10µm (Figs 17, 20).

FIGURES 22–26: *Ctenophora pulchella*

SEM micrographs, Fig. 22, external view of whole valve; Fig. 23, internal view of whole valve; Fig. 24, detail of pole, internal view showing, virgae, vimines and sternum; Fig. 25, details of pole, external view of ocellulimbus, rimoportula and areolae; Fig. 26, detail of striae, external view of virgae, vimines, sternum and closing plates. Scale bars = 1µm (Figs 24–26), 10µm (Figs 22, 23).

FIGURES 27–31: *Ctenophora pulchella* ("*Exilaria licmoidea* Breb., *Exilaria pulchella* Ralfs ~~?~~ ! 160", herb. Diat. 2542!)

SEM micrographs, Fig. 27 and 30, detail of central area showing buttressed central area (arrows); one plaque in the series indicated with dashed arrow. Fig. 28, details of pole with VC *in situ*, arrow indicated where arms meet; Fig. 29, detail of VC, white arrows indicating area of attachment to valve, irregular plaques indicated by dashed arrow; Fig. 31, detail of VC with attachment points to valve, undulating to fit virgae, plain to fit central area (arrows). Scale bars = 1µm (Fig. 28), = 2µm (Figs 27, 29, 30, 31).

FIGURES: 32–52: *Ctenophora saxonica*

FIGURES: 32–39: Fig. 32, reproduction of the original drawing of *Synedra saxonica* (from Kützing 1844: pl. 15, fig. XIV); Fig. 33, reproduction of the original description of *Synedra saxonica* (from Kützing 1844: 68); Fig. 34, packet for 'Kützing 166' ("Salzsee"); Figs 35–37, LM for specimens from BM 18344; Figs 38, 39, reproduction of figure for *Synedra pulchella* var. *saxonica* (Kütz.) Grunow in Van

Heurck 1881: pl. 41, fig. 3 , Fig. 38 the original, Fig. 39, from Van Heurck's annotated archived copy). Scale bars = 10μm.

FIGURE 40–44: SEM micrographs, *Ctenophora saxonica*, Fig. 41, internal view of whole valve; Fig. 41, detail of buttressed central area; Figs 42, 43, detail of poles, for rimoportula, virgae and vimines; Fig. 44, external detail of pole with narrow sternum, areolae ornamentation, rimoportula (arrow) and ocellulimbus. Scale bars = 2μm (Figs 41, 42, 44), = 1μm (Fig. 43), = 10μm (Fig. 40).

FIGURE 45–48: SEM micrographs, *Ctenophora saxonica*, Fig. 45, internal view of pole, with rimoportula, ocellulimbus, and striae; Fig. 46, detail of central area from valve and girdle view (arrows); Fig. 47, whole valve in girdle view; Fig. 48, details of VC and copula at pole, plain arrows indicating open bands and dashed arrows their ornamentation. Scale bars = 1μm (Fig. 45), = 2μm (Figs 46, 48), = 10μm (Fig. 47).

FIGURES 49–51: Fig. 49, *Exilaria fasciculata* sensu Kütz. (1834b [1833]: Dec. VIII, no. 74) in BR; Fig. 50, reproduction of description for *E. fasciculata* sensu Kützing (1833: 561); Fig. 51, reproduction of drawing for *E. fasciculata* Kütz. (1834a: taf. 15, fig. 40). Scale bar = 10μm

FIGURES 52–56: *Ctenophora vertebra*

Fig. 52, reproduction of drawing for *Synedra vertebra* Gregory (1855: pl. 4, fig. 22); Figs 53–56, LM micrographs of *C. vertebra*, BM 24988, 'lacustrine sands, Glenshira, near Inverary, Scotland'. Scale bar = 10μm; Fig. 57, reproduction of *Synedra acicularis* W. Sm. (1853: 70, pl. 11, fig. 86; Fig. 58, reproduction of *Synedra socialis* Rabenh. (1853: 56, pl. 4, fig. 22).

FIGURES 59–64: SEM micrographs

Figs 59, 60, *Fragilaria* sp., external and internal view of plain central area; Fig. 61, *Tabulariopsis australis* (M. Perag.) D.M.Williams (1988: 249), detail of central area; Figs 62, 63, *Hannaea baicalensis* Genkal *et al.* (2008: 322), detail of central area, Fig. 62, external view, Fig. 63, internal view, with robust buttressed area; Fig. 64, *Fragilaria* sp. (Lake Baikal), whole valve, external view of plain central area. Scale = 1μm (Figs 59, 60), Scale = 2μm (Fig. 63), Scale = 3μm (Fig. 61), Scale = 5μm (Fig. 62, 64).

FIGURE 65A–C: Cladogram for the relationships of *Ctenophora*; Fig. 65a, modified from Williams & Round (1988); Fig. 65b, modified from Williams (2021), Fig. 65c, modified from Ma Dolores Belando *et al.* (2018); *Tabularia*[1], *Tabularia*[2], *Tabularia*[3], and *Tabularia*#1 are all 'parts' of the paraphyletic Tabularia *sensu* Williams & Round.

956 **TABLE 1:** The four slides in BM catalogued for *Synedra pulchella*
957

BM no.	Kützing no.	Locality	Collector	Taxon name
18308	1731	Falaise, France	Brébisson	*Synedra pulchella* [*pulcherimma*]
18309	1571	Mortain, France	Brébisson	*Synedra pulchella*
18310[4]*	193	[Penzance]	Ralfs	*Synedra pulchella*
18311	1340	Vire, France	Brébisson	*Synedra pulchella* [*Exilaria licmoidea*]

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[4] With an extra label on the reverse of the slide: "*Synedra pulchella* Kg. det. R. Patrick"

960 **TABLE 2:** Slides from Miles Joseph Berkeley in Kützing's collection
961

BM no.	Kützing no.	Locality	Collector	Taxon name
None	946	Penzance	Ralfs	*Gomphonema dichotomum*
18575	947	Ilfracombe	Ralfs	*Encyonema prostratum*
17938*	948	Penzance	Ralfs	*Diatoma vitreum*
19285*	949	Penzance	Ralfs	*Striatella unipunctata*

962

963 **TABLE 3:** Slides in Kützing's collection from Penzance
964

BM no.	Kützing no.	Locality	Collector	Taxon name [date from catalogue]
18644	360	Penzance	Ralfs	*Gomphonema dichotomum* [March 1844]
18670	377	Penzance	Ralfs	*Gomphonema minutum* [1842]
18953	479	Penzance		*Berkeleya fragilis* [March 1843]
19284	729	Penzance		*Striatella unipunctata* [Nov. 1842]
19301	744	Penzance		*Rhabdonema arcuatum*
17883	1347	Penzance		*Striatella*

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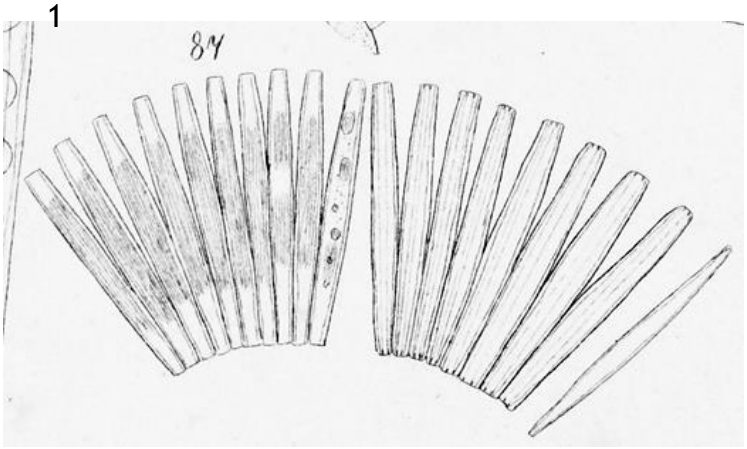
966

TABLE 4: Synonyms *Exilaria fasciculata* according to Kützing (1833, 1834a); in Kützing 1834b [1833] only the two Greville publications are noted (marked here with a *)

Exilaria fasciculata	Grev.	*Scottish cryptogamic flora*	5, pl. 298, fig. 3a	1827*
	Kütz.	*Algarum aquae dulcis Germanicarum*	[no.74] Dec.VIII	1834b [1833]
Echinella fasciculata	Jürg.	*Algae Aquatica…*	Dec. XI [p. 3, no. 8]	1822
	Grev.	*Scottish cryptogamic flora*	1, pl. 16, figs 1—3	1823*
	Hornem.	*Icones plantarum sponte nascentium in Regno Daniae* (*Fl. Dan.)*	Tab. 1957, fig. 3?	1810
Diatoma fasciculatum	C.Agardh	*Conspectus Criticus Diatomacearum*	p. 51	1832
		Exilaria fasciculata"β *Frustulis longioribus*"		
Frustulia parasitica	C.Agardh	*Syst. Alg.*	p. 2	1824
Diatoma parasiticum	C.Agardh	*Algarum aquae dulcis Germanicarum*	p. 50	1832

[Landscape table 4 on separate file]

1



2

56. SYNEDRA PULCHELLA. Taf. 29. Fig. 87. ($4\frac{1}{2}^{o}$). S. mediocris tabulis apice flabellatim disruptis; bacillis laevibus a latere primario utrinque sensim attenuatis, apice truncatis, a latere secundario anguste lanceolatis.

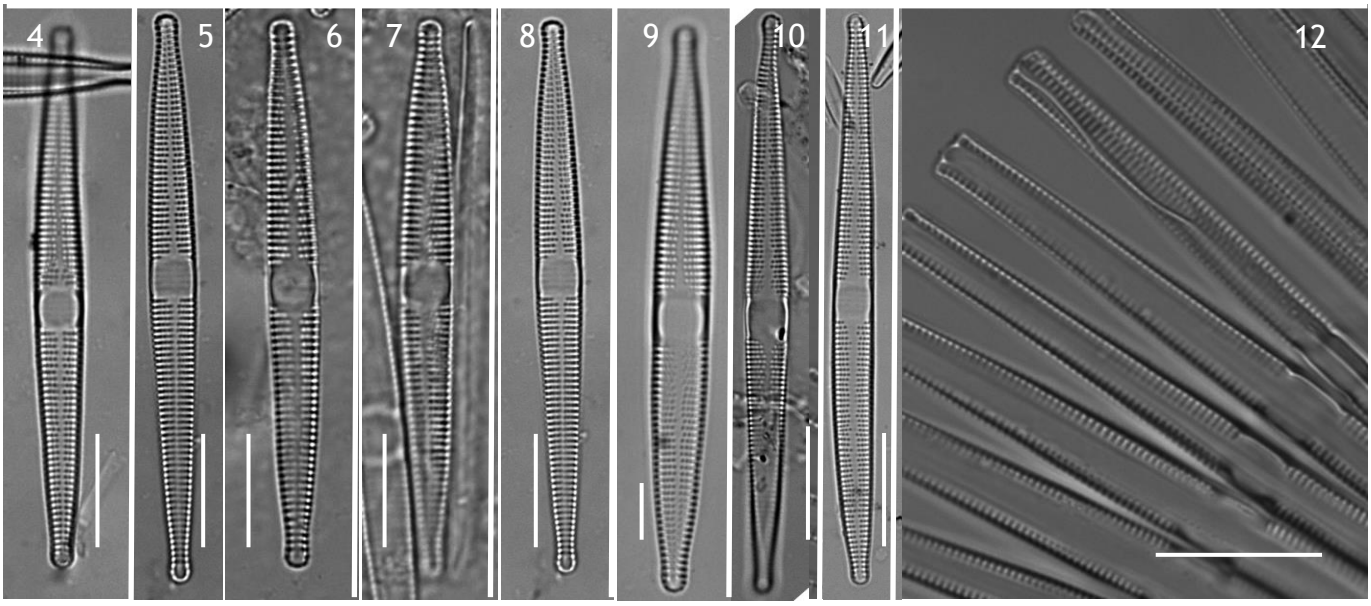
Exilaria pulchella *Ralfs*! (ex specim.).

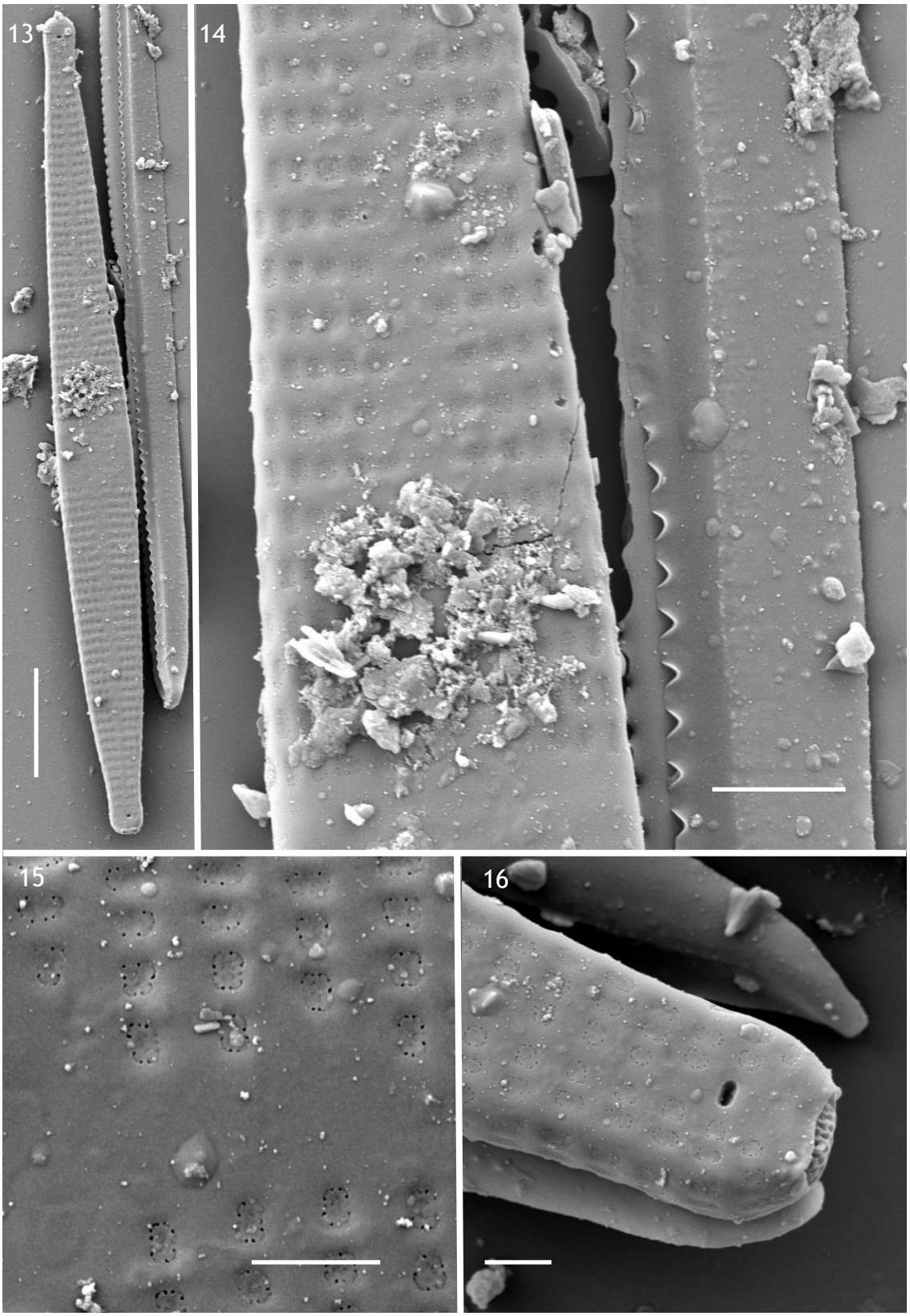
An Conferven in England. Originalexemplare wurden mir von dem Hrn. Berkeley mitgetheilt. — Länge $\frac{1}{15}'''$.

3

Var. *E. viridescens* Breb. No

3. E. LICMOÏDEA *Nob.* Vire.

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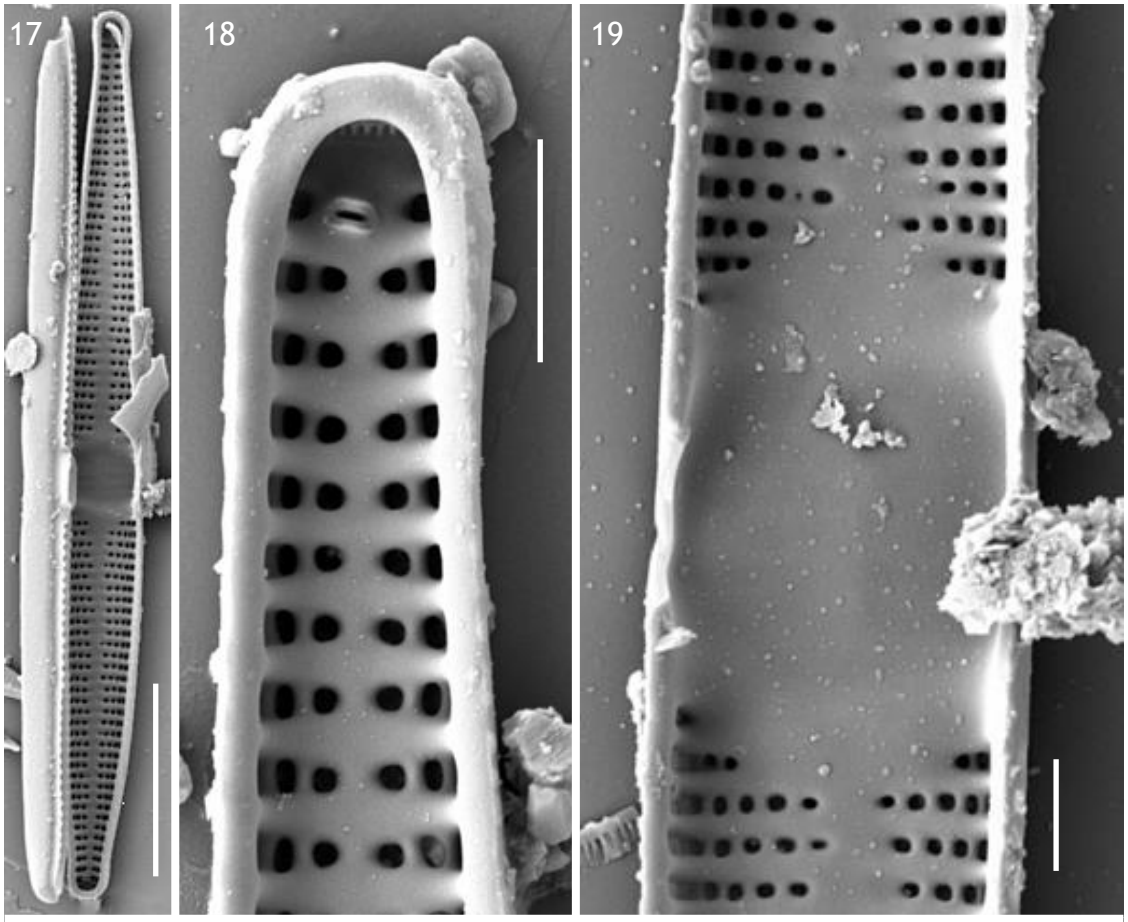
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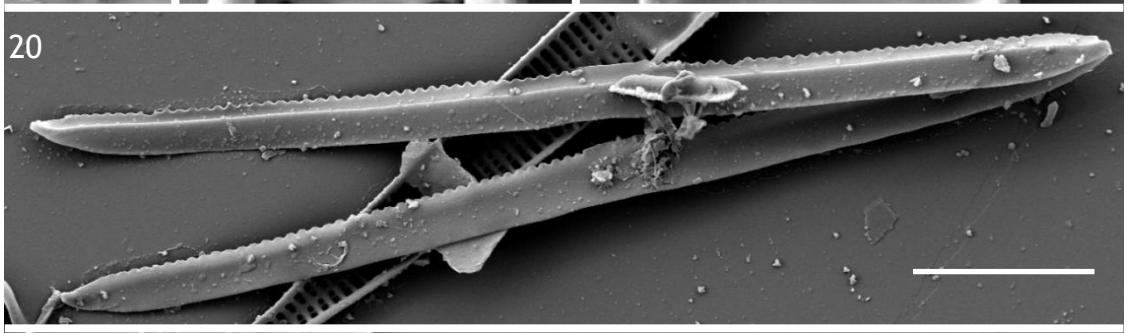
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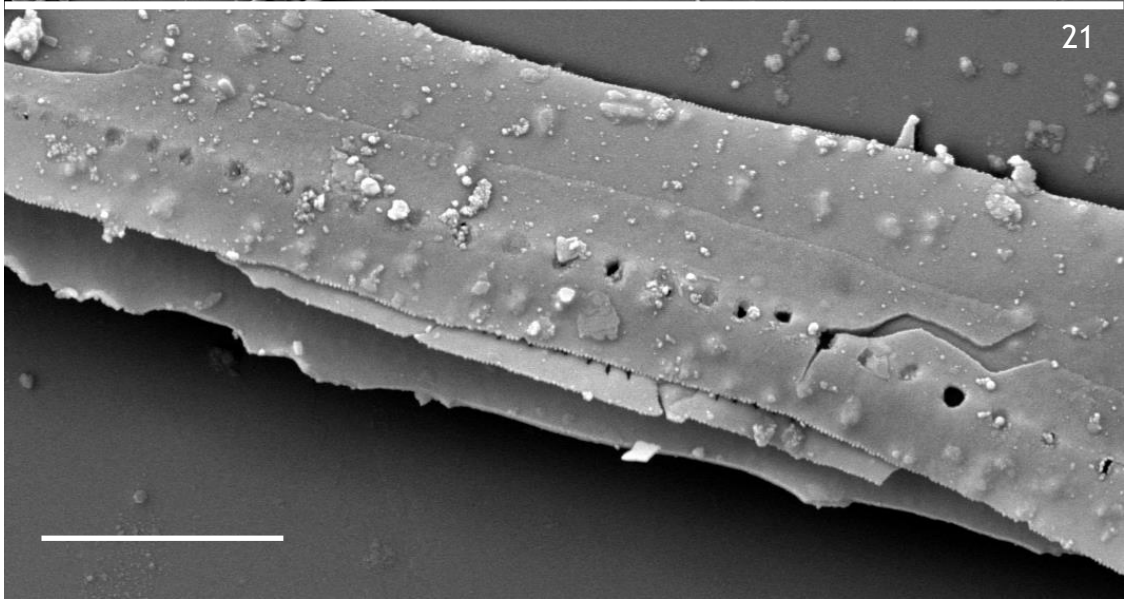
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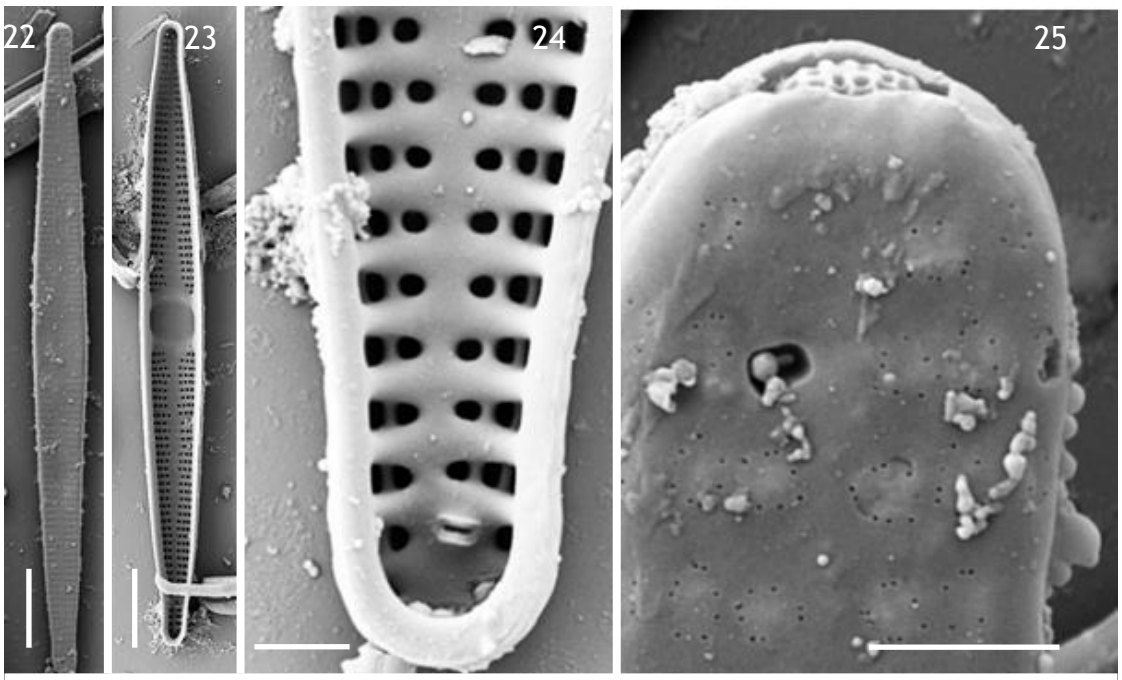
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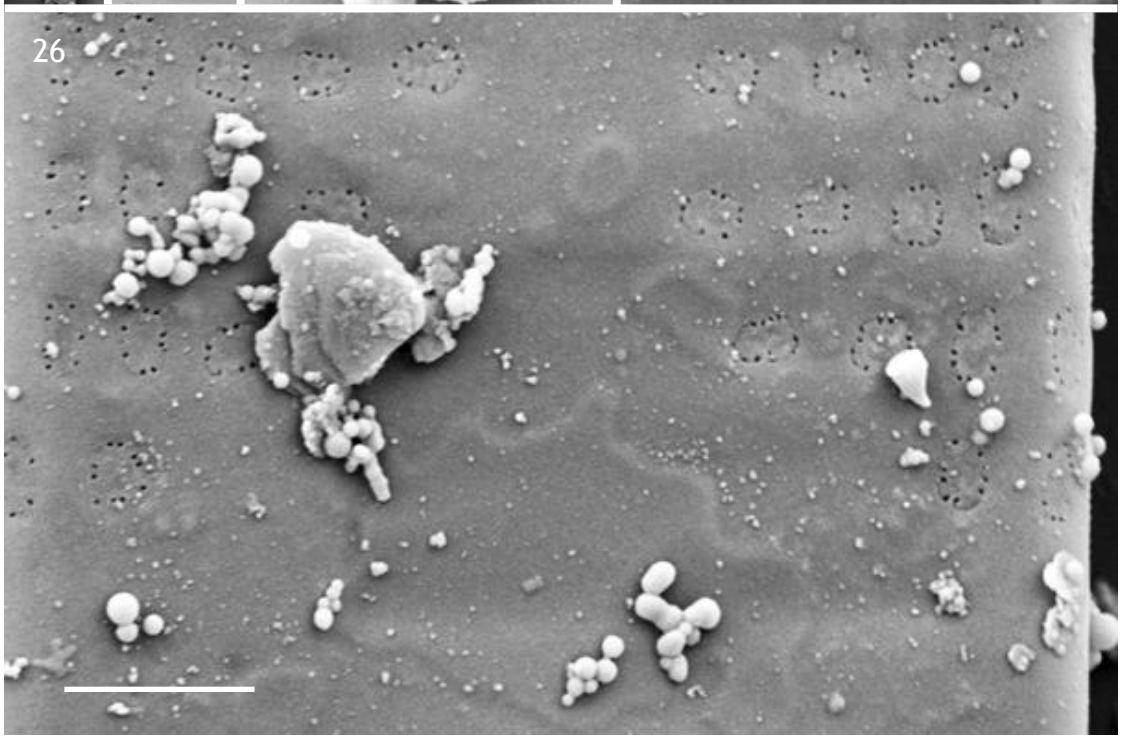
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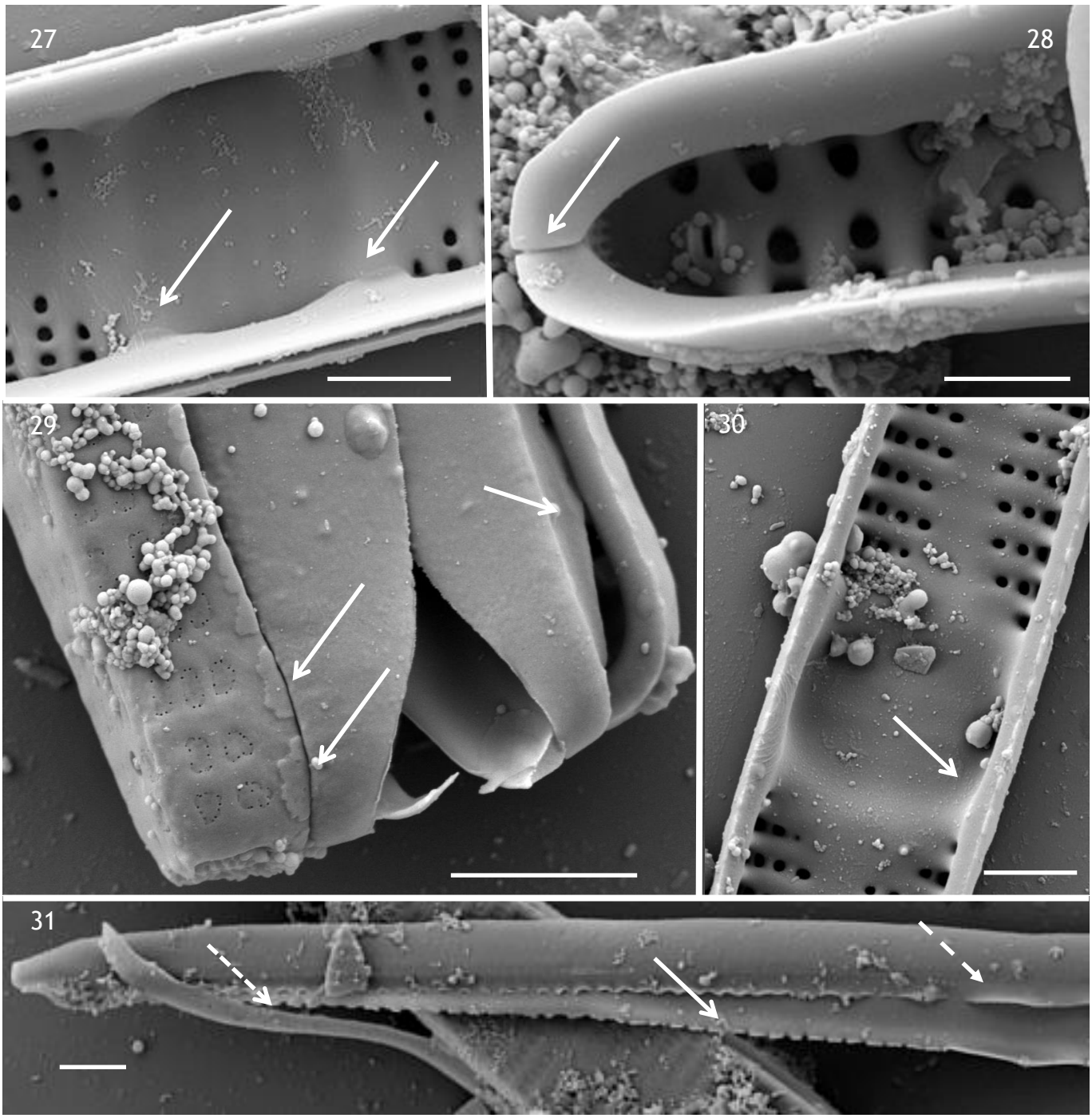
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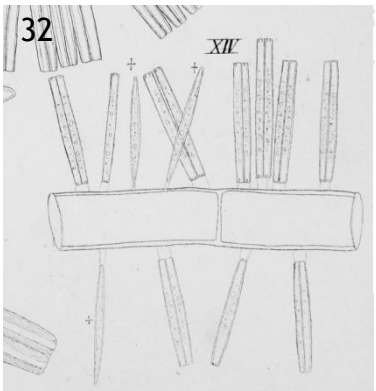


33

64. SYNEDRA SAXONICA. Taf. 15. Fig. XIV. ($\frac{4}{1}$°). S. mediocris, gracilis, linearis, a latere primario apice truncata, latere secundario anguste lanceolata; stipite parum elongato.

Exilaria fasciculata *Kg.* Dec. No. 74.

Im salzigen See bei Eisleben an Cladophora flavescens! im Flensburger Meerbusen an Ectocarpus: Binder! — Länge $\frac{1}{11}$.'''

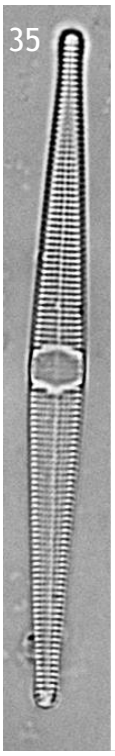
166 Synedra saxonica Taf 15 fig XIV an Conf. flavescens Salzsee d. auch 354

4

34

10µm

35



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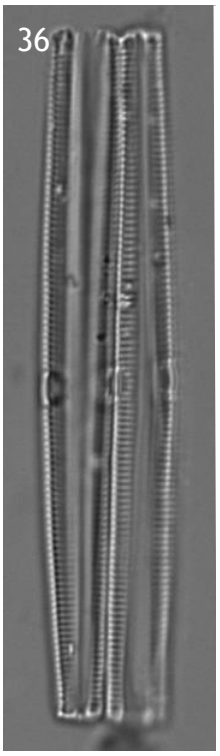

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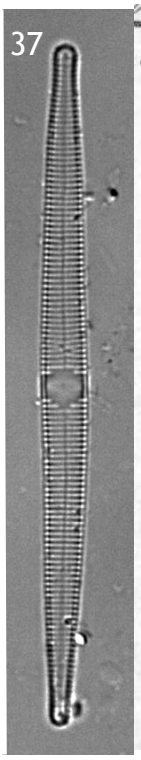
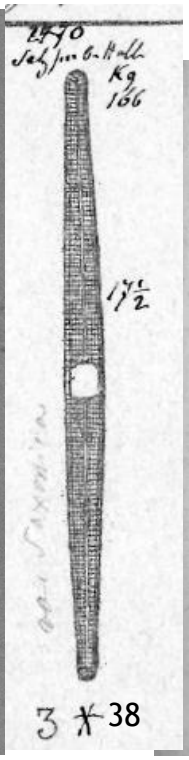
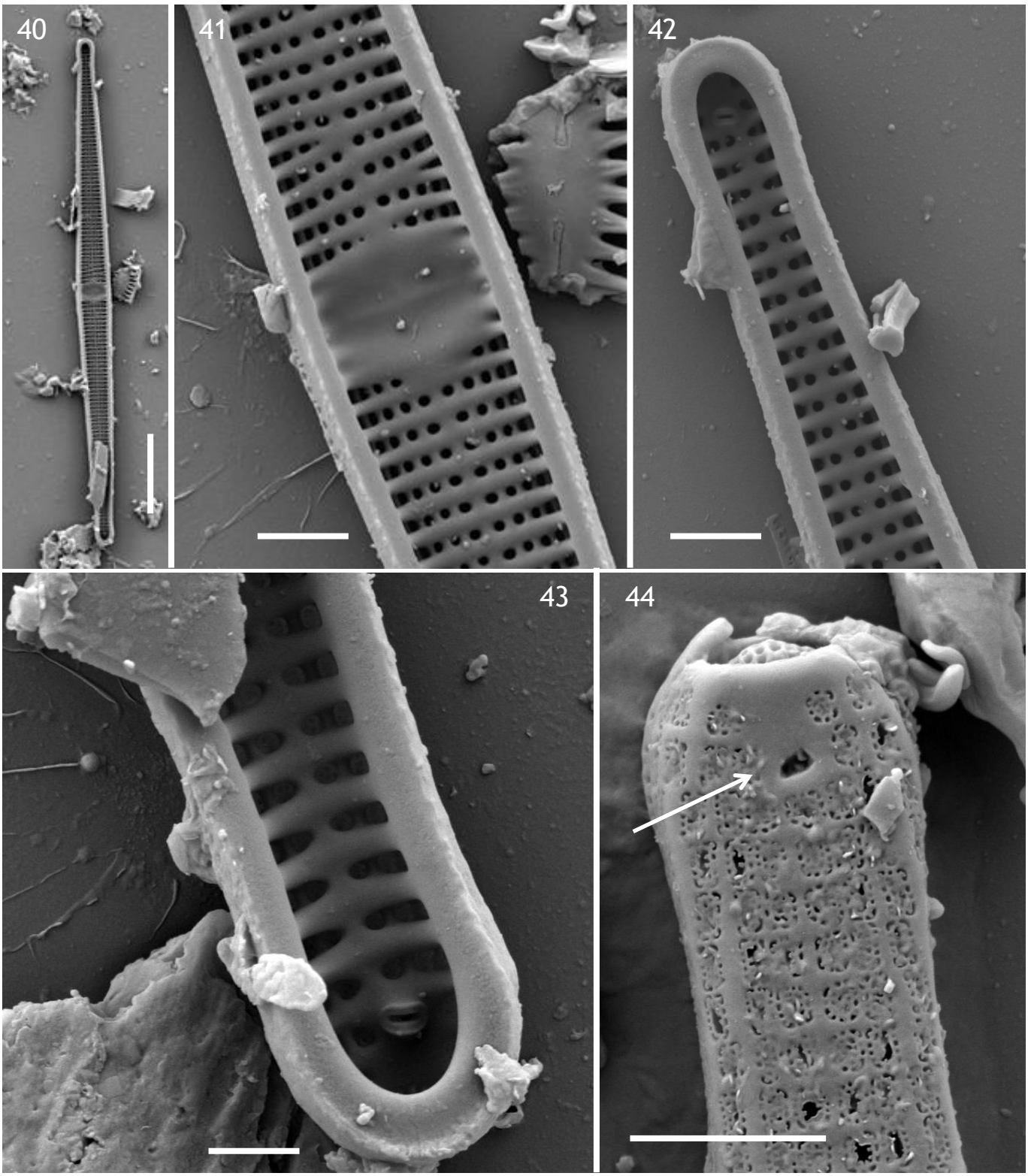




3 38

3 39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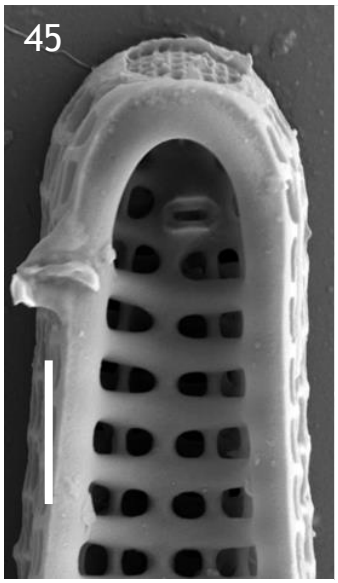
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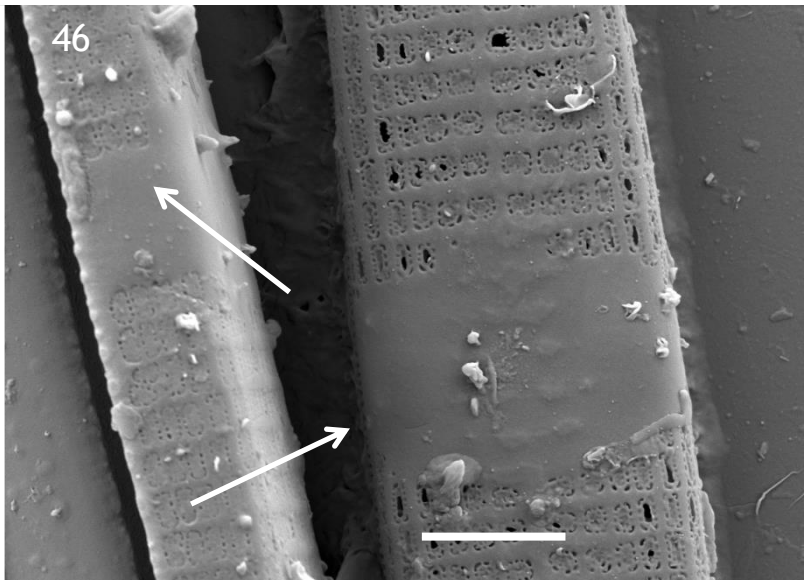
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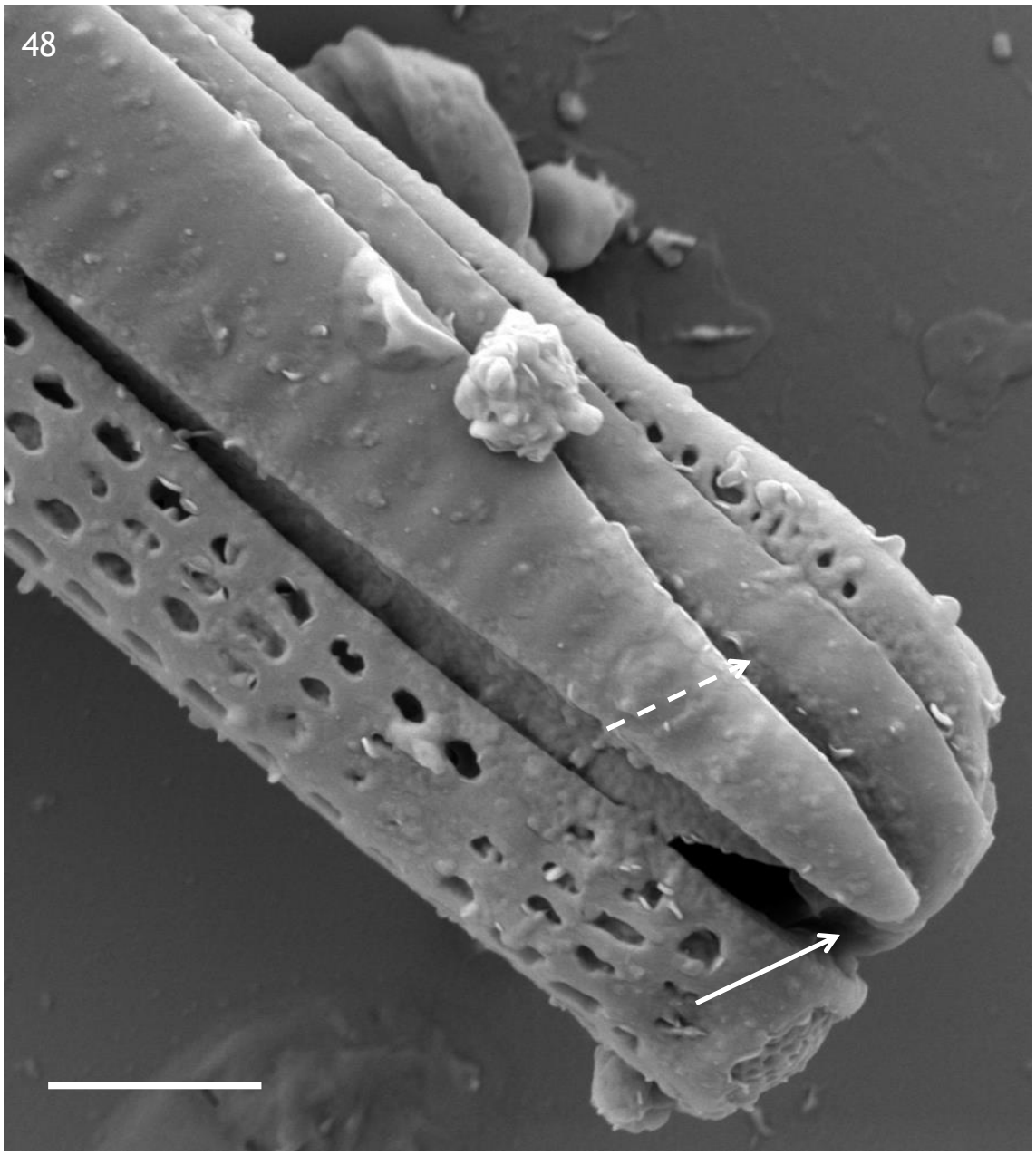
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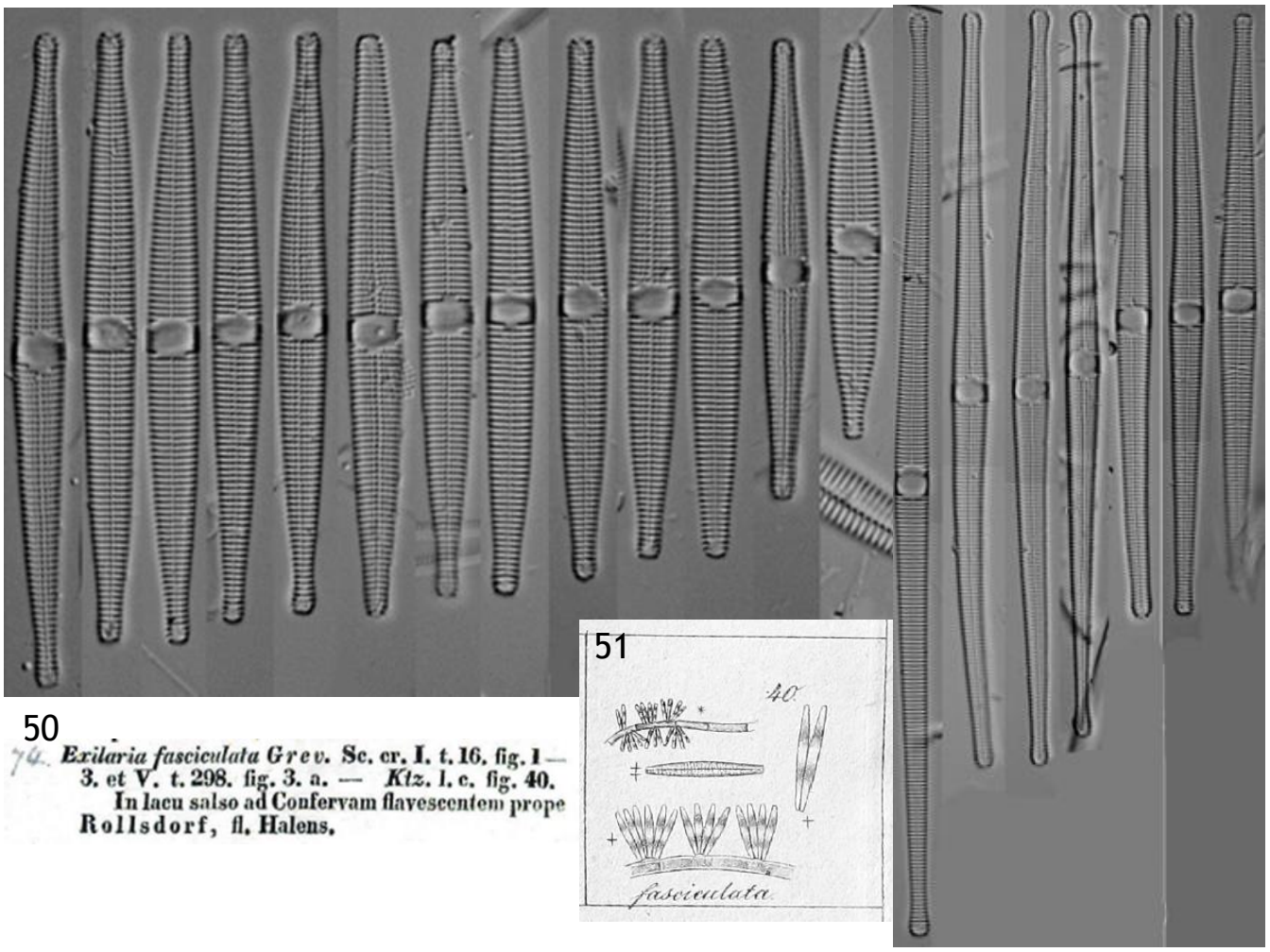
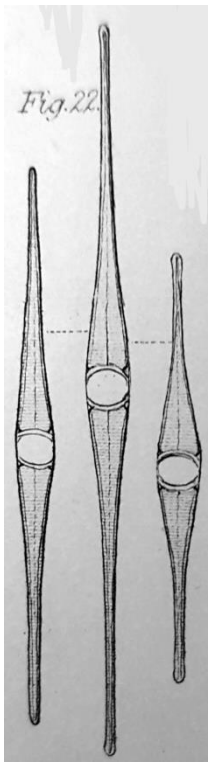


50

74. *Exilaria fasciculata Grev.* Sc. cr. I. t. 16. fig. 1—3. et V. t. 298. fig. 3. a. — *Ktz.* l. c. fig. 40.
In lacu salso ad Confervam flavescentem prope Rollsdorf, fl. Halens.

51

52



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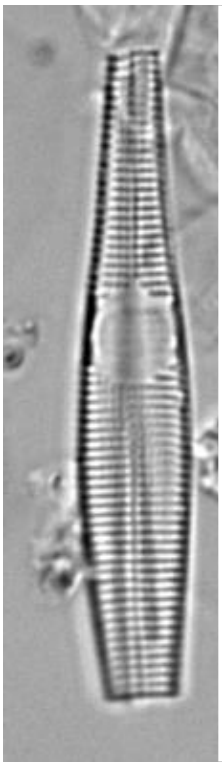

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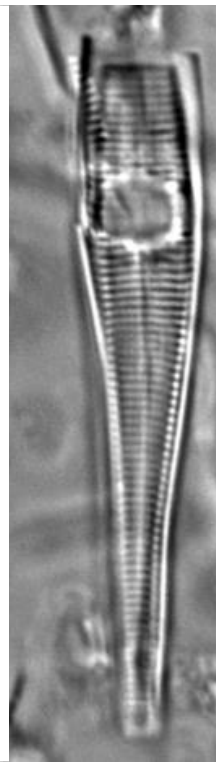

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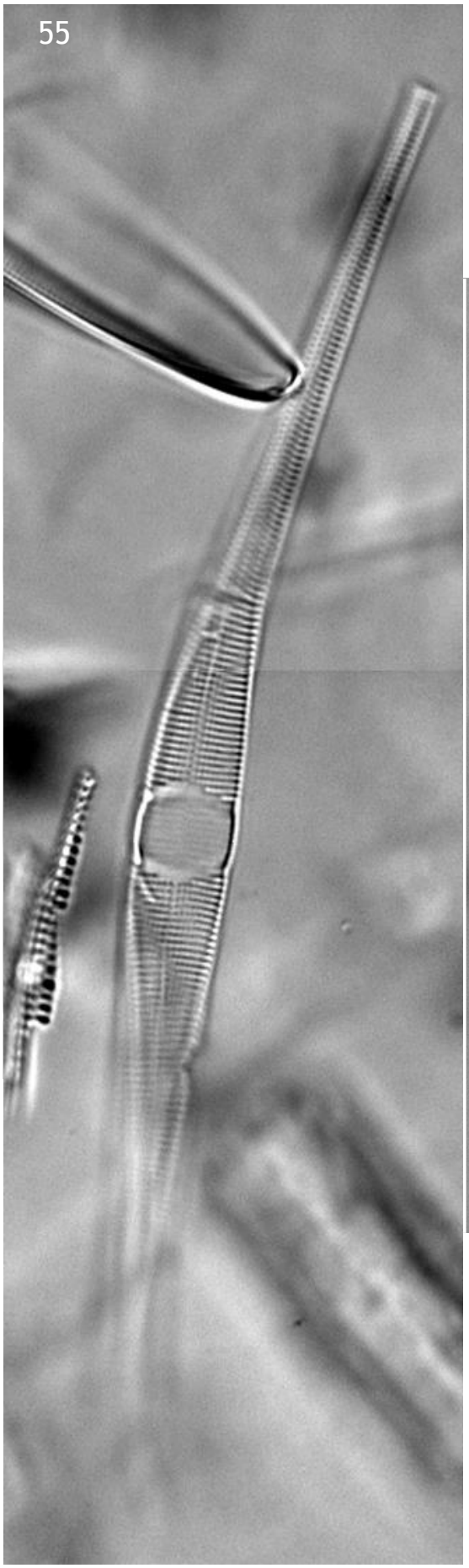

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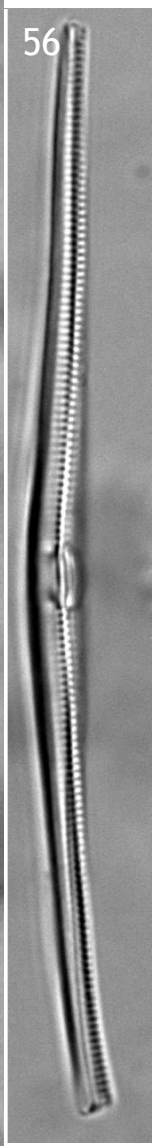
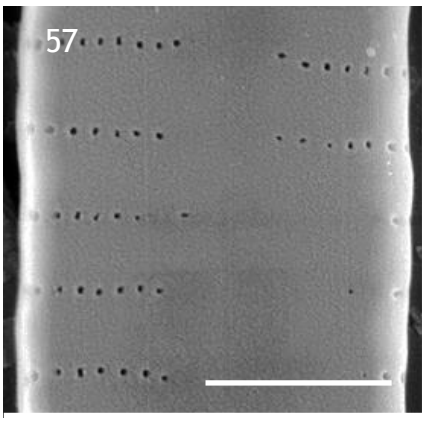


10µm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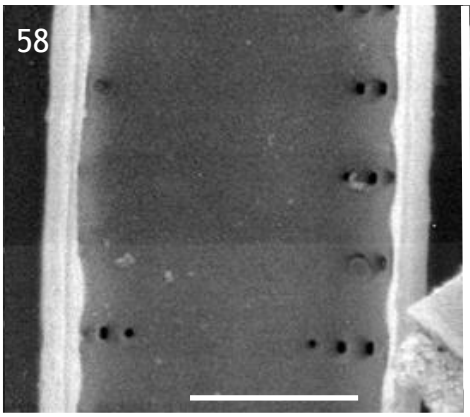
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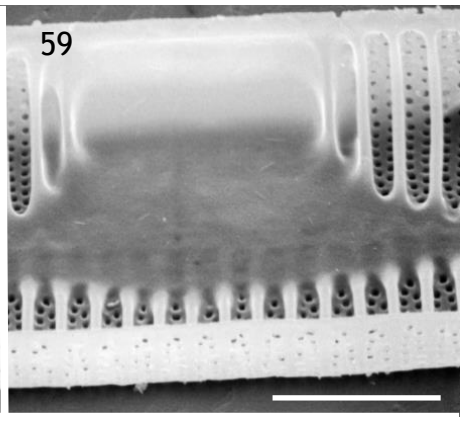
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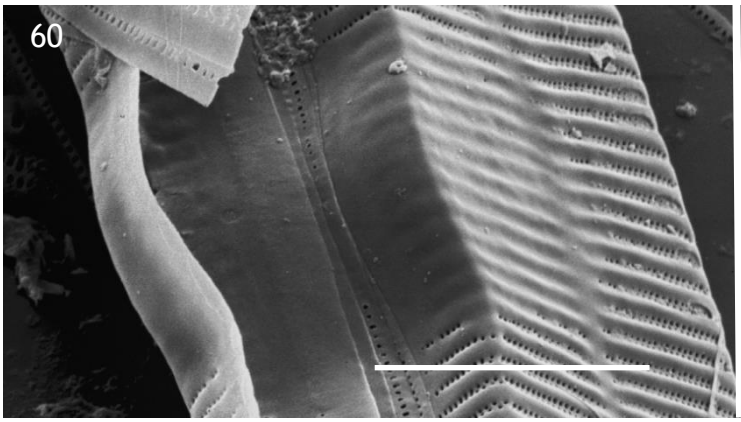
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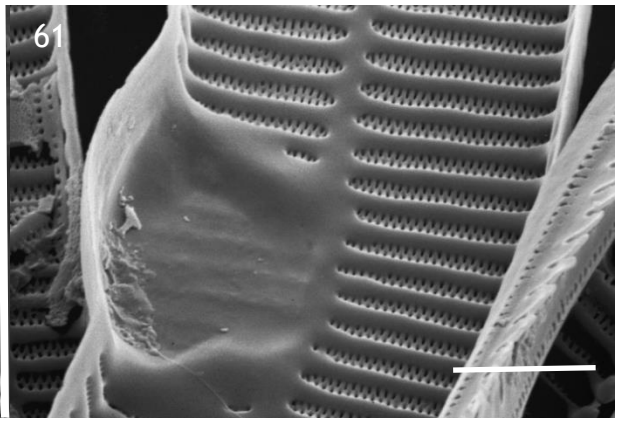
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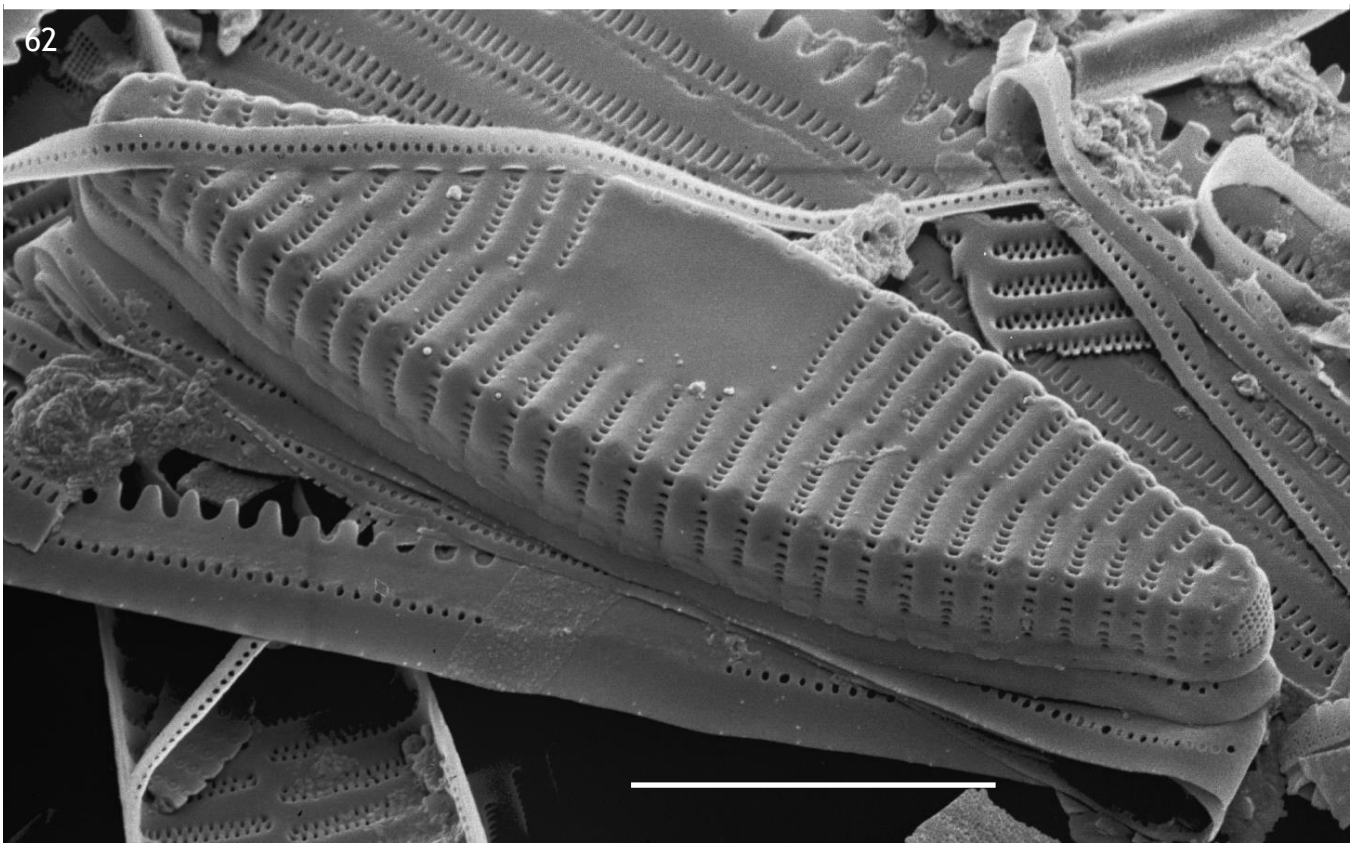
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Figure 63a

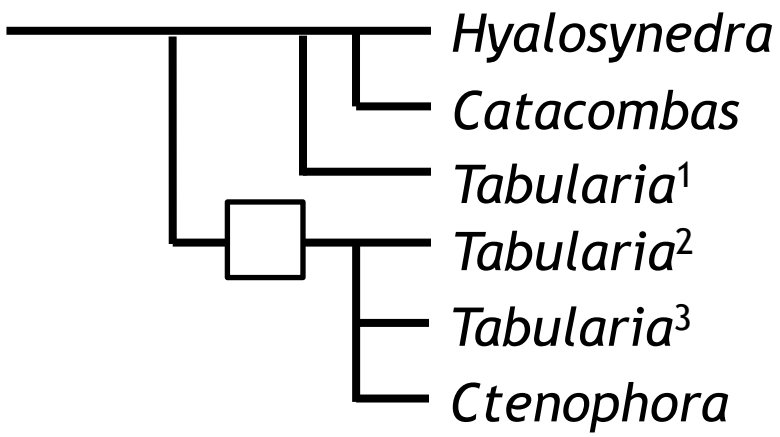

Figure 63b

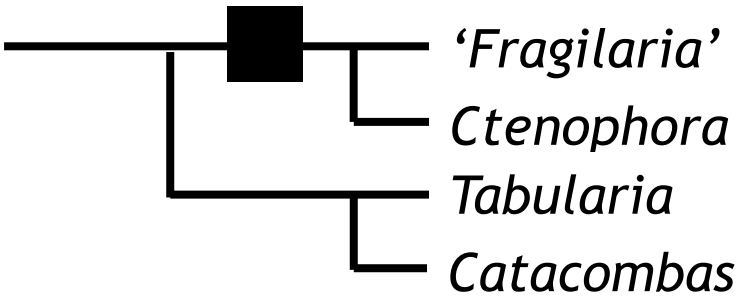

Figure 63c