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Valve ultrastructure of *Rhopalodia constricta* (W.Smith) Krammer (Rhopalodiales, Bacillariophyceae) and a consideration of its systematic placement

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Light microscope (LM) observations of specimens of *Rhopalodia constricta* (W.Smith) Krammer are made from the holotype slide. LM and scanning electron microscope (SEM) observations from Rabenhorst's material of this species are also presented. The two populations are similar in size and ornamentation. Many features seen in the SEM are presented here for the first time, including documentation of the valve interior and the girdle bands. A flap from the valvocopula extends onto the valve exterior at the apices and covers the raphe end—this is the first time this feature has been documented in the Rhopalodiales. *Rhopalodia constricta* is compared and contrasted with other, small species of the genus. It lacks features seen in the generitype, *R. gibba*, suggesting it might be phylogenetically dissimilar to the type species of the genus.

Keywords: *Rhopalodiales*, scanning electron microscopy, type material, *Bacillariophyta*, morphology

Introduction

Rhopalodia constricta was first described by Smith (1853) as *Epithemia constricta* W. Smith, from Exceat-Sussex, U.K. Its systematic position within *Epithemia*, and subsequently *Rhopalodia*, has been debated. It was made a variety of *E. musculus* by Van Heurck (1885) and of *Rhopalodia gibberula* by Cleve-Euler (1952). Müller (1899) considered some interpretations of *E. constricta* as *E. musculus* ['Die vorher citirten Abbildungen der *E. constricta* von W. Smith und C. Janisch, sowie diejenigen von Pedicino aus Fusaro, endlich meine eigene Tafel XI, Figur 8 und 16, gehöören zum Formenkreise der *Rh. Musculus*; die Abbildungen in Van Heurck, Syn. t. 32, 16–18, als *E. succincta* Breob. (*E. constricta* Breob. nee W. Sm.) bezeichnet, zu dem von *Rh. gibberula*'; Müller 1899, p. 279]. On the other hand, Lange-Bertalot & Krammer (1987) and Krammer (1988b) considered specimens identified as *R. musculus* (Fricke in Schmidt 1905, Germain 1981) and *R. musculus* var. *vanheurckii* (Hustedt 1930) the same as *R. constricta*. Krammer (in Lange-Bertalot & Krammer 1987) transferred this taxon to *Rhopalodia* at the level of species, naming it *Rhopalodia constricta*.

Despite (or perhaps because of) the relative lack of scanning electron microscope (SEM) observations, differences between *R. constricta* and these other taxa with which it had been aligned, as well as *R. brebissonii*

Krammer (see Lange-Bertalot & Krammer 1987 and Krammer 1988b) have not been well documented. Lange-Bertalot & Krammer (1987) offer 3 SEM images of *R. constricta* while Krammer (1988b) does not illustrate this species with any SEM images. Previously published SEM images of *R. constricta* are external views only; there has not been any images or discussion of the valve interior or the girdle bands of this taxon.

Although Eulensteini (in Rabenhorst 1870) suggested *E. constricta*, *E. gibberula* and *E. gibba* formed a natural group, Müller (1895) excluded *E. constricta*, *E. gibberula* and *E. musculus* from *Rhopalodia* when he first described the genus, suggesting they were transitional forms and would be better left within *Epithemia*. *Rhopalodia constricta* was assigned to the 'Gibberula' group of *Rhopalodia* (Krammer 1988a, 1988b). The taxa referred to this 'group' share only one point; they are not included in the *Rhopalodia gibba* group. Hustedt (1938, p. 459) suggested the structure of the valves would not help distinguish between species, and that only shape differences would be useful ('Hinsichtlich der Struktur bieten die Rhopalodia-Arten mit weniger Ausnahmen keinewesentlichen Unterschiede, so dass man in der Systematik lediglich auf die Form von Zellen und Shalen angewiesen ist'). While Krammer (1988b) addressed the taxonomy of members assigned to the Gibberula group, he did not recognize one

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or more features to distinguish this group from the Gibba group (as typified by *R. gibba* (Ehrenberg) O.Müller). Some members of the Gibberula group were shown to be separate from *R. gibba* and its close allies using molecular data (Ruck *et al.* 2016).

In the present study we provide light microscope (LM) and SEM observations on type specimens as well as specimens identified originally as '*Epithemia constricta*' and included Rabenhorst's *Algen Europa*'s, number 2121 (Rabenhorst 1870).

Methods and materials

BM Diatom Collection slide number 23050, 'Exect Sussex, Mar. 16 1852, W.S.'

Material from Rabenhorst 2121, Borkum Island from stagnant seawater, Northern Germany, part of COLO collection (A-5004).

Material from the Rabenhorst collection at COLO was cleaned in concentrated HNO₃, rinsed 5 times until neutral, and then air-dried onto coverslips. For light microscopy, the air-dried material was made into permanent slides with Hyrax. Observations were made with an Olympus BX-51 light microscope equipped with DIC optics and a 1.40 NA 100X objective. Images were captured with an Olympus DP71 digital camera. For the SEM, material on coverslips were attached to aluminium stubs with double-sided carbon tape, and sputter coated with ca. 4 nm of Au-Pd with a Cressington 108 sputter coater (Cressington Scientific Instruments Ltd., Watford, UK). The coated material was viewed with a Hitachi SU SU3500 VP (Variable Pressure) SEM (Hitachi High Technologies, America, Inc.) with an accelerating voltage of 15 kV at the Nanomaterials Characterization Facility, University of Colorado, Boulder. Slides made from the Rabenhorst material reside in the Kociolek Diatom Collection at the University of Colorado, Boulder.

Results

Rhopalodia constricta (W.Smith) Krammer in Lange-Bertalot & Krammer 1987, p. 77–78

Lectotype: The Natural History Museum Collection slide number 23050, 'Exect Sussex, Mar. 16 1852, W.S.' (designated here).

Basionym: *Epithemia constricta* Smith 1853, p. 14, fig. 248

Homotypic synonyms: *Epithemia musculus* var. *constricta* (W.Smith) Van Heurck 1885; *Cystopleura constricta* (W.Smith) Kuntze 1891; *Cystopleura musculus* var. *constricta* (W.Smith) De Toni 1892; *Rhopalodia gibberula* var. *constricta* (W.Smith) Cleve-Euler 1952

Non *Epithemia constricta* Grunow 1878 (later homonym)

Figs 1–35

With Light microscopy:

The specimens from the Type slide (Figs 1–8) and the Rabenhorst material (Figs 9–18) are morphologically similar in shape, size and in the density of costae and striae. Frustules are segment-like, wider at the dorsal margin, narrower at the ventral margin. Valves with a strongly convex dorsal margin and nearly straight ventral margin, with a strong or abrupt change in the plane of the surface of the valve, making it difficult to get the entirety of the valve face in focus. Valves 23.0–57.5 µm long, 9.5–13.0 broad in the type population, 23.5–63.0 µm long, 10–14 µm broad in the Rabenhorst material population. Apices straight to deflected slightly towards the ventral margin. Striae distinctly punctate, the striae becoming less organized and more coarse from the dorsal margin to the ventral margin, 3–6 rows of striae between two adjacent costate fibulae, 12–14/10 µm. Costate fibulae narrow but distinct, 4–6/10 µm.

With scanning electron microscopy: Externally (Figs 19–25), the frustule is segment- or wedge-shaped, with the face on one of side of the raphe system being at a more acute angle and shorter and the other at a less acute angle and longer. The raphe opening is a fine slit located in a distinct keel running the length of the valve. The proximal raphe ends are deflected ventrally and covered by a flap at the centre of the valve, and the distal raphe ends are deflected ventrally and covered by flap originating on the valvocopula. When the top of the keel is removed, the rounded portulae are evident. Striae are comprised of alternating rows of areolae. The areolae are c-shaped, containing volae that occlude most of the opening. In some specimens the areolar openings appear round, with the volae not formed or otherwise lacking.

Internally (Figs 26–31), the valve has narrow costate fibulae; secondary costae are absent or indistinct. There is a short tube-like extension of the canal at the apices. Portulae of the canal raphe are rounded, except near the central area where they are more elongated. Each areolar opening contains a vola that makes the opening c-shaped.

There are numerous girdle bands associated with each valve (Figs 32–35). The girdle bands bear one or more rows of perforations. Narrow bands are of the open type and taper to fine points at the ends. A broader closed band fits flat under the valve at the apices and has an opening that corresponds to the opening near the end of the canal raphe. The wider part of the band occurs along most of the length of the valve. A small external flap of the band extends over the very terminus at each end of the valve. The openings are very small or organized together into distinct ellipsoid shapes separated equidistantly around the girdle band. No extensions from the girdle bands overlap onto the costate fibulae. Septa are absent.

Discussion

Our observations support the conclusions of Krammer (1988b) that *R. constricta* can be distinguished from

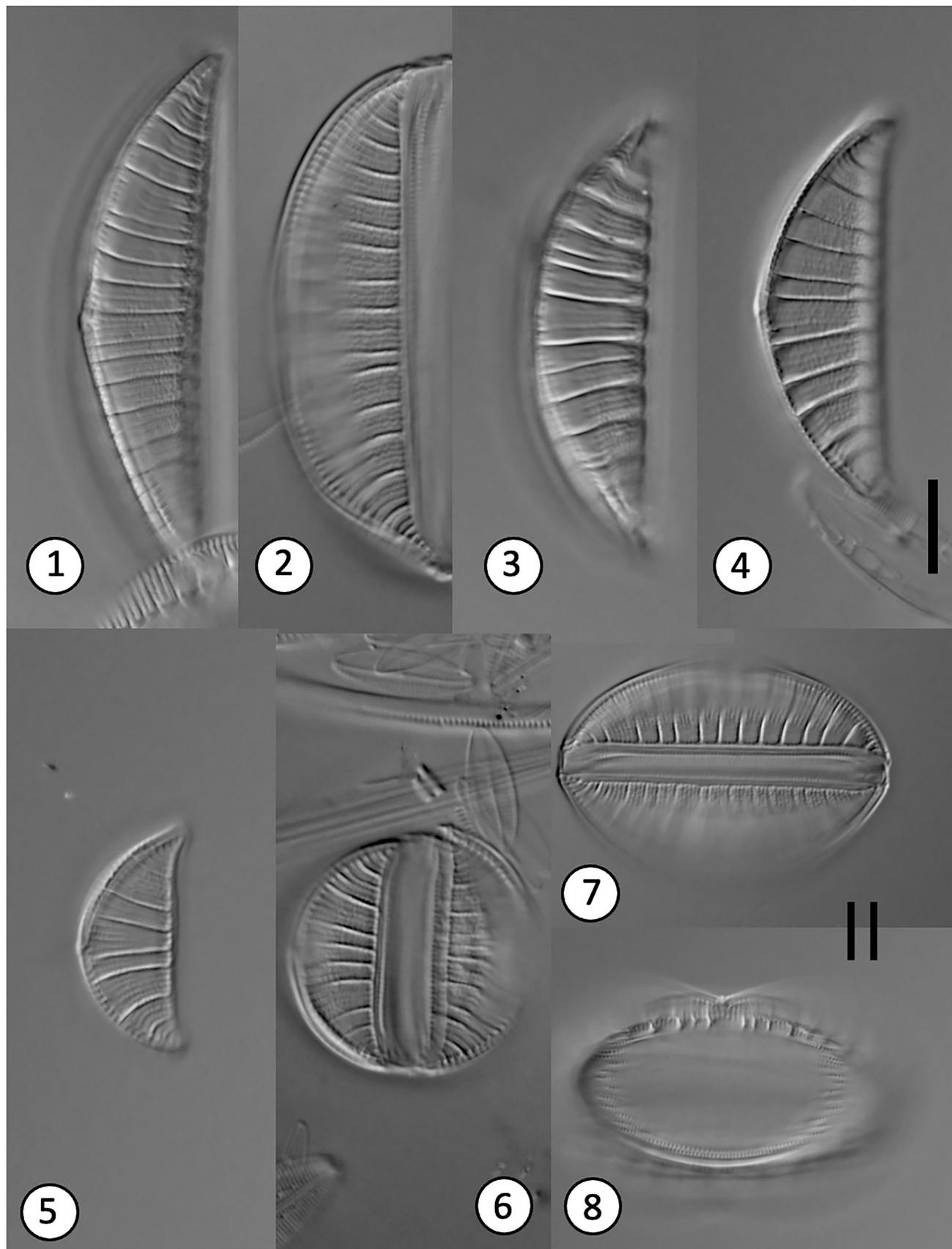


Plate 1. *Rhopalodia constricta*. Light microscopy. Figs 1–8. Specimens from the Type Slide (BM 23050, ‘Exect Sussex, Mar. 16 1852, W.S.’). || indicates images of the same specimen. Scale bar = 10 µm for all specimens.

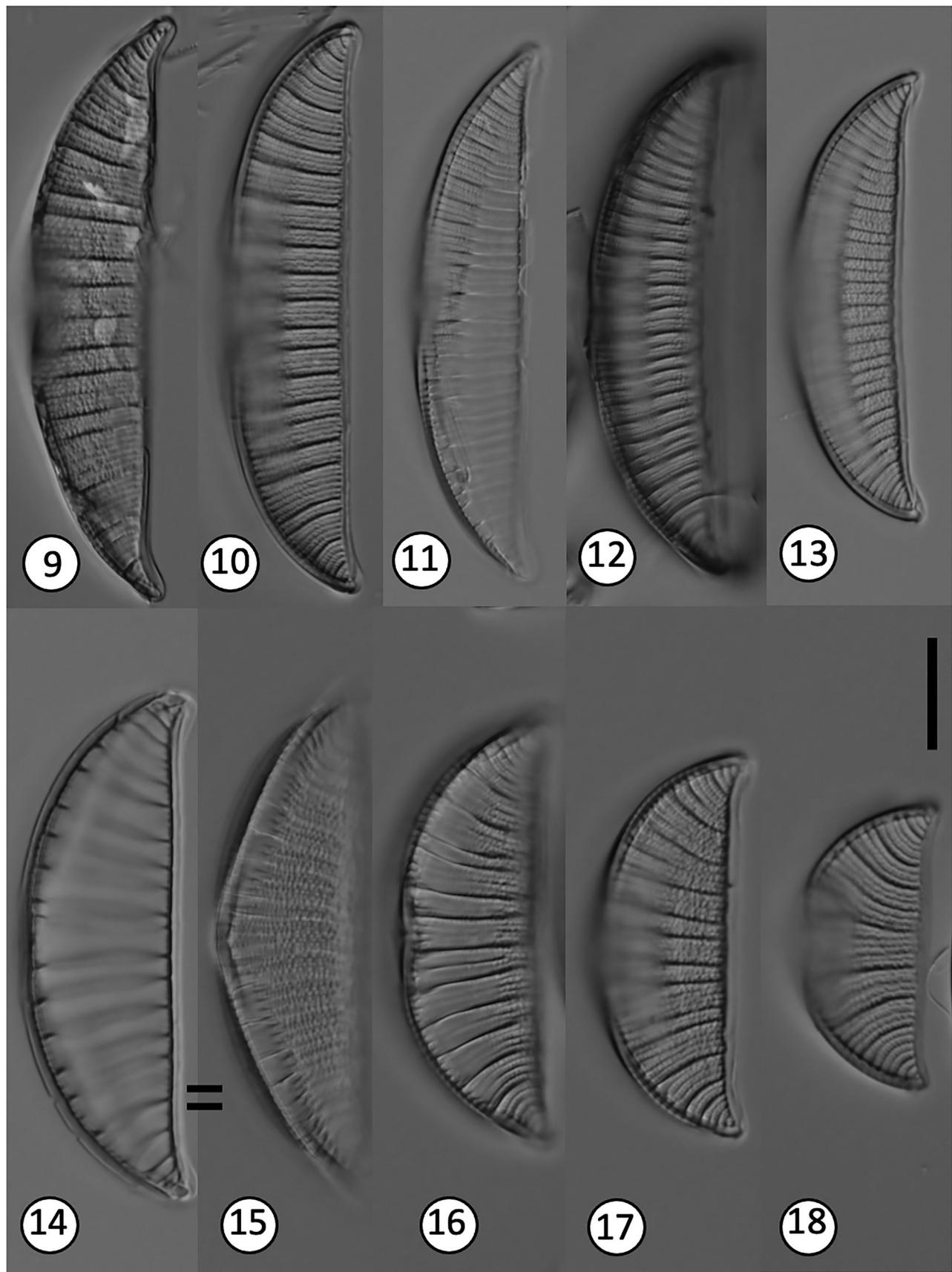


Plate 2. *Rhopalodia constricta*. Light microscopy. Figs 9–18. Specimens from Rabenhorst 2121, Borkum Island from stagnant sea-water, northern Germany, part of JPK collection (A-5004), University of Colorado, Boulder (COLO). = indicates images from the same specimen. Scale bar = 10 μ m for all specimens.

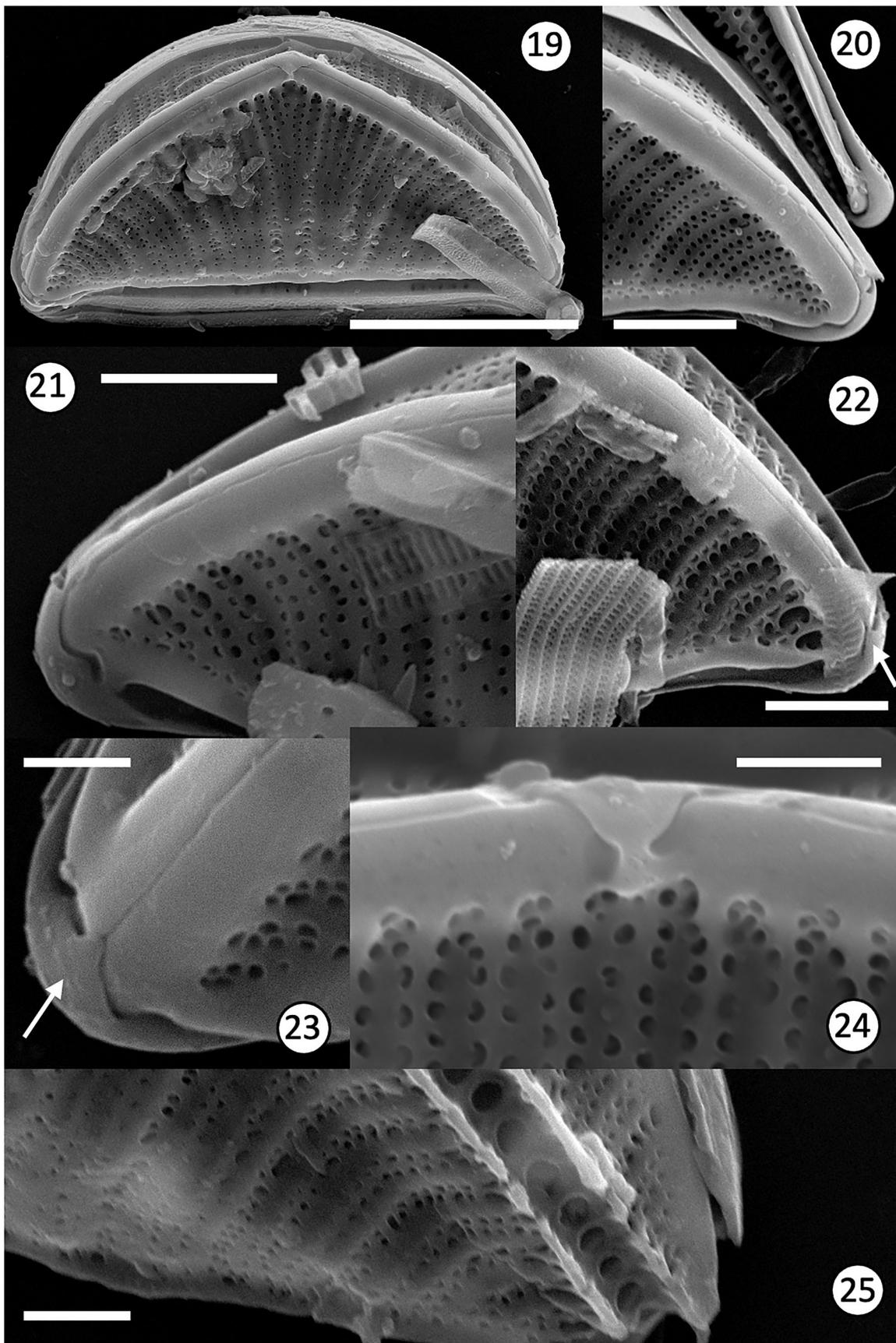


Plate 3. *Rhopalodia constricta*. Scanning electron microscopy. Figs 19–25. External Views. Fig. 19. Entire valve view, showing raphe elevated in a keel with distinct fibulae and disorganized striae. Figs 20–23. Apices of the valve, with flap of silica covering distal raphe end (arrows). Areolae are c-shaped or round holes. Fig. 24. Centre of the raphe showing fold in the constricted central region. Fig. 25. Raphe with top of keel pulled away showing canal with portules. Scale bars = 10 µm for fig. 19; 2.5 µm for figs 20, 21, 22, 25; 1 µm for figs 23, 24.

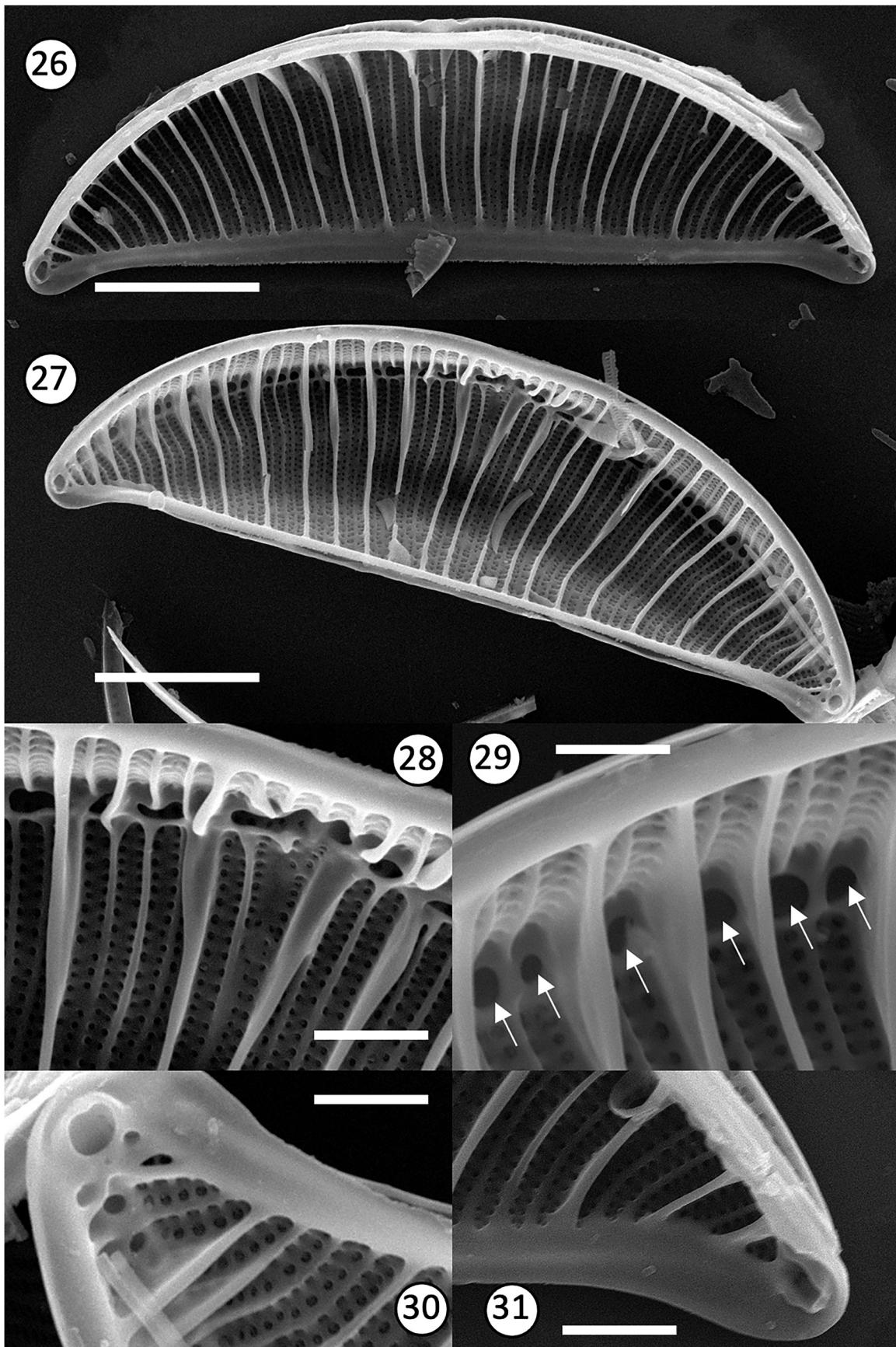


Plate 4. *Rhopalodia constricta*. Scanning electron microscopy. Figs 26–31. Internal Views. Figs. 26, 27. Whole valve showing distinct costate fibulae and tube-like, round openings at the apices. Fig. 28. Valve centre with primary and secondary fibulae. Fig. 29. Canal raphe showing portulæ (arrows). Figs 30, 31. Apices with extended, round openings. Scale bars = 10 µm for figs 26, 27; 2.5 µm for figs 28–31.

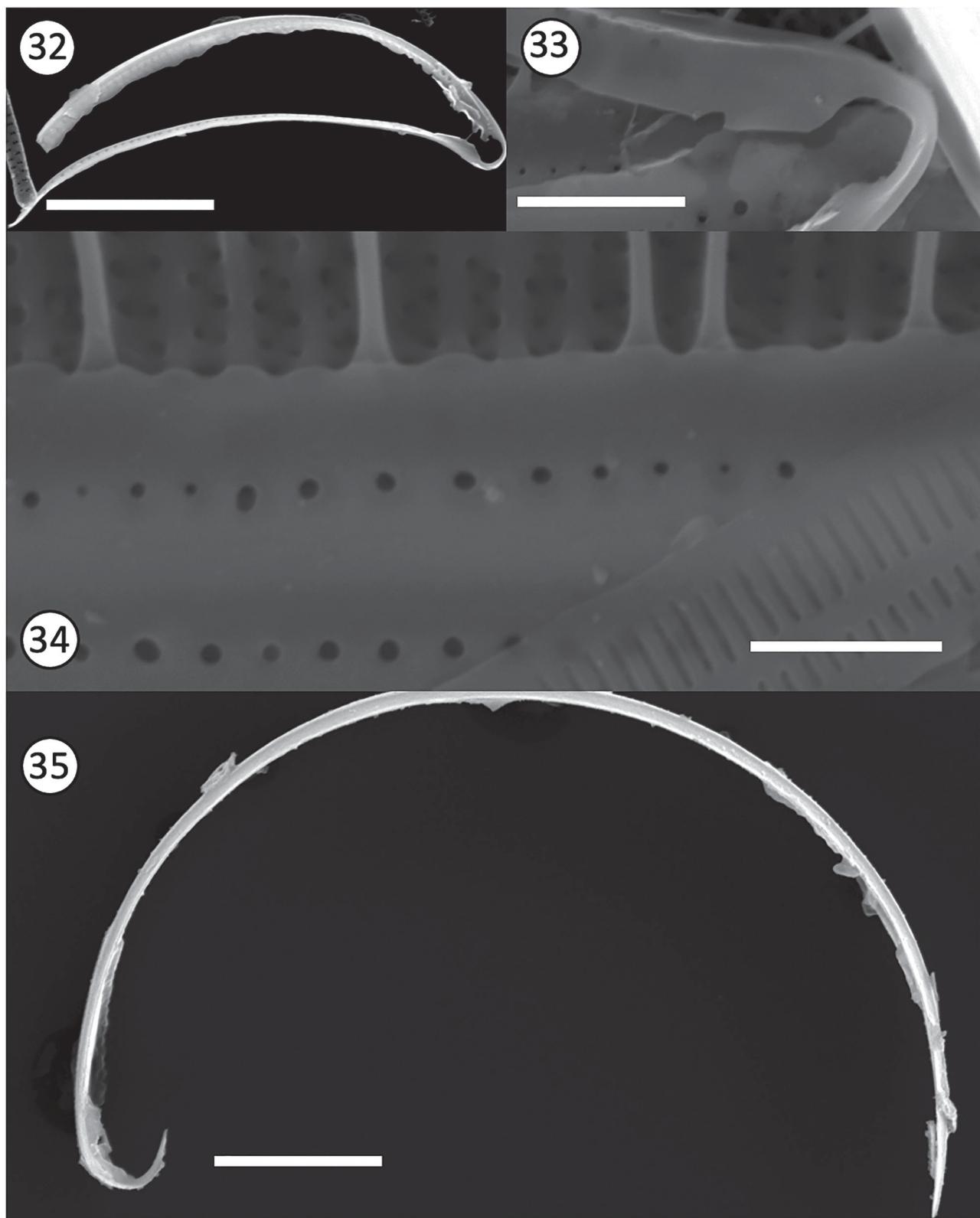


Plate 5. *Rhopalodia constricta*. Scanning electron microscopy. Figs 32–35. Girdle bands. Figs 32, 33. Valvocopula with expanded band and flattened apex. Fig. 34. Valvocopulae laying against the valve. Margin is undulate but without extensions overlaying the fibulae. Fig. 35. Copula of the open type with fine, tapered ends. Scale bars = 10 μ m for fig. 32; 2.5 μ m for fig. 33; 2.0 μ m for fig. 34; 5 μ m for fig. 35.

Table 1. Comparison of *Rhopalodia constricta* with morphologically similar congeners using size metrics and valve features.

TAXA	Length; Breadth (μm)	Features					References
		Striae in 10 μm	Costae in 100 μm	Apical Flaps	Apical Fold		
<i>R. constricta</i>	23.5–63.0; 10–14	12–14	40–60	YES	YES	1	
	23.0–57.5; 9.5–13.0 type	12–15	40–60	N/A	N/A	1	
	24–75; 9–18	15–20	35–60	YES	YES	2,3	
<i>R. gibberula</i>	25–100; 5–12	12–19	30–100	YES	NO	2,4	
<i>R. sculpta</i>	23–52; 6–12	15–18	40–70	N/A	NO	3	
<i>R. rumrichiae</i>	19–72; 6–12	15–19	30–50	N/A	NO	3	
<i>R. acuminata</i>	22–112; 10–16	15–20	40–60	N/A	NO	2	
	22–112; 7.5–11.0	16–19	40–60	N/A	NO	3	
<i>R. brebissonii</i>	15–40; 5.0–8.5	11–22	35–60	N/A	NO	2,5	
<i>R. musculus</i>	12–80; 10–16	15–20	30–50	YES	NO	2	

1 = Data provided herein; 2 = Krammer & Lange-Bertalot (1988); 3 = Lange-Bertalot & Krammer (1987); 4 = Patrick & Reimer (1975); 5 = Krammer (1988b)

N/A = not available; specimens on mounted slides only.

other, previously described taxa assigned to the *Rhopalodia gibberula* group (sensu Krammer 1988b). Specimens observed in the type material and in the Rabenhorst material agree in all aspects with the specimens illustrated in Lange-Bertalot and Krammer (1987) and Krammer (1988b), except the report of valves reaching up to 18 μm in breadth. Also, our stria counts suggest them to be a bit more coarse (down to 12/10 μm and not more than 15) versus the report of them up to 20/10 μm. Krammer & Lange-Bertalot (1988) did not indicate the populations they reviewed that had such a high density of striae; perhaps those specimens or populations represent a different species.

While similar to other species in the Gibberula group, *R. constricta* differs with respect to valve metrics based on valve shape, structure of the striae and areolae, and valve ultrastructure. *Rhopalodia constricta* can be distinguished from species that are most similar morphologically, including *R. gibberula* (Ehrenberg) O. Müller, *R. sculpta* Krammer, *R. rumrichiae* Krammer, *R. acuminata* Krammer and *R. brebissonii* Krammer. These taxa are compared in Table 1. Based on the interpretation of these taxa presented by Krammer and Lange-Bertalot (1988), *R. constricta* is differentiated from *R. brebissonii* by being larger and, although both species have ventrally-deflected apices, they are more pronounced in *R. brebissonii*. *Rhopalodia acuminata* has narrow apices like *R. constricta*, but they are straight, not deflected. Both *R. sculpta* and *R. rumrichiae* differ from *R. constricta* by having concave ventral margins (Lange-Bertalot & Krammer 1987). Müller (1899) considered *R. constricta* a synonym of *R. musculus* (Kützing) O. Müller, but figures of *R. constricta* presented herein of the type population and from the Rabenhorst material, as well as in Krammer (1988b) and Krammer & Lange-Bertalot (1988), show these two taxa are easily separated by the curvature of the ventral margin; in *R. constricta* the ventral margin is straight or nearly so, in *R. musculus* the

ventral margin is distinctly concave. The two also differ in the structure of the central part of the dorsal margin and in the density of striae.

Müller (1895) first created the genus *Rhopalodia* for *R. gibba* and its allies, including endemics from the East African Rift Valley lakes. He then assigned species allied with *R. gibberula* to the genus, including *R. gibberula* and *R. musculus*. Müller (1899, 1900) considered many taxa within the range of forms expressed by *R. musculus* (and described four groups within that species complex that contained 29 taxa, of which 25 were described as new subspecific taxa; Müller 1899, 1900). His lumping of *E. constricta* within *R. gibberula* meant that he never formally transferred the taxon to *Rhopalodia*. This was first done by Cleve-Euler (1952) as *R. gibberula* var. *constricta*, following Müller's suggestion having *R. constricta* as a variety of *R. gibberula*. It was Krammer (in Lange-Bertalot & Krammer 1987) that recognized *R. constricta* as a distinct species within the genus.

Members of the Gibberula group are quite diverse morphologically (Krammer 1988b). For example, while most species are segment-like and asymmetrical in their organization (including *R. constricta*), there are some that are segment-like but symmetrical (similar in their organization to *R. gibba*) (Müller 1899; Fricke in Schmidt 1904; Krammer 1988b). In addition, *R. constricta* lacks any extensions from the girdle bands. Extensions of the girdle bands that overlay the costate fibulae are found in *Epithemia* Kützing (Sims 1983; Kocielek et al. accepted), *Tetralunata* Hamsher et al. (2014) and the lineage containing *R. gibba* (e.g., Lange-Bertalot & Krammer 1987) and this may represent a difference between the Gibba and Gibberula groups. In terms of the raphe structure, the raphe of *R. constricta* and other species in the Gibberula group (e.g., *R. brebissonii*, *R. acuminata*; Krammer & Lange-Bertalot 1988) is biarcuate and visible at a particular plane of focus; this structure is

not seen in other species of the Gibberula group or in *R. gibba*, where the keel of the raphe is positioned along the valve face: mantle interface (Lange-Bertalot & Krammer 1987; Krammer 1988a). A similar biarcuate raphe structure, where the raphe extends from the middle of the apices to the dorsal margin, can be seen in the Cistula group of *Epithemia*, but not in other species of that genus (Lange-Bertalot & Krammer 1987; Krammer & Lange-Bertalot 1988; Kociolek et al. accepted).

R. constricta and *R. gibberula* have been shown by Lange-Bertalot and Krammer (1987) and Krammer and Lange-Bertalot (1988) to have a flap like extension of the keel covering the external proximal raphe ends. This feature is also shown in *R. guettingeri* Krammer (Krammer 1988b), but has not been documented in other members of *Rhopalodia* (e.g., *R. rupestris* (W.Smith) Krammer or *R. operculata* (Agardh) Håkansson, see Krammer 1988b). This feature, if found in other species of the Gibberula group may also serve to help distinguish it from the Gibba Group (i.e., *Rhopalodia sensu stricto* as typified by *R. gibba*).

Most members of the Gibberula group have c-shaped volate occlusions, similar to the rest of the Rhopalodiales. In some of Krammer's (1988b) images, volae are absent (for example in *R. constricta*) or appear to be modified and not c-shaped. In some specimens of *R. constricta* we observed herein, the areolae appear to be without occlusions. In *R. musculus*, the exterior areolae openings are large and have very small occlusions recessed within them (see Krammer & Lange-Bertalot 1988, plate 110, Fig. 4). Absence of areolar occlusions can be seen in other species of the Rhopalodiales that are either from exsiccatae over 150 years old (e.g., Kociolek & Van De Vijver 2023), dissolved in fossil taxa (e.g., Kociolek et al. accepted) or not yet developed in extant material (Kociolek et al. accepted).

Molecular data indicate species of the Gibberula group, as well as some unnamed taxa, are outside the lineage containing *R. gibba* (the type species of the genus) and its allies (Ruck et al. 2016), but despite this Ruck et al. (2016) proposed to lump all *Rhopalodia* species into *Epithemia*, based on their idea that lumping the genera together was a more 'conservative' approach nomenclaturally versus separating out two new genera which, in their words would minimize 'overall disruption to the taxonomy of this group' (Ruck et al. 2016). This approach was endorsed by Cocquyt et al. (2018), though they recognized a new subgenus for species described originally from Africa, though did not place this group relative to others in *Epithemia*. Vigneshwaran et al. (2021) noted that the disruption of the taxonomy may be greater due to the many taxonomic changes (hundreds!) necessitated by lumping taxa. Again, the molecular data suggest that the groups (most unnamed and undocumented by Ruck et al. 2016) are not closely related to *Rhopalodia sensu stricto* (let alone *Epithemia*). Observations presented herein on *R. constricta* valve

morphology provide further evidence that it differs from *R. gibba* and allies. Additional data, on both morphological diversity and molecular sequence data with increased taxon sampling, should help elucidate the relationships among diatoms that have been referred to as *Rhopalodia*.

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