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Light and Scanning Observations on a *Denticula* species reported from South Africa and endemism of the diatom genus *Tetralunata* (Rhopalodiales, Bacillariophyceae)

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Abstract

Denticula costata Hustedt was originally described from fossil material from Sumatra and later assigned to the genus *Tetralunata*. Although *Tetralunata* was thought to be endemic to Indonesia, *D. costata* has been reported from wetwalls from South Africa. This disparity in locality prompted us to investigate the *D. costata* in South Africa further. *D. costata* (now *T. costata*) specimens and the species reported from South Africa were different in size, shape, and structure of the raphe system. These differences, as well as comparisons to other *Denticula* species, allowed us to determine that the South African specimens have not been described previously. Valve ultrastructure, including the canal raphe, areolae with volate occlusions, and presence/structure of the septa suggest this new species belongs to the genus *Tetralunata*. This is the first report of *Tetralunata* from outside of Indonesia. Herein, we describe *Tetraluanata schoemanii sp. nov.* and its systematic placement close to, but separate from, *Epithemia*. This first report of *Tetralunata* from outside of Indonesia, increases our understanding of the genus range and displays a unique biogeographical pattern that warrants further investigation in the future.

Key words: Morphology, SEM, Epithemiaceae, new species, biogeography, *Tetralunata*, *Denticula*, *Epithemia*

Introduction

Denticula Kützing (1844: 43) was considered a member of the Rhopalodiales, along with two other genera, *Rhopalodia* O. Müller (1895: 57) and *Epithemia* Brébisson ex Kützing (1844: 33). These genera share the presence of a canal raphe (Karsten 1928) and the harboring of blue-green algal symbionts (Geitler 1977; Patrick & Reimer 1975; Krammer & Lange-Bertalot 1988). Hustedt (1928, 1930) and Patrick & Reimer (1975) considered *Denticula* within the Rhopalodiales, with *Denticula* being more closely related to *Epithemia* than either was to *Rhopalodia*. Simonsen (1979) thought *Denticula* was a member of the Bacillariales, being a close ally of *Nitzschia* Hassall (1845: 435). Lange-Bertalot & Krammer (1987) and Krammer & Lange-Bertalot (1988) considered *Denticula* to be a link between the Bacillariales and the Rhopalodiales (a close relative of the Surirellales), by virtue of them possessing a canal raphe. Molecular data has shown the Bacillariales and Rhopalodiales+Surirellales to be distantly related, with the evolution of the canal raphe being homoplasious between the two lineages (Ruck & Theriot 2011; Hamsher *et al.* 2014). A

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single *Denticula* species, *D. kuetzingii* Grunow 1862: 546) was included in a large analysis of the relationships of the Bacillariales and nested deep within one lineage of the polyphyletic genus *Nitzschia* (Mann *et al.* 2021).

Brun (1891) and Hustedt (1935, 1937) described several *Denticula* species from Sumatra. *Denticula* species from Sumatra were suggested by Sims (1983) to be morphologically similar to *Epithemia*, though no data were shown to support that contention. Also, Geitler (1977) showed that one of the Indonesian species, *D. vanheurckii* Brun (1891: 25), possessed blue green algal symbionts, adding further support to the idea that the *Denticula* species from Indonesia were closely allied to the Rhopalodiales. Hamsher *et al.* (2014) documented several species of *Denticula* from Indonesia with volate occlusions of the areolae, similar to those found in members of the Rhopalodiales. Based on a formal phylogenetic analysis of morphological data, the diatom genus *Tetralunata* was proposed by Hamsher *et al.* (2014) for species originally described in the genus *Denticula* from fossil and recent collections around Lake Toba, on the island of Sumatra, Indonesia (Brun 1891; Hustedt 1935, 1937). Hamsher *et al.* (2014) showed that *Denticula sensu lato* was paraphyletic, with some species belonging to the Bacillariales and others, like those described from Indonesia, belonging to the Rhopalodiales. Many new taxa were described from Pleistocene sediments and recent material from the caldera lake formed by a supervolcano about 75,000 years ago. *Tetralunata* has been considered an endemic to Indonesia (Hamsher *et al.* 2014; Kociolek 2019).

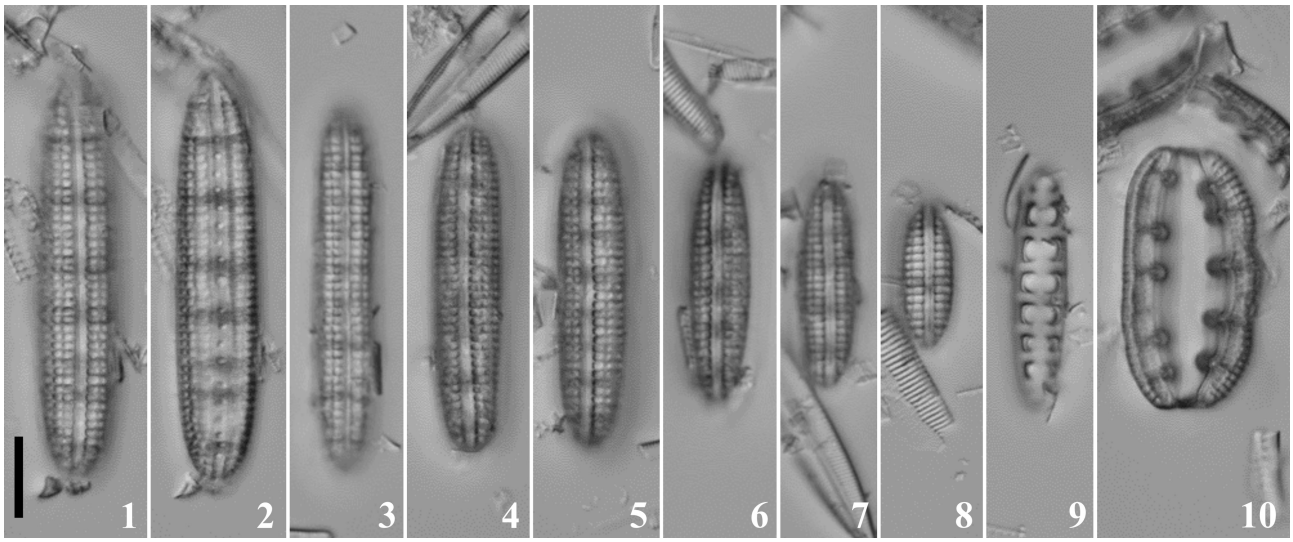
In 1973, Schoeman reported *Denticula costata* Hustedt (1935: 170) from damp rock faces in cave-like cliff in Lesotho, South Africa, a species originally described from Sumatra (Hustedt 1935). This species had previously been reported from South Africa by Cholnoky (1957). In this paper, we present light and scanning electron microscopical observations of the *Denticula* specimens studied by Schoeman to determine whether: (1) the species from Lesotho, South Africa, is conspecific with *D. costata* from Indonesia, and (2) *Tetralunata* occurs in South Africa as well as Indonesia.

Materials and methods

The Schoeman material from Lesotho from which *Denticula costata* was reported ("Lesotho 78, about 2 miles from the Maluti treks camp, situated on the banks of the Senqunyane River, on the road to Marakabei. Sides of hollow, cave-like cliffs below the road, damp rock faces") was obtained from the South African National Diatom Collection, North-West University, Potchefstroom. The material was cleaned by boiling in concentrated nitric acid, then rinsed and settled for a 24-hour period over a period of 5 days. The cleaned and rinsed material was then air-dried onto glass coverslips, which were then mounted onto microscope slides with Hyrax. Light microscopic observations were made with an Olympus BX-51 light microscope outfitted with Differential Interference Microscopy optics and a 100X, 1.40 NA objective. Digital images were taken with an Olympus DP-71 digital camera. Cleaned material was also air-dried onto small coverslips which were then attached to aluminum stubs with double-sided carbon tape. The stubs containing the material were sputter-coated with ca. 4 nm of Platinum 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.) at an accelerating voltage of 15 kV at the Nanomaterials Characterization Facility, University of Colorado, Boulder.

Results

Light microscope observations on the specimens from South Africa identified by Schoeman as *Denticula costata* are presented in Figures 1–10. In the light microscope, specimens from South Africa are linear in shape with apices tapered and narrowly rounded. Length ranges from 23–55 µm and breadth 7–10 µm. The raphe is placed medianly, with indistinct raphe branches. The proximal ends terminate close to one another. Distally, the raphe branches extend onto the mantle at the apices. Costae are robust, 1–3 / 10 µm. Striae are parallel, composed of 4–6 areolae, and number 8–10 / 10 µm. In girdle view, "capitate costae" are visible. Also evident in girdle view are Häutung valves, wherein a single new valve is produced within a frustule. Häutung valves appear arched or undulate but otherwise are structured similar to vegetative valves.



FIGURES 1–10. *Tetralunata schoemanii*, *sp. nov.* Light Microscopy. Figs 1–8. Size diminution series, valve views, from Holotype slide. Fig. 9. Septa. Fig. 10. Frustule in girdle view showing Häutung valve. Scale bar = 10 μm for all specimens.

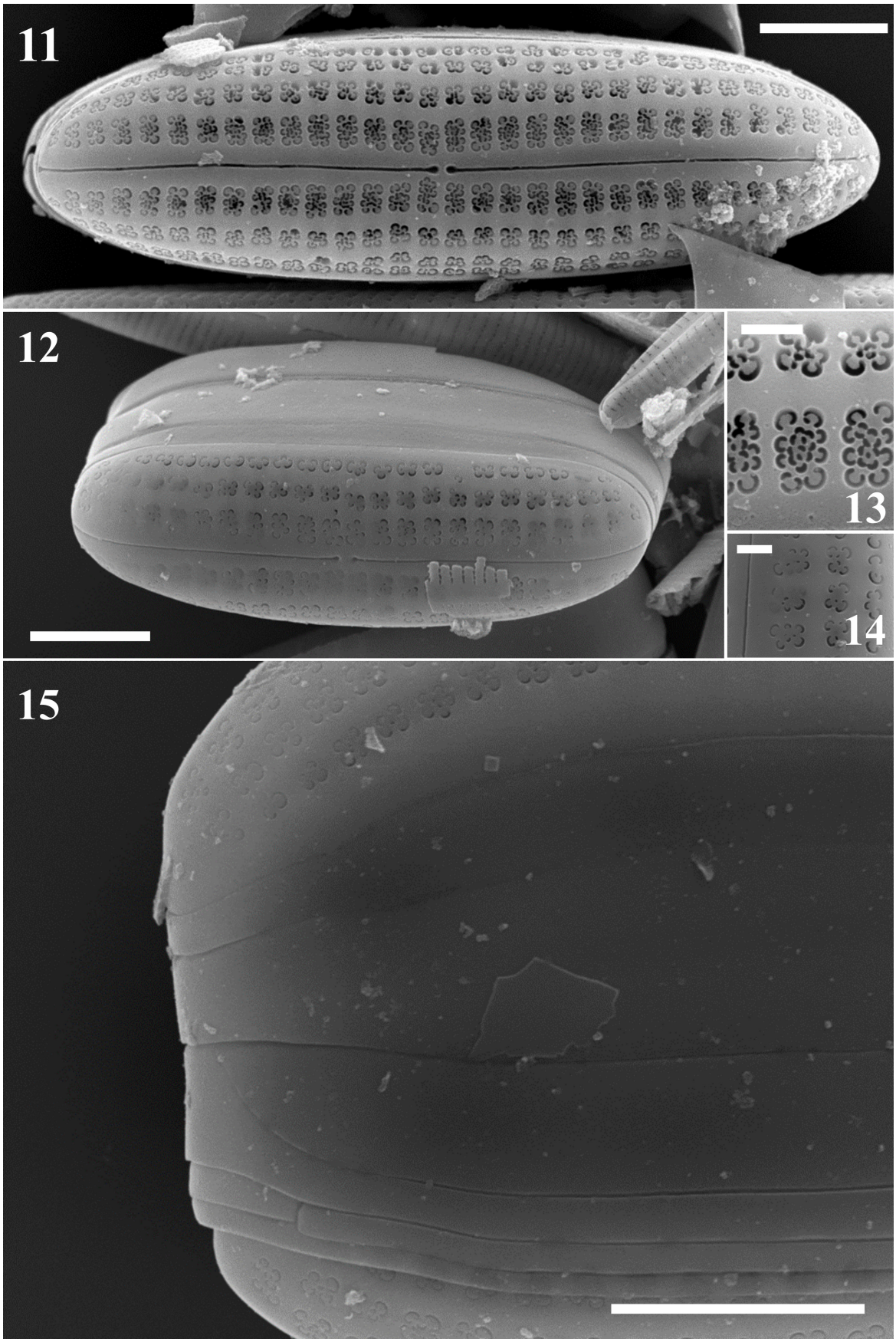
In the SEM, the exterior (Figs 11–15) valves are pill-shaped, with a rounded valve face. Striae are composed of 3–5 rows of areolae (Fig. 11). The lunate areolae (see Hamsher *et al.* 2014) have complex volae with a 'domed cap' and areolar strut structure, more or less in divisions of four sections or groups (Figs 13, 14). The raphe is straight, with the proximal ends terminating in close proximity to each other, appearing dilated and rounded (Figs 11, 12). Distal raphe ends extend onto the valve mantle and are also dilated and rounded. In girdle view, valve face is rounded (Fig. 15). Striae extend from the valve face to the mantle (Figs 12, 15). Cingulum elements can be narrow or broad, and they lack poroids (Fig. 15).

Internally (Figs 16–21), the valve is dominated by robust costate fibulae, swollen slightly in the middle. The canal raphe is wide, and contains small portulae, except in the center where the opening into the canal is wider (Figs 16, 17). The raphe is interrupted to form the proximal raphe endings internally (Fig. 19). Septa are closed at the apices and interrupted in the middle of the extensions across the valve face (Figs 17, 18). One side of a septum is smooth, the other is grooved. The grooved side of the septum overlays the costate fibulae (Figs 20, 21). In section, the grooved side of the septa can be seen to cover the costate fibulae, creating the "capitate costae" as named by Patrick and Reimer (1975) (Fig. 21).

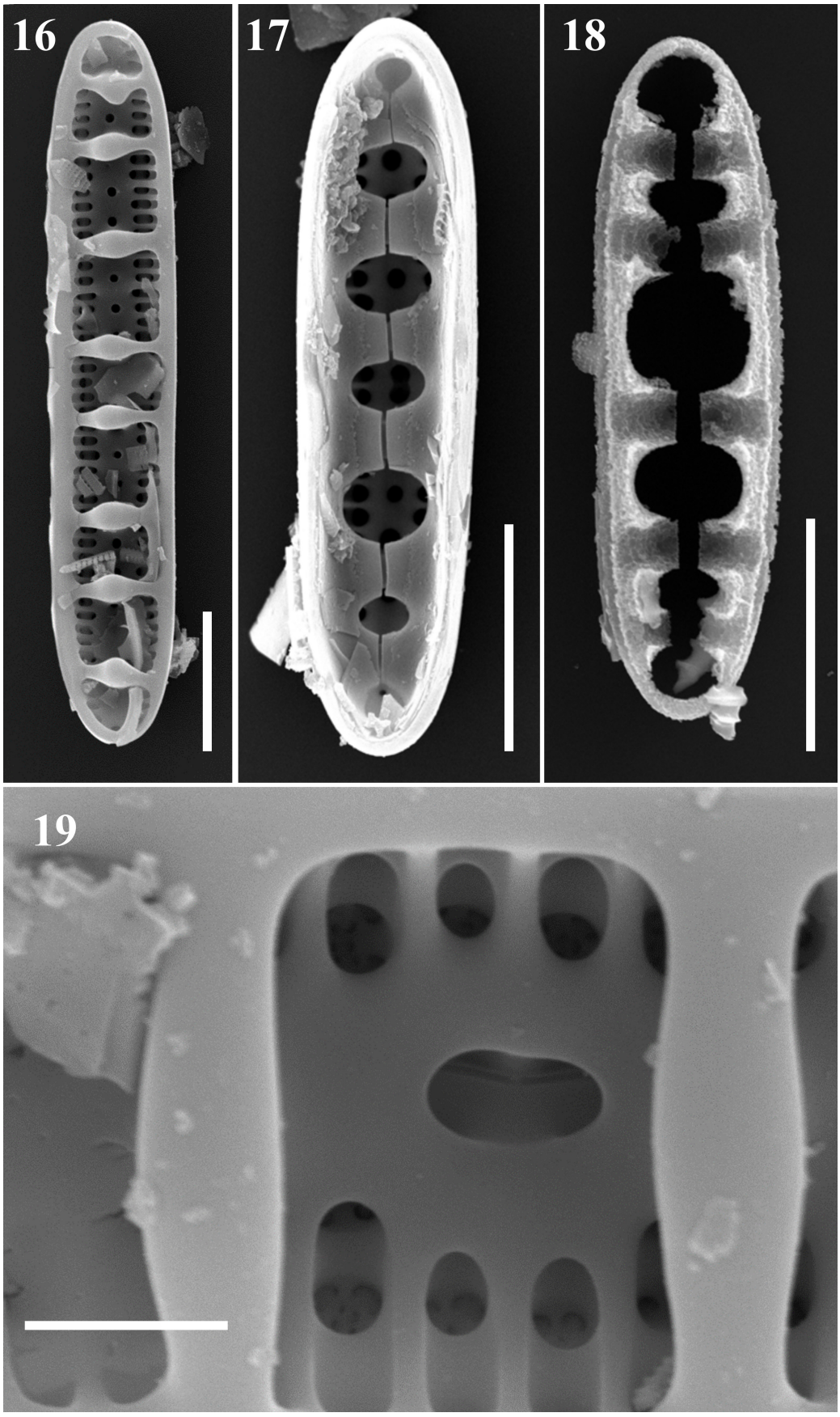
Discussion

Specimens observed in material from South Africa are inconsistent with those described as *D. costata* by Hustedt from Sumatra based on differences in valve shape and proportions. In comparing our specimens with those of depicted by Hustedt (1935, Plate IV, fig. 25) and published by Simonsen (1987, plate 282, figs 1–5) the two have similar outlines but differ in several features. *Denticula costata* has striae comprised of 1 or 2 areolae, the raphe is somewhat undulate, and the axial area is much wider than in the specimens from South Africa. Further, Hustedt does not mention, nor illustrate, the presence of Häutung valves in the material from Sumatra. However, this type of valve was reported by Fricke (in Schmidt 1906, plate 266, fig. 23) as "Anomale Schale, Gurtelbandseite" for *D. vanheurckii* from Java, a species quite distinct from the one in South Africa. None of the other *Denticula* species described from Sumatra appear to be conspecific with the specimens from South Africa. Based on these differences, we propose the specimens from South Africa to be a new species.

Based on similarities in raphe placement and complexity of the areolae and volae (lunate areolae structure), the specimens from South Africa clearly belong to the genus *Tetralunata*, originally described from Sumatra. In addition, septa interrupted in the middle and with swollen centers are also features shared between specimens from the two localities in the southern hemisphere. The specimens from South Africa do not appear to be similar to the genus *Denticula*, as typified by *D. tenuis* Kützing.



FIGURES 11–15. *Tetralunata schoemanii*, *sp. nov.* Scanning electron microscopy. Valve exterior. Figures 11, 12. Valve view of entire cell. Scale bars = 5 µm. Figs 13, 14. Higher magnification view of volae occluding areolae, on valve face and mantle, respectively. Scale bars = 1.5 µm. Fig. 15. Girdle view showing the girdle bands near the valve apex. Scale bar = 2.5 µm.



FIGURES 16–19. *Tetralunata schoemanii*, *sp. nov.* Scanning electron microscopy. Internal views. Fig. 16. Valve view with costae evident. Scale bar = 10 µm. Fig. 17. Valve with septum overlaying valve. Scale bar = 5 µm. Fig. 18. Septum. Scale bar = 5 µm. Fig. 19. High magnification view of the center of the valve showing proximal raphe ends. Scale bar = 1 µm.

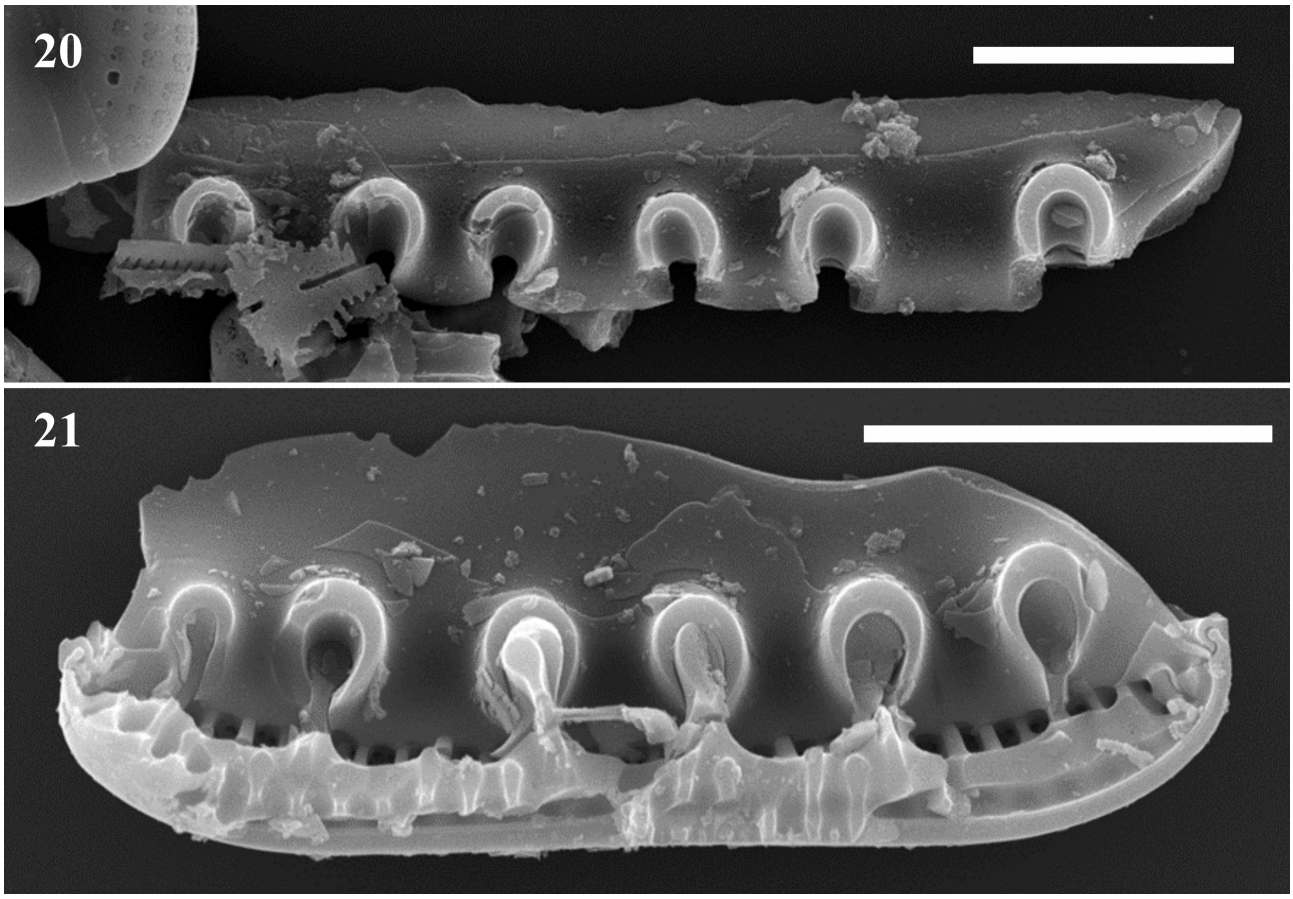


FIGURE 20, 21. *Tetralunata schoemanii*, *sp. nov.* Septum, cross section. Fig. 20. Septum only. Fig. 21. Valve with costa and septum overlaying the valve. Scale bars = 5 µm.

Based on the features of the South African specimens, we propose a new species of *Tetralunata*:

Bacillariophyta
Bacillariophyceae Haeckel 1878
Rhopalodiales D.G. Mann in Round *et al.* 1990
Epithemiaceae Karsten in Engler & Prantl 1928
Tetralunata Hamsher *et al.* 2014

Tetralunata schoemanii, *sp. nov.*
Figures 1–21

Description: Valves are linear in shape with apices tapered and narrowly rounded. Length ranges from 23–55 µm and breadth 7–10 µm. The raphe is placed medianly, with the raphe branches indistinct. The proximal ends terminate close to one another. Distally, the raphe branches extend onto the mantle at the apices. Costae are robust, 1–3 / 10 µm. Striae are parallel, composed of 4–6 areolae, and number 8–10 / 10 µm. Areolae clover-shaped with 4–8 c-shaped occlusions with those closer to the raphe having more occlusions and complexity. In girdle view, "capitate costae" are visible. Also evident in girdle view are Häutung valves, with a single new valve produced within a frustule. Häutung valves appear arched or undulate but otherwise are structured similar to vegetative valves.

Type:—SOUTH AFRICA**.** Lesotho, about 2 miles from the Maluti treks camp, situated on the banks of the Senqunyane River, on the road to Marakabei. Sides of hollow, cave-like cliffs below the road, damp rock faces. (Holotype COLO! 652039, here illustrated as Fig. 3; isotypes BM! 82423, South African National Diatom Collection! 84/1673).

Etymology:—Named in honor of F.R. Schoeman who collected and first reported this diatom.

The production of Häutung valves as initially reported was thought to be unique to the genus *Epithemia* (Thaler

1972; Sims 1983), although Fricke (1906 in Schmidt) had illustrated it in *Denticula vanheurckii* (=*T. vanheurckii* (Brun) Hamsher *et al.* 2014: 361). Häutung valves were first described by Geitler (1927) and later in greater detail by Thaler (1972) as a single valve produced within a frustule that more or less resembles the vegetative valves, distinguishing it from Innenschalen (e.g. Geitler 1980; Kociolek *et al.* 2011) and valves produced within cells of *Eunotia* Ehrenberg (1837: 44) (e.g. Von Stosch & Fecher 1979). These valves may have undulate valve faces, making them distinct in the light microscope. The reason for their production is uncertain, but they may be reactions to osmostic stress or serve as a resting stage (Thaler 1972).

Observations on the *Tetralunata* species from South Africa confirms their close relationship to *Epithemia*, as suggested by Hamsher *et al.* (2014). Evidence for a close relationship to *Epithemia* is evidenced with respect to the presence and similarity in structure in the volae, septa, septa that clasp the costate fibulae forming 'capitate costae', lack of a keel, no poroids in the girdle bands, frustules that are planar and not segment-like in their organization, and production of Häutung valves (Sims 1983, Kociolek *et al.* submitted).

In terms of biogeography, Kociolek (2019) had indicated *Tetralunata* was endemic to Indonesia. Reporting the genus in South Africa here for the first time, as a species endemic to southern Africa, expands the known distribution of the genus considerably. Our current understanding is that the members of the Rhopalodiales have verified fossil records that extend back 30 mya (Benson *et al.* 2012). Given the wide separation in both space and time of SE Asia and South Africa during the breakup of the continents (McLoughlin 2001), earth history dynamics would not be useful to identify a mechanism for this disjunct distribution. Further research will be necessary to attain an understanding of the separate locations for this rare genus.

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