

***Epithemia hirudiniformis* and related taxa  
within the subgenus *Rhopalodiella* subg. nov. in  
comparison to *Epithemia* subg. *Rhopalodia* stat nov.  
(Bacillariophyceae) from East Africa**

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**Abstract** – *Epithemia hirudiniformis* and three morphologically related taxa, described in *Rhopalodia* by O. Müller from material collected in East Africa at the end of the 19<sup>th</sup> and the beginning of the 20<sup>th</sup> century were re-evaluated and lectotypes designated. *Rhopalodiella* as a new subgenus is proposed which refines O. Müller's infrageneric classification and to which all these taxa belong. In addition, the type of *Epithemia rhopala*, described by Ehrenberg from Egypt, was studied to examine the assumed synonymy, introduced by Hustedt, with some of Müller's species. This study, using light and scanning electron microscopy, was not only based on historic material but also more recent material from Africa, including samples from the Island of Reunion from which the new species *Epithemia vandevijveri* is described. The distribution of *Epithemia* subg. *Rhopalodiella*, known to be restricted to tropical Africa, is discussed based on literature data and own observations. Corresponding to recent molecular-based studies, *Rhopalodia* is given a new status as subgenus.

**Classification / diatoms / East Africa / new species / new subgenera / *Rhopalodia* / taxonomy / typification**

## INTRODUCTION

*Rhopalodia* O. Müll. taxa are, like the representatives of the genus *Iconella* Jurily, formerly subsumed under the genus name *Surirella* Turpin (Ross, 1983; Jahn *et al.*, 2017), typical components of the East African Rift diatom flora. Of the about 100 new diatom taxa Müller described from this region (Müller, 1904a, 1904b, 1905, 1910; Jahn, 2002), 26 taxa are belonging to the family Rhopalodiaceae, a family recently subsumed under the order Surirellales (Ruck *et al.*, 2016a). Re-investigation of Müller's taxa was possible as a large part of the samples taken during the German "Nyassa-See- und Kinga-Gebirgs-Expedition" (Müller, 1904a, b) and considered as lost were discovered at the Botanical Museum Berlin-Dahlem (for details see Jahn, 1996, 2002); these samples were used to typify Müller's Surirellaceae taxa (Cocquyt & Jahn, 2005, 2007a, 2007b, 2007c, 2007d, 2014). Among the

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discovered material are also some samples – unfortunately not all – from the earlier Emin-Pascha-Expedition to Lake Victoria which were collected by Stuhlmann and which served for the description of the new genus *Rhopalodia* by Otto Müller. Unfortunately, the material Müller (1899) examined from saline ponds and springs in El Kab, located 20 km beneath Edfu in Upper Egypt on the East side, was not between the discovered material. Nevertheless, Otto Müller published good drawings and explicit descriptions of his new genus and species so that his taxa can be rediscovered in the mentioned samples or, if the respective samples do not contain this species, his drawings can be lectotypified and epitypes can be selected from among his other material in which he mentioned the species to occur.

The nine *Rhopalodia* taxa Müller (1899) described from saline ponds and springs of Egypt are all related to *Rhopalodia gibberula*, and belong to the infrageneric *Rhopalodia* “Sippe” *Epithemioideae*, one of the two sections Müller distinguished within the genus. The *Rhopalodia* taxa considered in the present paper are from the region of Lake Victoria (Müller, 1895) and Lake Malawi (Müller, 1904a) and belong to the second infrageneric “Sippe” Müller distinguished, the *Eurhopalodiae*. It concerns four species, *R. ascoidea*, *R. asymmetrica*, *R. hirudiniformis* and *R. vermicularis*, and three varieties of *R. hirudiniformis*. The differences between the two sections *Epithemioideae* and *Eurhopalodiae* as given by Müller (1895) are summarized in Table 1.

Table 1. The differences between the sections *Epithemioideae* (= subgenus *Rhopalodia*) and *Eurhopalodiae* (= subgenus *Rhopalodiella*) according to Müller (1895)

|                     | <i>Epithemioideae</i>   | <i>Eurhopalodiae</i>                                     |
|---------------------|---|--|
| Valve shape         | reniform, sickle- or clamp-shaped   | ascus like to irregular worm-shaped                      |
| Girdle view         | elliptic to linear  | club- to pear-shaped                                     |
| Transapical section | trapezoidal, roof-like with acute angle                                     |  |
| Symmetry            | bilateral symmetric, mirror symmetry of thecae against the transapical face | asymmetric, against the valve face or totally asymmetric |

As in our previous re-investigation of Müller’s material, e.g. *Iconella* and *Surirella* (= *Surirella* and *Cymatopleura* taxa) (Cocquyt & Jahn, 2005, 2007a, 2007b, 2007c, 2007d, 2014), we made Müller’s drawings and detailed descriptions of the taxa belonging to the section *Eurhopalodiae* more accessible by translating his original German descriptions and lectotypifying each taxon. We discussed which of Müller’s taxa can be accepted and placed them according to a current system within the genus *Epithemia*. Moreover, we give additional information on morphological characters using light microscopy and electron microscopy, based on historic as well as on modern samples. This investigation led to the description of a species new to science.

In addition to this paper, nomenclatural information will be made available via the AlgaTerra Information System (Jahn & Kusber, 2008) and PhycoBank (Kusber *et al.*, 2017).

## MATERIAL AND METHODS

Concerning the material used by O. Müller, which is kept at B (Botanical Museum Berlin-Dahlem), the original samples of Stuhlmann and Fülleborn were

oxidized with Hydrogen peroxide and embedded in Naphrax<sup>®</sup> to obtain new permanent microscopic slides. The samples studied in this paper are given below with collection information in accord with the list of collectors, collecting localities and details as published by Müller (1904a) and translated from German. Current names of the localities are put in square brackets. The last two numbers of the samples, refer to the numbering used by Müller (1904a).

- B 52 000017 [<http://herbarium.bgbm.org/object/B52000017>]: Lake Nyassa [Lake Malawi], Langenburg [Old Langenburg], plankton 2 km from the coast at 95-130 m depth, 1-2 m above the bottom. Calm. Collected by F. Fülleborn on 23 August 1899 at 10:00 am.
- B 52 000023 [<http://herbarium.bgbm.org/object/B52000023>]: Lake Nyassa [Lake Malawi], near the peninsula of Kanda [Tanzania], hillside North of Langenburg [Old Langenburg]. On gneiss boulders in the surge zone. Collected by F. Fülleborn in 1899. [Due to lake level rises at the end of the 19<sup>th</sup> century, the city of Langenburg was relocated in 1900 during the German colonial rule in the highland at 1500 asl. This new town, known as Neu-Langenburg, is the actual Tukuyu. The geocode for the original, Old Langenburg where Dr. Fülleborn collected algal material is 9.566667°S and 34.133333°E.]
- B 52 000026 [<http://herbarium.bgbm.org/object/B52000026>]: Lake Nyassa [Lake Malawi], Kota-Kota [Nkhotakota, Malawi], mud on the shore, soil and mud sample. Collected by Fülleborn on 1 February 1900.
- B 52 000032 [<http://herbarium.bgbm.org/object/B52000032>]: River Baka [River Mbaka], Konde-Land [Tanzania], plankton. Collected by Fülleborn in December 1898.
- B 52 000100 [<http://herbarium.bgbm.org/object/B52000100>]: Lake Victoria Nyansa [Lake Victoria], at Island Djuma [Mwanza region, Tanzania], upwelling, No.1, algae and protozoa. Collected by Stuhlmann on 13 March 1892.
- B 52 000101 [<http://herbarium.bgbm.org/object/B52000101>]: Lake Victoria Nyansa [Lake Victoria], upwelling, No.3, algae and protozoa. Collected by Stuhlmann on 13 March 1892.
- B 52 000102 [<http://herbarium.bgbm.org/object/B52000102>]: Usegua, Rukagara River (Mbusine) [Tanzania]. Collected by Stuhlmann on 8 August 1888.

Concerning Ehrenberg's material, the following materials from the Ehrenberg collection at BHUPM (Museum für Naturkunde, Berlin) were investigated:

- EC Mica strips 100501e orange, 100505d red, 100506a orange from Lake Garag, Fajum [Fayyum], Egypt.
- Drawing sheet 1135.

Modern materials and slides from the Cocquyt and the Van de Vijver collections are kept at the Botanic Garden Meise (BR). They include additional samples and/or slides from other localities in tropical Africa to obtain information on the species variability in different populations:

- CCA Luichi17-03-2003: Material from the Luichi River (Tanzania) (4.8988 °S and 29.7155 °E) near the bridge on road Kigoma-Malagarazi River at around 7.5 km from its flowing into Lake Tanganyika; phytoplankton collected with a phytoplankton net (mesh wide 10 µm) by

C. Cocquyt on 17 July 2003. Raw material was stained with Rose Bengal and embedded in Naphrax without any treatment.

- BM 479: Réunion (Island and region of France located in the Indian Ocean), Saint-Joseph Cascade de Grande Galet (Langevin River). Wet wall covered with mosses in the splash zone of the 30 m high waterfall (21.311833° and S 55.641889° E). Collected on 26 December 1999 by B. Van de Vijver.
- BM 481: Réunion (Island and region of France located in the Indian Ocean), Sainte-Rose, Anse des Cascades. Wet wall covered by mosses, behind the waterfall (21.184056° and S 55.826556° E). Collected on December 26, 1999 by B. Van de Vijver.

Wherever possible stable identifier for specimens according to Güntsch *et al.* (2016) are used. Names and nomenclatural novelties are databased in PhycoBank (Kusber *et al.*, 2017), additional data is published in the AlgaTerra Information System (Jahn & Kusber, 2017).

## RESULTS

Taxa belonging to the Müller's genus *Rhopalodia* have a complex valve structure and symmetry which is well explained by Müller in his description of this genus (Müller, 1895). A translation of some of his symmetry terminology in the present paper is, in our opinion, not superfluous. It allows for a better understanding of the translation we made of the original description of the *Rhopalodia* species belonging to the section ("Sippe") *Eurhopalodiae* discussed here (see also Table 1).

a) Pervalvar axis (Fig. 1): The ideal straight line cutting, from the centre of the cell in epithecal and hypothecal direction, through the central point of both valves; the bent axis is derived from the ideal axis.

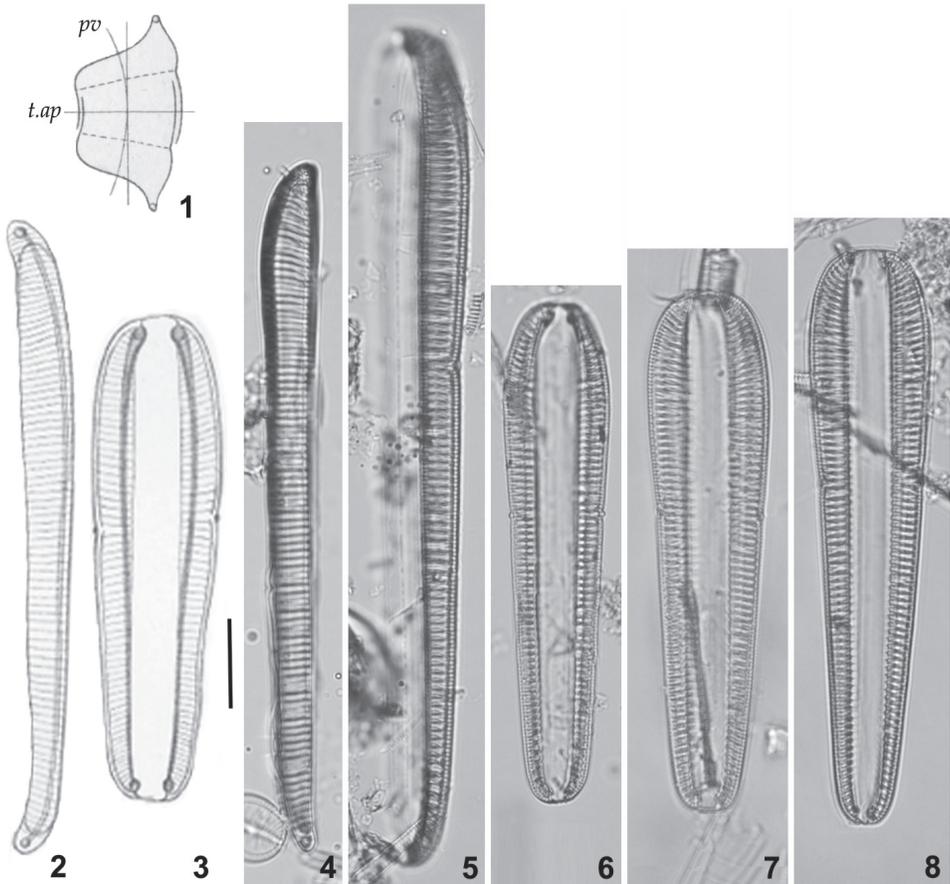
b) Apical axis: The ideal straight line sitting perpendicular (right-angle) on the pervalvar axis and going through the apical sides (apices) of the theca (entire cell wall); the bent axis is derived from the ideal axis.

c) Transapical axis (Fig. 1): The straight line which sits perpendicular (right-angle) on the intersection of both other axes (pervalvar and apical axis) and does not go through the apical wall of the theca.

d) Mirror-symmetry: taken against the face of a theca, which is divided by this face into two equal parts, which are perverted against each other. Perversion is present when one half is wrongly oriented to the homologous side axis of the other half (becoming negative).

e) Diagonal-symmetry: taken against the face of a theca, which is divided by this face into two equal parts, which are inverted against each other. Inversion is present when by half a turn of a half around one of its three dimension axes, both other dimension axes are inverted against the homologous axis of the other half (becoming negative).

In his description of new *Rhopalodia* taxa of the "Sippe" *Eurhopalodiae*, published on 19 November 1895, Müller (1895) treated the taxa according to their symmetry. The valves of *Rhopalodia ascoidea*, *R. hirudiniformis* and *R. vermicularis* have mirror-symmetry against the valve face and are asymmetric against the apical



Figs 1-8. *Epithemia* (subg. *Rhopalodiella*). 1. Symmetry axes on a transverse section of *E. hirudiniformis*, original drawing by Müller (1895); pv: pervalvar axis, t. ap: transapical axis. 2-8. *Epithemia* (subg. *Rhopalodiella*) *ascoidea*. 2-3. Original drawings by Müller (1895). 3. Lectotype. 4-8. LM, cells from epitype material B52 000026. 6. Valve representing the epitype on slide slide B 40 0042020. Scale bar = 20  $\mu\text{m}$ .

and transapical face. Valves of *Rhopalodia asymmetrica* possess an asymmetry against all three faces.

***Epithemia* subg. *Rhopalodia* (O. Müll.) Cocquyt, Kusber & R. Jahn, stat. nov.**

*Basionym*: *Rhopalodia* O. Müll. in *Bot. Jahrb. Syst.* 22: p. 57. 1895, nom. cons.

*Lectotype* (vide Boyer, 1927): *Rhopalodia gibba* (Ehrenb.) O. Müll.

- *Rhopalodia* [unranked] *Epithemioideae* O. Müll. in *Bot. Jahrb. Syst.* 22: p. 63. 1895.

*Note*: The new subgenus is in accordance with Art. 21B.4 of McNeill *et al.* (2012) in contrast to Müller's "Sippe" *Epithemioideae* which includes the type of *Rhopalodia* O. Müll.

*Registration*: <http://phycobank.org/100125>

Table 2. Overview of some morphometric characteristics of *Epithemia* taxa morphologically related to *E. hirudiniiformis*

| <i>Epithemia</i>                               | Reference        | Length<br>[ $\mu\text{m}$ ] | Width<br>Valve [ $\mu\text{m}$ ] | Width<br>Girdle [ $\mu\text{m}$ ] | Costae<br>in 10 $\mu\text{m}$ | Ribs in<br>between<br>costae | L/W<br>valve | L/W<br>girdle |
|--|------------------|-----------------------------|----------------------------------|-----------------------------------|-------------------------------|------------------------------|--------------|---------------|
| <i>E. ascoidea</i>                             | Müller 1895      | 126-150                     | 18                               | 22-28                             | 5.5-6.0                       | 1-2                          | —            | —             |
| <i>E. hirudiniiformis</i>                      | Müller 1895      | 67-130                      | 16-22                            | 25-54                             | 6                             | 1-3                          | 4.0-6.0      | 1.8-4.0       |
|  | Müller 1905      | 63-200                      | —                                | —                                 | —                             | —                            | —            | —             |
|  | Cocquyt 1998     | 58-113                      | 10-12                            | 24-35                             | 5                             | 2                            | —            | —             |
|  | Cocquyt unpubl.  | 85-254                      | —                                | 27.7-39.0                         | 5-6                           | 1-3                          | —            | 2.7-4.4(6.7)  |
| <i>R. hirudiniiformis</i><br>var. <i>parva</i> | Müller 1895      | 28-50                       | 12-14                            | 23-31                             | —                             | —                            | 2.8-3.6      | 1.0-1.7       |
|  | Müller 1905      | 44-55                       | —                                | —                                 | —                             | —                            | —            | —             |
|  | Cocquyt 1998     | 40-52                       | 8-10                             | 25-27                             | 7-8                           | 2                            | —            | —             |
| <i>E. vermicularis</i>                         | Müller 1895      | 122-227                     | 13-20                            | 26-37                             | 6                             | 4-2                          | 8.0-12.5     | 4.0-7.0       |
|  | Müller 1905      | 180-217                     | —                                | —                                 | —                             | —                            | —            | —             |
|  | Cocquyt 1998     | 220                         | 13                               | 46                                | 5                             | 2                            | —            | —             |
|  | Gasse 1986       | 200                         | 16.3                             | 45                                | 4                             | 2                            | 12.3         | 4.4           |
|  | Hustedt 1949     | — 360                       | —                                | —                                 | —                             | —                            | —            | —             |
| <i>E. asymmetrica</i>                          | Müller 1895      | 80-185                      | 12-13                            | 14-18                             | 6                             | 1-2                          | —            | —             |
|  | Müller 1905      | 143-200                     | —                                | —                                 | —                             | —                            | —            | —             |
| <i>E. rhopala</i>                              | Müller 1895      | 94.1-170.5                  | —                                | 28.2-30.6                         | 4.5-5.0                       | —                            | —            | 3.1-3.7       |
| <i>E. vandevijveri</i>                         | This publication | 99.4-140.7                  | —                                | 29-40                             | 4.7-5.5                       | —                            | —            | 3.0-4.6       |

***Epithemia gibba*** (Ehrenb.) Kütz., *Kieselschal. Bacill.*, p. 35. 1844.

*Basionym*: *Navicula gibba* Ehrenb. in *Abh. Königl. Akad. Wiss. Berlin* 1831: p. 80. 1832.

*Synonym*: *Rhopalodia gibba* (Ehrenb.) O. Müll. in *Bot. Jahrb. Syst.* 22: p. 65. 1895.  
*Lectotype* (vide Jahn & Kusber, 2004): [icon] Part of Ehrenberg's drawing sheet No. 560a in BHUPM.

Müller (1895) published several occurrences of this widely distributed species.

***Epithemia* subg. *Rhopalodiella*** Cocquyt, Kusber & R. Jahn, **subg. nov.**

- *Rhopalodia* [unranked "Sippe"] *Eurhopalodiae* Müller (1895), nom. inval. according to Art. 21.3 of McNeill *et al.* (2017).

*Holotype* (designated here): *Epithemia hirudiniformis* (O. Müll.) Rimet *et al.* (vide infra).

*Registration*: <http://phycobank.org/100126>

*Diagnosis*: The valve morphology resembles *Epithemia* subg. *Rhopalodia* except for its symmetry. Taxa of *Epithemia* subg. *Rhopalodiella* are ascus like to irregular worm-shaped in valvar view and asymmetric against the apical and transapical face. The valve shape in girdle view is club- to pear-shaped, symmetrical or asymmetrical. *Epithemia* subg. *Rhopalodiella* comprises African, mostly tropical East-African, freshwater taxa.

***Epithemia ascoidea*** (O. Müll.) Cocquyt & R. Jahn, **comb. nov.** **Figs 2-8**

*Basionym*: *Rhopalodia ascoidea* O. Müll. in *Bot. Jahrb. Syst.* 22: p. 66, pl. 1, figs 31-33; pl. 2, figs 8, 9. 1895.

*Lectotype* (designated here): [Icon!] Pl. 2 fig. 9 in *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 22. 1895; given here as Fig. 3.

*Epitype* (designated here): slide B 40 0042020, Botanical Museum Berlin-Dahlem (B) [<http://herbarium.bgbm.org/object/B400042020>]; the valve representing the epitype is illustrated as Fig. 6.

*Locality of the epitype*: Nkhotakota, Lake Malawi, Malawi, (sample B 52 0000026).

*Habitat*: mud on the shore of Lake Malawi, on stalks.

*Registration*: <http://phycobank.org/100127>

Translated from German, Müller's description reads: "Pervalvar axis bent, heteropolar; apical axis curved, isopolar; transapical axis heteropolar. Valve side ascus-like, towards one pole of the apical axis broader developed (the head pole) than towards the other pole (the foot pole), with ventrally curved, and rounded apices. The dorsal side of the valve is more convexly curved, the ventral side weakly curved or straight, both sides not undulating or irregularly bent. Raphe strongly dorsal, the central raphe endings displaced towards the head pole. Girdle side club-shaped with rounded corners; the sides (keel with raphe) only curved near the poles, for the rest forming a straight line. Central raphe endings somewhat sunken, the terminal raphe endings located on the strongly distinct paravalvar apical costae. Costae 5.5-6.0 in 10 µm; in between the costae 1-2 fine, delicately dotted ribs. Length 126-150 µm. Broadest width of the valve 18 µm, of the girdle view 22-28 µm. Lives in Mhonda (Unjura), in the catchment area of the Wami, common (Stuhlmann); in Lake Victoria Nyansa [Lake Victoria] near Bukoba under *Cladophora* (Stuhlmann); in the Rukagara river near Mbusine (Usegua) in calm water (Stuhlmann).

Differs from *R. vermicularis* by the smooth sides of the valves, which are not irregularly curved, and in the stronger ventrally curved head pole.”

In 1905, Müller added the distribution in the area of Lake Malawi: “Lake Nyassa near Langenburg, surface plankton (1, 6, 7, 12, 18), near Wiedhafen, surface plankton (9), near Langenburg in the plankton at 5-8 m depth (13), near Langenburg at 40-70 m depth (14), near Langenburg in mud at 200 m depth (24), near Likoma at 333 m depth (25), in mud of Kota-Kota, shore (26), in the river Baka, plankton (32), in Lake Malombe (38), in Uluguru mountains at Mdansa (48), Uluguru mountains at 1000m high (50), in Lake Rukwa, Uhehe? (57), in Lake Rukwa, Ussangu ? (58).”

*Distribution*: This taxon is reported by Müller from the region of Lakes Victoria and Malawi only.

***Epithemia asymmetrica* (O. Müll.) Cocquyt & R. Jahn, comb. nov.      Figs 9-14**

*Basionym*: *Rhopalodia asymmetrica* O. Müll. in *Bot. Jahrb. Syst.* 22: p. 68, pl. 1, figs 49, 50; pl. 2, figs 12, 13, 20. 1895.

*Lectotype* (designated here): [Icon!] Pl. 2 fig. 12 in *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 22. 1895; given here as Fig. 9.

*Epitype* (designated here): slide B 40 0042021 [<http://herbarium.bgbm.org/object/B400042021>], Botanical Museum Berlin-Dahlem (B); the valve representing the epitype is illustrated as Figs 11-13.

*Locality of the epitype*: Lake Malawi, near the peninsula of Kanda [Tanzania], hillside North of Langenburg [Old Langenburg], (sample B 52 0000023).

*Habitat*: on gneiss boulders in the surge zone of Lake Malawi.

*Registration*: <http://phycobank.org/100129>

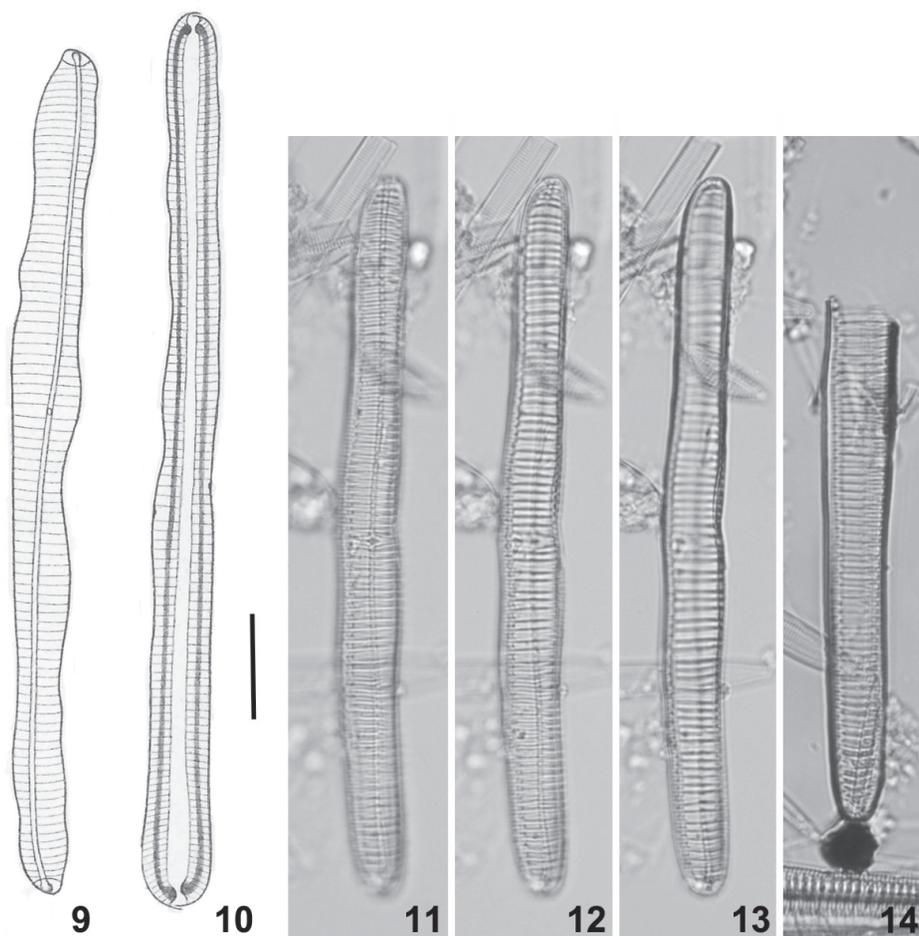
Translated from German, Müller’s description reads: “Pervalvar axis hardly bent, heteropolar. Apical axis irregularly curved, heteropolar; transapical axis heteropolar. Valve side irregularly baton shaped, with bluntly or sharpened rounded apices, a broader head pole not or only a little bit distinguishable. The valve side irregularly undulated. The raphe runs in the axial axis or slightly diagonal. Girdle side linear, not significantly broader than the valve side, the side (keel with raphe) irregularly undulated: a broader head pole can be distinguished. The central raphe endings on both sides not always at the same height, terminal raphe endings located on the more distinct paravalvar apical costae. Costae 6 in 10  $\mu\text{m}$ , in between 1-2 finer, delicately dotted ribs. Length 80-185  $\mu\text{m}$ , width valve 12-13  $\mu\text{m}$ , girdle view 14-18  $\mu\text{m}$ . Lives in Victoria Nyansa [Lake Victoria] near Bukoba among *Cladophora* (Stuhlmann).”

In 1905, Müller added the distribution in the area of Lake Malawi: “in the river Mbasi (34)”.

*Remarks*: No other reports of this taxon are found in the literature. This taxon was only sporadically observed in sample B 52 0000023. The valve designated here as epitype fits the dimensions given by Müller, e.g., length of 140  $\mu\text{m}$  and width of 12.1  $\mu\text{m}$ , as do the number of costae in 10  $\mu\text{m}$  (5.5-6.0 costae). There are 11-12 striae in 10  $\mu\text{m}$ .

***Epithemia hirudiniformis* (O. Müll.) Rimet, D.G. Mann, R. Trobajo, J. Zimm. & R. Jahn in *Fottea* 18(1). 2018.      Figs 15-30, 59-76**

*Basionym*: *Rhopalodia hirudiniformis* O. Müll. in *Bot. Jahrb. Syst.* 22: p. 67-68, pl. 1, figs 40-46, 51-52; pl. 2, figs 15-17. 1895.



Figs 9-14. *Epithemia* (subg. *Rhopalodiella*) *asymmetrica*. **9-10**. Original drawings by Müller (1895). **9**. Lectotype. **11-14**. LM, cells from epitype material B 52 000023. **11-14**. Valve representing the epitype on slide B 40 0042021 from material taken at different foci. Scale bar = 20  $\mu$ m.

*Lectotype* (designated here): [Icon!] Pl. 2 fig. 15 in *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 22. 1895; given here as Fig. 16.

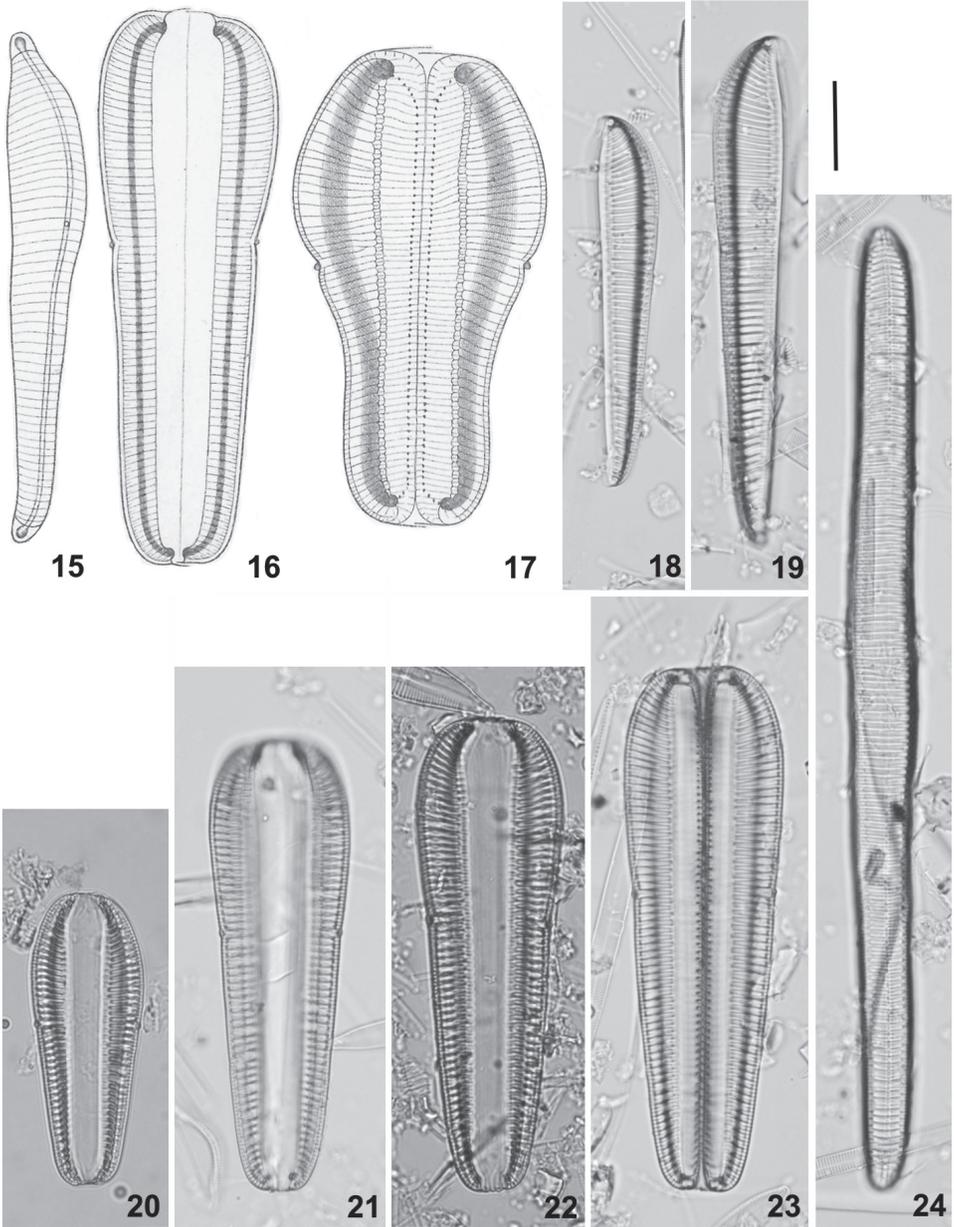
*Epitype* (designated here): slide B 40 0042022, Botanical Museum Berlin-Dahlem (B) [<http://herbarium.bgbm.org/object/B400042022>]; the valve representing the epitype is illustrated as Fig. 21.

*Locality of the epitype*: Lake Malawi, near the peninsula of Kanda [Tanzania], hillside North of Langenburg [Old Langenburg], (sample B 52 0000023).

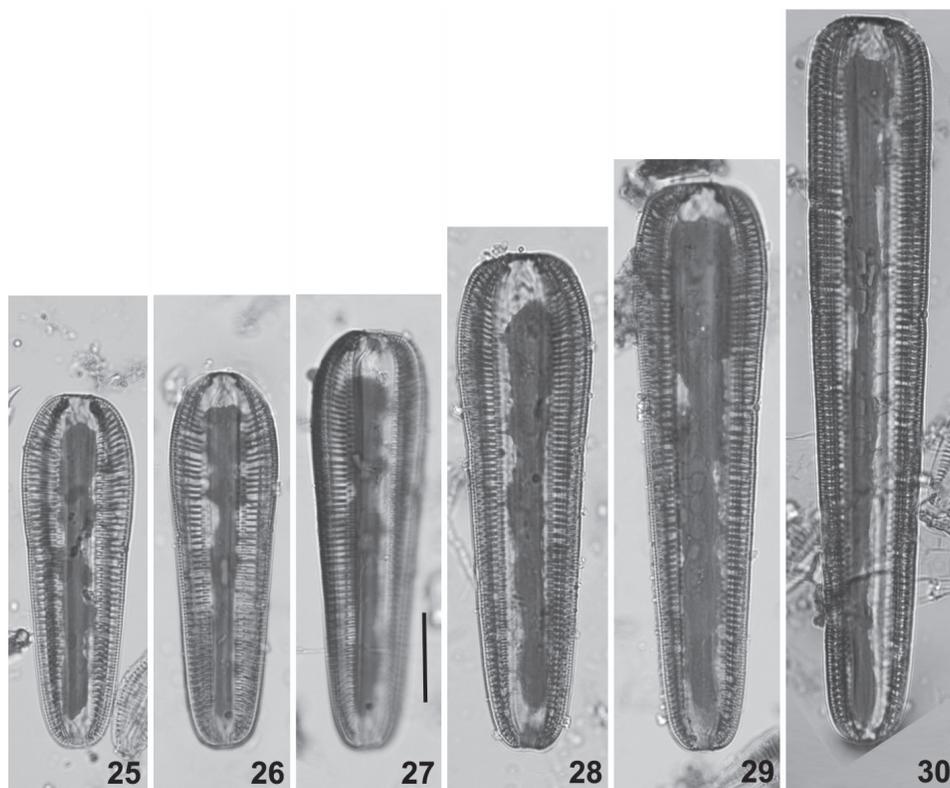
*Habitat*: on gneiss boulders in the surge zone of Lake Malawi.

*Registration*: <http://phycobank.org/100131>

*Synonyms*: *Rhopalodia hirudiniformis* var. *capiticonstricta* O. Müll.; *Rhopalodia hirudiniformis* var. *pediconstricta* O. Müll.; *Rhopalodia hirudiniformis* var. *parva* O. Müll.

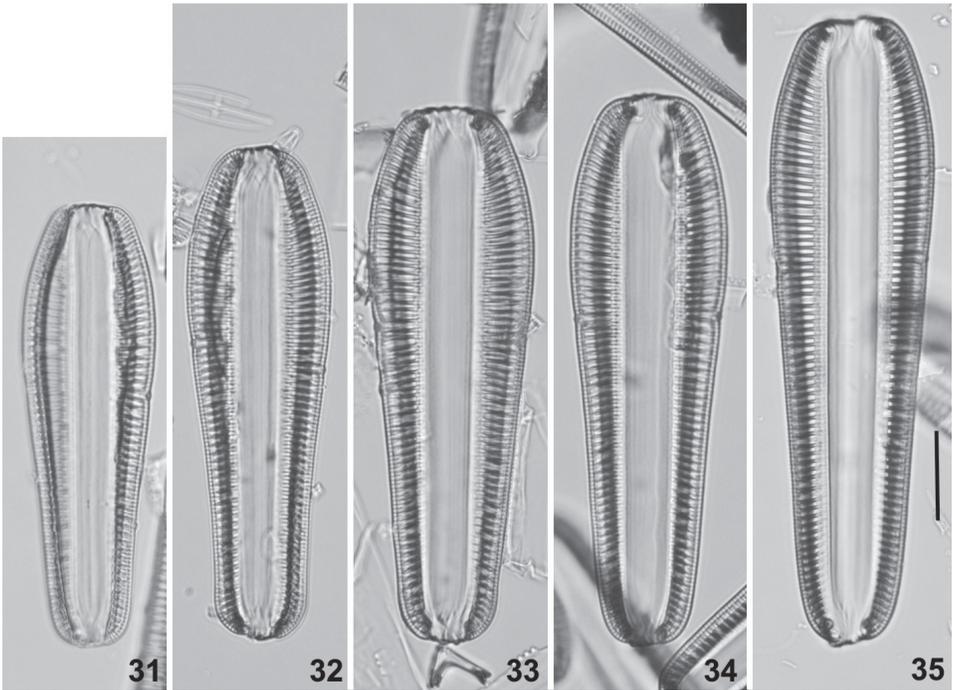


Figs 15-24. *Epithemia* (subg. *Rhopalodiella*) *hirudiniformis*. **15-17**. Original drawings by Müller (1895). **16**. Lectotype. **18-24**. LM, cells from epitope material B 52 0000023. **21**. Valve representing the epitope on slide B 40 0042022. Scale bar = 20 µm.



Figs 25-30. *Epithemia* (subgen. *Rhopalodiella*) *hirudiniformis*. LM. Slide CCA Luichi17-03-2003, material from the Luichi River, Tanzania, phytoplankton net 10  $\mu\text{m}$ , 17 July 2003. Girdle views showing the cell variability and the single plate-like plastid with highly lobed margins. Scale bar = 20  $\mu\text{m}$ .

Translated from German, Müller's description reads: "Pervalvar axis bent, heteropolar; apical axis irregularly curved, heteropolar; transapical axis heteropolar. Valve side leech shaped, much wider near the head pole of the apical axis, both apices slightly or not at all ventrally curved. The dorsal side of the valve strongly convex at the head pole, irregularly swollen at the foot pole, the ventral side nearly straight or slightly undulated and curved. Raphe strongly dorsal, the central raphe endings concurrently displaced towards the head pole, the terminal raphe endings located on the strongly distinct paravalvar apical costae. Girdle view pear shaped, near the head pole more or less wide, sometimes strongly swollen, near the foot pole unevenly narrower. The sides (keel with raphe) form on the head pole a strongly convex, now and then almost a circular line, which sinks towards the central raphe endings, and from there is concavely bent towards the foot pole. Costae 6 in 10  $\mu\text{m}$ , in between 1-3 finer, delicately dotted ribs. Length 67-130  $\mu\text{m}$ . Largest width of the valve 16-22  $\mu\text{m}$ , of the girdle view 25-54  $\mu\text{m}$ . Length-to-width ratio: valve 1:4 to 1:6, girdle 1:1.8 to 1:4. – Lives in Victoria Nyansa [Lake Victoria] near Bukoba among *Cladophora* (Stuhlmann); in the River Rukagara near Mbusine in calm water (Stuhlmann); in the Tararo Stream near Undussuma at 1051 m (Stuhlmann). – Differs

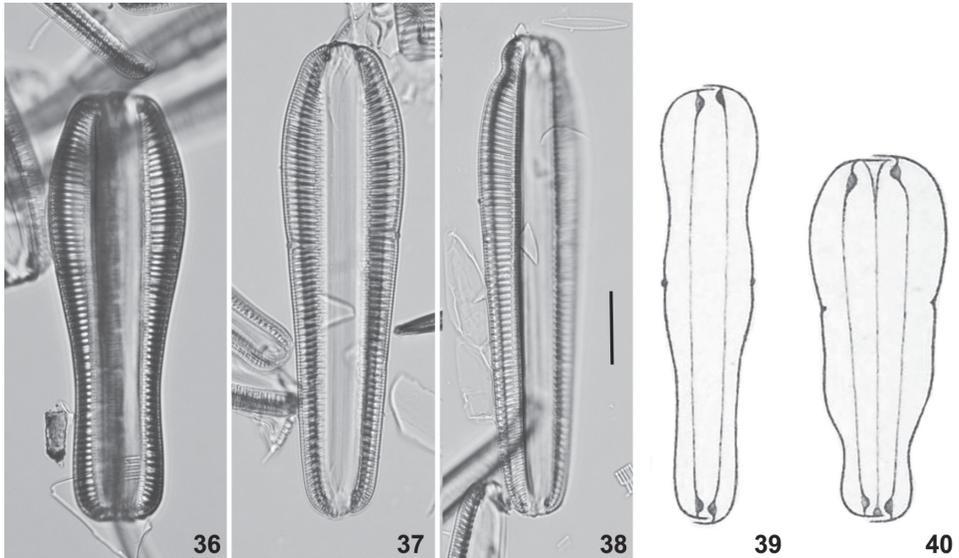


Figs 31-35. *Epithemia vandevijveri* sp. nov. LM. Material from Reunion. **32.** Valve representing the holotype on slide BR 4493. **31-35.** Girdle views from type material BM 481 showing the cell variability and the diminishing series. Scale bar = 20  $\mu$ m.

from *R. vermicularis* by its pear shape in girdle view, the much stronger bulging and curvation of the valve near the head pole, and the smaller total length and length to width ratio.”

In 1905, Müller added the information that this taxon lives partly on stalks, partly free, and its distribution in the area around Lake Malawi: “Lake Nyassa near Langenburg, surface plankton (6, 18), near Wiedhafen, surface plankton (9), near Langenburg in the plankton at 40-70 m depth (14), 80-90 m depth (16), 95-130 m depth (17), near the peninsula Kanda, in the surge zone (23), near Langenburg in mud at 200 m depth (24), in mud of Kota-Kota, on the shore (26 m), near Langenburg, pool (27), near Wiedhafen, pool (29), in the river Lumbira (31), in the river Baka, plankton (32), in the river Mbasi (33, 34), in the river Songwe (36), in Lake Malombe (37, 39), in Lake Malombe, plankton (40), in the river Rufidji, Pangani rapids (51), in Utengule, watercourse (53), in Lake Rukwa, Uhehe? (57).”

**SEM:** First SEM pictures of this taxon were presented by Güttinger (1994-1996) of material from Lake Victoria he indicated as *Rhopalodia* “*hirundiniformis*” [sic] (2.07.02-5). On the outside of the valve face the areolae are simple rounded openings. Two rows, rarely one row, of areolae are present between the costae. Details of the central raphe endings are not well discernible, but they seem straight. The central nodule is slightly sunken. Small spines can be observed on the raphe keel but no detail is given.

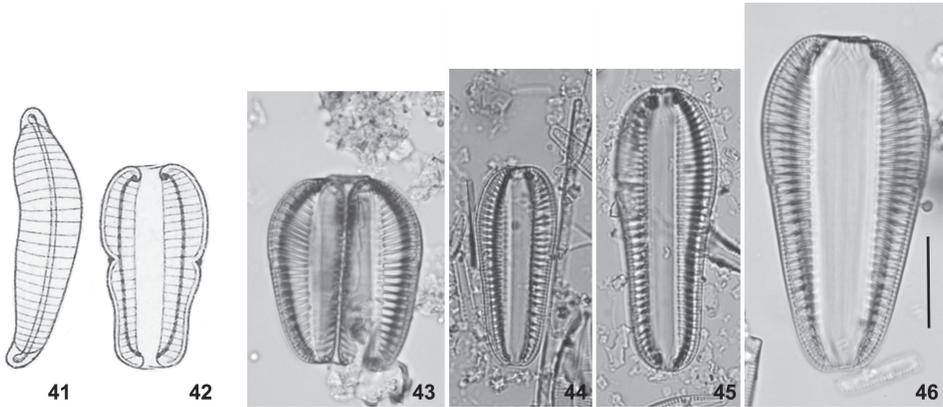


Figs 36-40. *Epithemia vandevijveri* sp. nov. and varieties of *Rhopalodia hirudiniformis*. 36-38. LM. *Epithemia vandevijveri*, material BM 481 from Reunion. 37-38. Girdle views showing constriction of the valve near the head pole. 39-40. Original drawings by Müller (1895). 39. Lectotype of *Rhopalodia hirudiniformis* var. *capiticonstricta*. 40. Lectotype of *Rhopalodia hirudiniformis* var. *pediconstricta*. Scale bar = 20  $\mu$ m.

Own SEM observations (Figs 59-76) from Müller's material (samples B 52 0000023, B 52 0000038, B 52 0000100): External view: striae composed of a double row of complex areolae (Fig. 69). Areolae occluded by flap-like occlusions only opening by crescent shaped slits, often 4 to 5 slits around a central slit giving a flower-like aspect to the areolae (Figs 63, 69-70). Eroded areolae rectangular with rounded corners (Fig. 68). Virgae raised forming transapical rib-like structure on the valve face (Figs 66-69, 73). Vimines well developed especially near the raphe forming longitudinal lines parallel to the raphe (Figs 61-62). Raphe straight, eccentric, not raised on a keel (Figs 64, 66-68). Flattened spines present at one side along the raphe at irregular distances (Fig 61), the largest ones near the head pole (Figs 67-68). On the edge of the valve slight elevations of the valve wall present at the end of the virgae, but not developed into spines (Figs 72-73). Central area formed by two striae shortened by one or two areolae (Fig. 62). Central raphe endings upwards on the raised part of the central nodule, expanded (Figs 62, 66). Terminal raphe endings straight, slightly expanded (Fig. 64). Small poroids present near the head pole, irregularly placed and continuing for a short distance on the valve edge (Fig. 76). No special pores observed that are responsible for the mucilage excretion forming stalks.

Girdle bands open. Valvocopula and the two other girdle bands without any perforation or ornamentation (Figs 59, 60, 65, 67, 71, 72, 75, 76).

*Distribution* (including all infraspecific taxa listed above as synonyms): Besides Lakes Malawi, Malombe, Rukwa and Victoria, Rivers Baka, Lumbira, Mbasi, Rufidji, Rukagara, Songwe and the Stream Tataro (Müller, 1895, 1905) this species



Figs 41-46. *Rhopalodia hirudiniformis* var. *parva*. 41-42. Original drawings by Müller (1895). 42. Lectotype. 43-47 LM. 43, 46. Girdle views from epitype material B 52 0000032. 46. Cell representing the epitype on slide B 40 0042024. 44-45. Cells from material B 52 0000023. Scale bar = 20  $\mu\text{m}$ .

was also reported from Lake Edward (Van Meel, 1954), Lake Malawi (West, 1907; Van Meel, 1954), Lake Tanganyika (West, 1907; Van Meel, 1954; Kufferath, 1956; Ross, 1983; Mpawenayo, 1986, 1996; Caljon, 1987; Cocquyt, 1991, 1998; Cocquyt *et al.*, 1991, Caljon 1992, Caljon & Cocquyt 1992), Lake Victoria (West 1907, Van Meel 1954), Burundi (Caljon, 1988; Mpawenayo, 1996), Congo (Zaire), Kenya, Madagascar (Metzeltin & Lange-Bertalot, 2002), Malawi (Van Meel, 1954), Mayotte (Frédéric Rimet), Reunion (this publication), Rwanda, Tanzania (Van Meel, 1954), Zimbabwe (Van Meel, 1954).

*Remark:* The epithet name of *Rhopalodia hirudiniformis* is often wrongly spelled as “*hirundiniformis*”. In 1954 this erroneous spelling appeared for the first time (Van Meel, 1954) and was later used by several authors (e.g., Cocquyt, 1998; Güttinger, 2002, website BRM).

Although *Rhopalodia hirudiniformis* var. *capiticonstricta*, var. *pediconstricta* and var. *parva* are here treated as taxonomic synonyms, for nomenclatural reasons they are here lectotypified. This is done as with the lectotypification of the varieties and forms of *Surirella engleri* O. Müller (Cocquyt & Jahn, 2007b). Only for the variety *parva* an epitype was designated here as it was the only variety we could observe in the available material Müller studied.

***Rhopalodia hirudiniformis* var. *capiticonstricta*** O. Müll. in *Bot. Jahrb. Syst.* 22: p. 68, pl. 1, fig. 47. 1895. **Fig. 39**

*Lectotype* (designated here): [Icon!] Pl. 1, fig. 47 in *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 22. 1895; given here as Fig. 39.

*Type locality:* Lake Victoria near Bukoba, actually located in Tanzania at around 1.34° S and 31.8° E.

*Habitat:* plankton.

*Registration:* <http://phycobank.org/100132>

*Synonyms:* *Rhopalodia dispar* Prudent (1906, p. 83) and *Epithemia dispar* (Prudent, 1906) according to F.W. Mills 1934, p. 654 (VanLandingham, 1978).

Müller writes (1895): “The side (keel with raphe), at the poles of the paratransapical axis, between the head pole of the apical axis and the central raphe endings, is concavely bent in girdle view so that this side looks swollen several times. Length 120  $\mu\text{m}$ , width of the girdle, largest 30  $\mu\text{m}$ , smallest 17  $\mu\text{m}$ . Lives in Bukoba, Victoria Nyansa (Stuhlmann).”

In material BM481 from Réunion, one valve was observed with a constriction near the head pole (Fig. 37) although the constriction is different from Müller’s drawing of *R. hirudiniformis* var. *capiticonstricta*. The constriction in the Réunion material concerns an accidental deformation during the valve formation and has no taxonomic value; valve depicted in Fig. 36 has only a slight indentation near the head pole. This let us suppose that this is also the case for the valve Müller described as *R. hirudiniformis* var. *capiticonstricta*.

Remarks: No others reports found.

***Rhopalodia hirudiniformis* var. *pediconstricta*** O. Müll. in *Bot. Jahrb. Syst.* 22: p. 68, pl. 1, fig. 48. 1895.

**Fig. 40**

*Lectotype* (designated here): [Icon!] Pl. 1, fig. 48 in *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 22. 1895; given here as Fig. 40.

*Type locality*: Lake Victoria near Bukoba, actually located in Tanzania at around 1.34° S and 31.8° E.

*Habitat*: plankton.

*Registration*: <http://phycobank.org/100133>

Müller writes (1895): “The concave curvature of the side of the girdle side, at the poles of the paratransapical axis, is located between the central raphe endings and the foot pole of the apical axis. Length 100  $\mu\text{m}$ , width of the girdle side, broadest 48  $\mu\text{m}$ , narrowest 19  $\mu\text{m}$ . Lives in Bukoba, Victoria Nyansa (Stuhlmann).”

Remarks: No others reports found.

The same remark as given for *R. hirudiniformis* var. *capiticonstricta* can be made here. However during our investigation no valve with an indentation near the foot pole could be observed.

***Rhopalodia hirudiniformis* var. *parva*** O. Müll. in *Bot. Jahrb. Syst.* 22: p. 68, pl. 1, figs 26-30; pl. 2, figs 18, 19. 1895.

**Figs 41-46**

*Lectotype* (designated here): [Icon!] Pl. 2 fig. 19 in *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 22. 1895; given here as Fig. 42.

*Epitype* (designated here): slide B 40 0042024, Botanical Museum Berlin-Dahlem (B) [<http://herbarium.bgbm.org/object/B400042024>]; the valve representing the epitype is illustrated as Fig. 46.

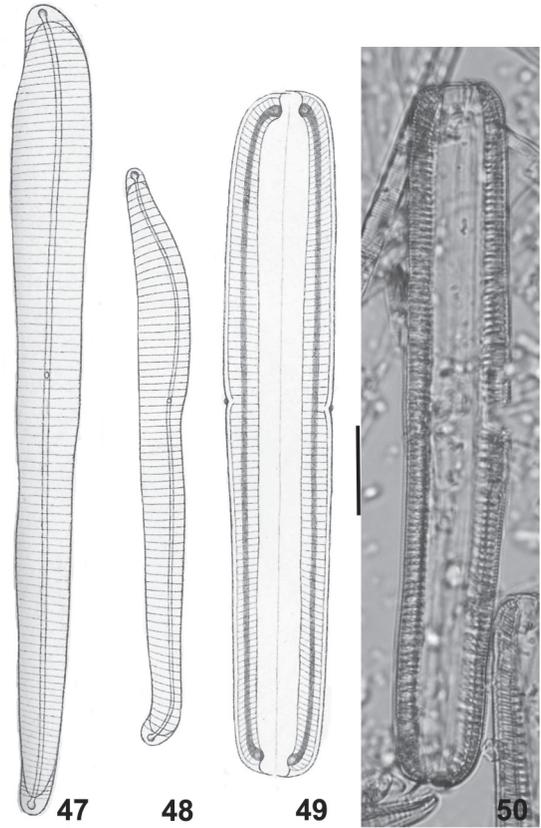
*Locality of the epitype*: the river Baka, Konde-Land [Tanzania], (sample B 52 0000032).

*Habitat*: plankton.

*Registration*: <http://phycobank.org/100134>

Müller writes (1895): “Differs from the type in the smaller size and the even more irregular shape of the valve margins. Length 28-50  $\mu\text{m}$ , largest valve width 12-14  $\mu\text{m}$ , girdle side 23-31  $\mu\text{m}$ , length-to-width ratio: valve 1:2.8 to 1:3.6, girdle side 1:1 to 1:1.7. Lives in Bukoba, Victoria Nyansa (Stuhlmann), in Tararo stream near Undussuma 1051 m (Stuhlmann).”

In 1905, Müller added the distribution in the area of Lake Malawi: “near Langenburg, surface plankton (6, 18), near Wiedhafen, surface plankton (9), near the



Figs 47-50. *Epithemia* (subg. *Rhopalodiella*) *vermicularis*. **47-49**. Original drawings by Müller (1895). **47**. Lectotype of *Rhopalodia vermicularis*. **50**. Girdle view, cell representing the epitype on slide B 40 0042023 from epitype material B 52 0000023. Scale bar = 20  $\mu\text{m}$ .

peninsula Kanda, in the surge zone (23), near Langenburg, pool (27), in the river Baka, plankton (32).”

*Remarks*: This taxon was reported from Burundi (Mpawenayo, 1996), Tanzania, Zimbabwe, Lake Malawi (Van Meel, 1954), Lake Tanganyika (Van Meel, 1954; Kufferath, 1956; Mpawenayo, 1986, 1996; Cocquyt, 1998) and Lake Victoria (Van Meel, 1954).

***Epithemia vermicularis* (O. Müll.) Cocquyt & R. Jahn, comb. nov. Figs 47-50**

*Basionym*: *Rhopalodia vermicularis* O.Müll. in *Bot. Jahrb. Syst.* 22: p. 67, pl. 1, figs 34-39; pl. 2, figs 10, 11, 14. 1895.

*Lectotype* (designated here): [Icon!] Pl. 2 fig. 11 in *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 22. 1895; given here as Fig. 49.

*Epitype* (designated here): slide B 40 0042023, Botanical Museum Berlin-Dahlem (B) [<http://herbarium.bgbm.org/object/B400042023>]; the valve representing the epitype is illustrated as Fig. 50.

*Locality of the epitype*: Lake Nyassa near the peninsula Kanda, surge zone on stalks, (sample B 52 0000023).

*Habitat*: surge zone in Lake Malawi, on stalks.

*Registration*: <http://phycobank.org/100135>

Translated from German, Müller's description reads: "Pervalvar axis curved, heteropolar; apical axis irregularly bent, heteropolar; transapical axis heteropolar. Valve side worm like, wider towards the head pole of the apical axis; the pole where this apex arise is often straightly erected or at least less bent ventrally compared to the apex of the foot pole. The dorsal side of the valve is more or less convexly curved and irregularly undulated bent, the ventral side is nearly straight, with minor irregular bendings. Raphe strongly dorsal, central raphe endings concurrently displaced towards the head pole, the terminal raphe endings located on the strongly distinct paravalvar apical costae. Girdle view linear with rounded, obtuse corners or at least club shaped, swollen in the direction of the head pole; the sides (keel with raphe) not bent pear shaped, from an almost (approach a) straight line, only the central raphe endings are somewhat sunken in. Costae 6 in 10  $\mu\text{m}$ , with 4-2 finer, delicately dotted ribs. Length 122-227  $\mu\text{m}$ . Broadest width of the valve 13-20  $\mu\text{m}$ , of the girdle view 26-37  $\mu\text{m}$ . Length to width ratio: valve 1:8 to 1:12.5; girdle 1:4 to 1:7. Lives in Victoria Nyansa [Lake Victoria] near Bukoba among *Cladophora* (Stuhlmann); in the River Rukagara near Mbusine in calm water (Stuhlmann). Differs from *R. ascoidea* in the irregularly bent sides of the valve and in the erected apex of the head pole; differs from *R. hirudiniformis* in the more slender shape and in the smaller swellings near the head pole, the larger total length and length to width ratio."

In 1905, Müller added the distribution in the area of Lake Malawi: "in Lake Nyassa near Wiedhafen, surface plankton (9), near the peninsula Kanda, surge zone on stalks (23), in mud of Kota-Kota, shore (26 m), in the river Baka, plankton (32), in the river Rufidji, Pangani rapids (51)"

*Remarks:* This taxon was reported from Ethiopia (Gasse, 1986), Kenya (Bachmann, 1938; Gasse, 1986), Rwanda (Gasse, 1986), Tanzania (Van Meel, 1954, Gasse, 1986), Uganda (Gasse, 1986), Zimbabwe, Lake Malawi (West, 1907) and Lake Victoria (West, 1907).

*Ecology:* According to Gasse (1986) this taxon "is a limnobiontic species which lives as a planktonic or a periphytic form in numerous lakes of moderate size. It seems to be a widely tolerant species with regard to the mineral content and alkalinity, since it was found in fresh waters and in hyper alkaline lakes as well. It lived in carbonate-bicarbonate waters, and seems to be indifferent to the cationic composition".

***Epithemia rhopala* (Ehrenb.) Cocquyt & R. Jahn, comb. nov. Figs 51-58**

*Basionym:* *Surirella rhopala* Ehrenb., *Mikrogeologie, Atlas*: pl. XXXIII: I: fig. 19; pl. XXXV A: X: fig. 3. 1854.

*Synonym:* *Rhopalodia rhopala* (Ehrenb.) Hust.

- *Surirella rhopala* Ehrenb. in *Ber. Bekanntm. Verh. Königl. Preuss. Akad. Wiss. Berlin* 1852: table to p. 620. 1852, nom. nud. (Art. 50B, McNeill *et al.* 2012).

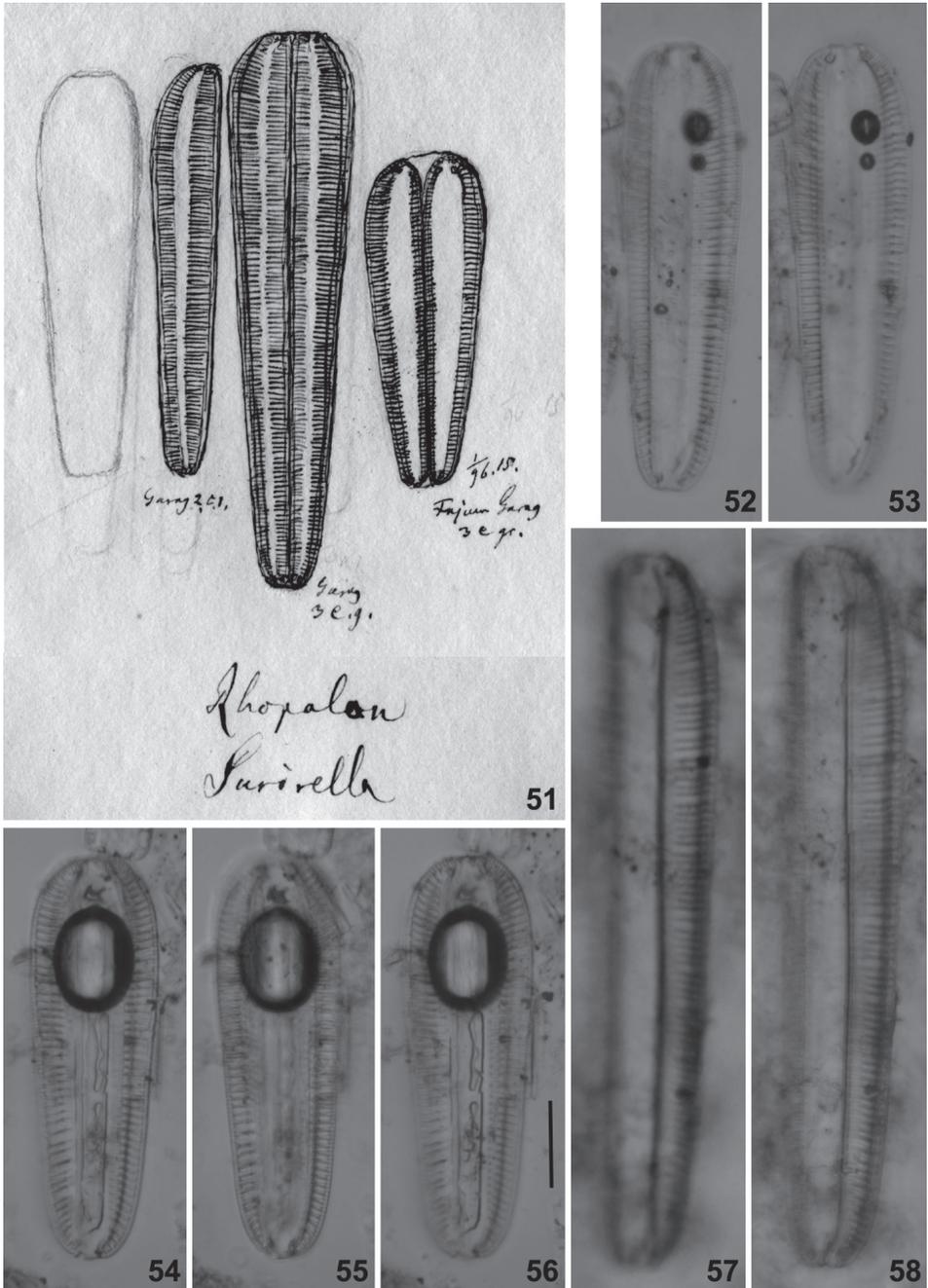
- *Surirella rhopala* Ehrenb. in *Ber. Bekanntm. Verh. Königl. Preuss. Akad. Wiss. Berlin* 1853: p. 201, 203. 1853, nom. nud. (Art. 50B, McNeill *et al.* 2012).

*Lectotype* (designated here): BHUPM EC mica strip 100505d red, given here as Fig. 52-53. Additional specimens in 100501e orange (Figs 54-56) and 100506a orange (Figs 57-58); drawing sheet No. 1135.

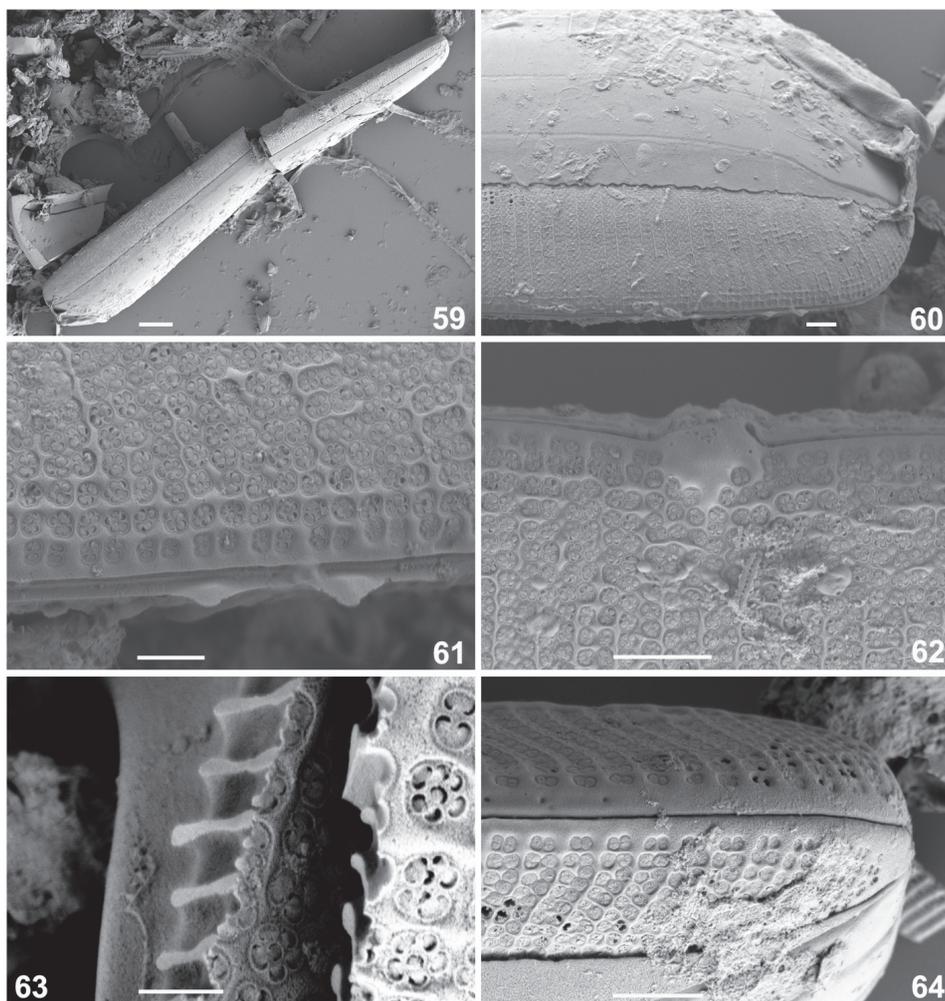
*Lectotype locality:* Egypt, Fajum, Lake Garag.

*Registration:* <http://phycobank.org/100137>

Many other *Rhopalodia* taxa were put into synonymy with *R. rhopala*: *R. vermicularis* and its formas *perlonga* Fricke and *recta* Rich, *R. ascoidea*, *R. asymmetrica* and *R. clavata* (Dickie) Forti 1910 (= *Epithemia clavata* Dickie 1879) Lake Nyassa leg. Dr. Laws.



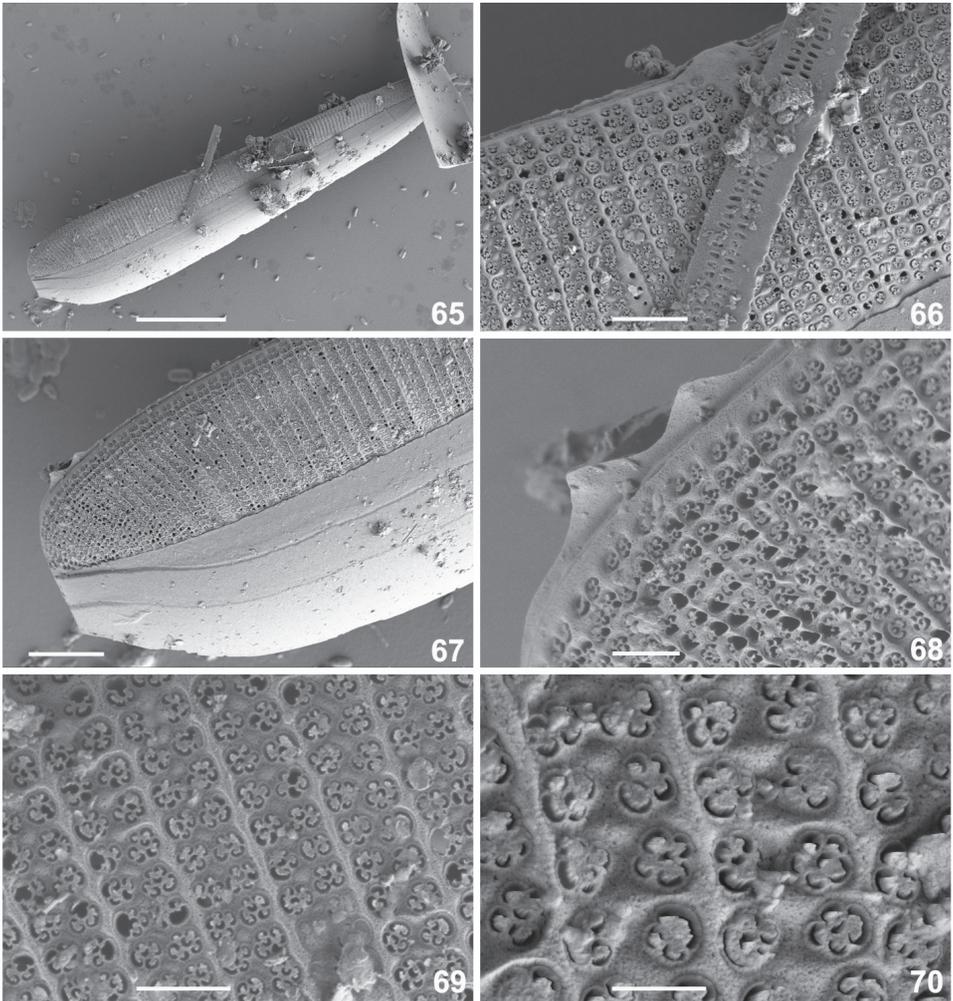
Figs 51-58. *Epithemia* (subg. *Rhopalodiella*) *rhopala*. **51**. Original drawing by Ehrenberg Drawing sheet No 1135 at BHUPM. **52-53**. Cell from mica strip BHUPM 100505d red, girdle view representing the lectotype taken at different foci. **53-57**. Girdle views from cells of mica strip BHUPM 100501e orange and BHUPM 100506a orange taken at different foci. Scale bar = 20  $\mu$ m.



Figs 59-64. *Epithemia* (subg. *Rhopalodiella*) *hirudiniformis*. SEM, external view. Material B 52 0000026. **59.** Overview of a frustule in girdle view. **60.** Detail of the head pole. **61.** Detail of the valve face showing the raphe and the flattened spines. **62.** Detail of the central area and the central raphe endings upwards on the raised part of the central nodule. **63.** Detail of the complex areolae with flap-like occlusions opening by crescent shaped slits and its flower-like aspect. **64.** Detail of the foot pole. Scale bar = 10  $\mu\text{m}$  (Fig. 59); 2  $\mu\text{m}$  (Figs 60, 62, 64); 1  $\mu\text{m}$  (Fig. 61); 0.5  $\mu\text{m}$  (Fig. 63).

Reported from many countries in Africa and from Lake Tanganyika (Mpawenayo, 1986; 1996; Cocquyt, 1991, 1998; Cocquyt *et al.*, 1991; Caljon & Cocquyt, 1992). *Ecology:* According to Chohnoky (1968) *Rhopalodia rhopala* is a tropical African species not only from the large lakes but also common in rivers. Its pH-optimum is between 7.8 and 8.2.

In-depth study of the *Epithemia hirudiniformis* material recently collected in Réunion let us conclude that this taxon is, based on morphological characteristics, a different species.



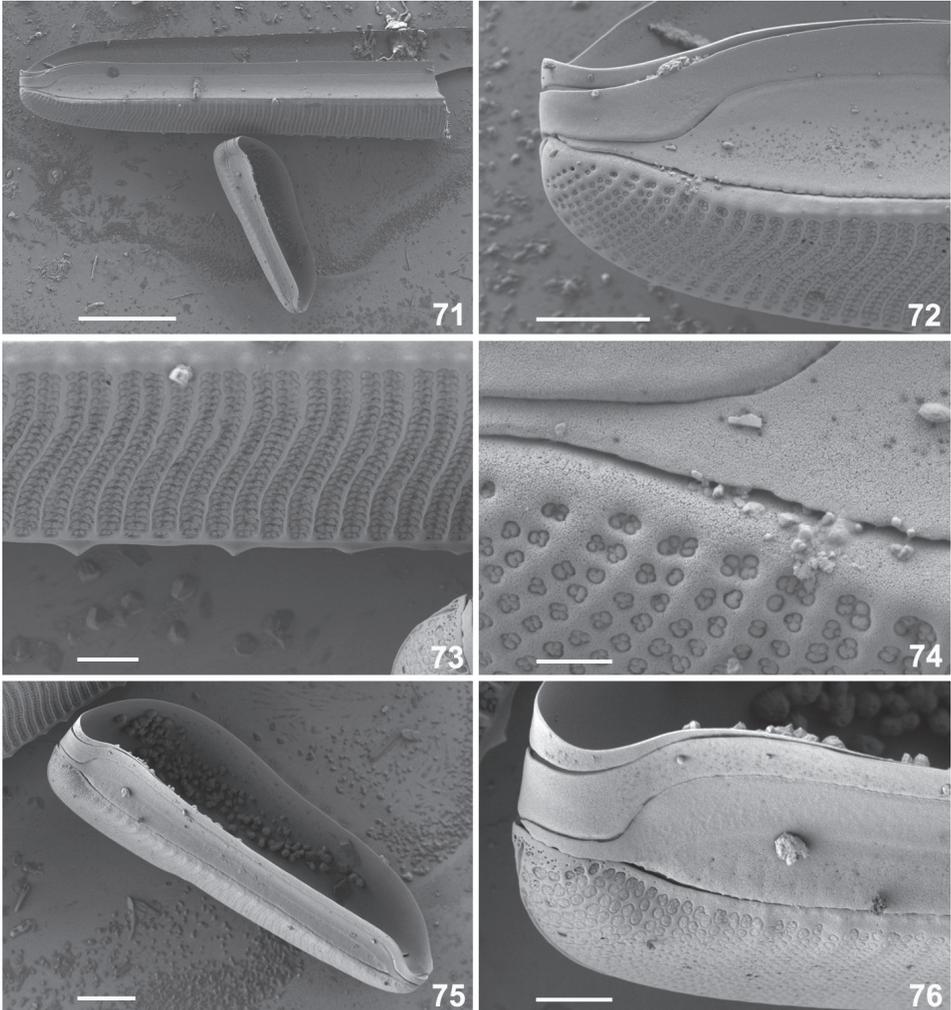
Figs 65-70. *Epithemia* (subg. *Rhopalodiella*) *hirudiniformis*. SEM, external view. Material B 52 0000100. **65.** Overview of a frustule in girdle view. **66.** Detail of the central area and of the central raphe endings upwards on the raised part of the central nodule. **67.** Detail of the head pole and the girdle bands. **68.** Detail of the valve face near the head pole showing the raphe and the large flattened spines. **69-70.** Detail of the valve face showing the biseriate stiae, composed of flower-like areolae, in between the raised virgae; note the well developed vimines. Scale bar = 20  $\mu\text{m}$  (Fig. 65); 5  $\mu\text{m}$  (Fig. 67); 2  $\mu\text{m}$  (Fig. 66); 1  $\mu\text{m}$  (Figs 68, 69); 0.5  $\mu\text{m}$  (Fig. 70).

***Epithemia vandevijveri* Cocquyt & R. Jahn, sp. nov.**

**Figs 31-38, 77-86**

*Holotype*: slide BR 4493 from material BM 481, Collected on December 26, 1999 by B. Van de Vijver, Botanic Garden Meise (BR); the valve representing the holotype is illustrated as Fig. 32.

*Isotype*: slide B 40 0042025 from material BM 481, Collected on December 26, 1999 by B. Van de Vijver, Botanical Museum Berlin-Dahlem (B) [<http://herbarium.bgbm.org/object/B400042025>].



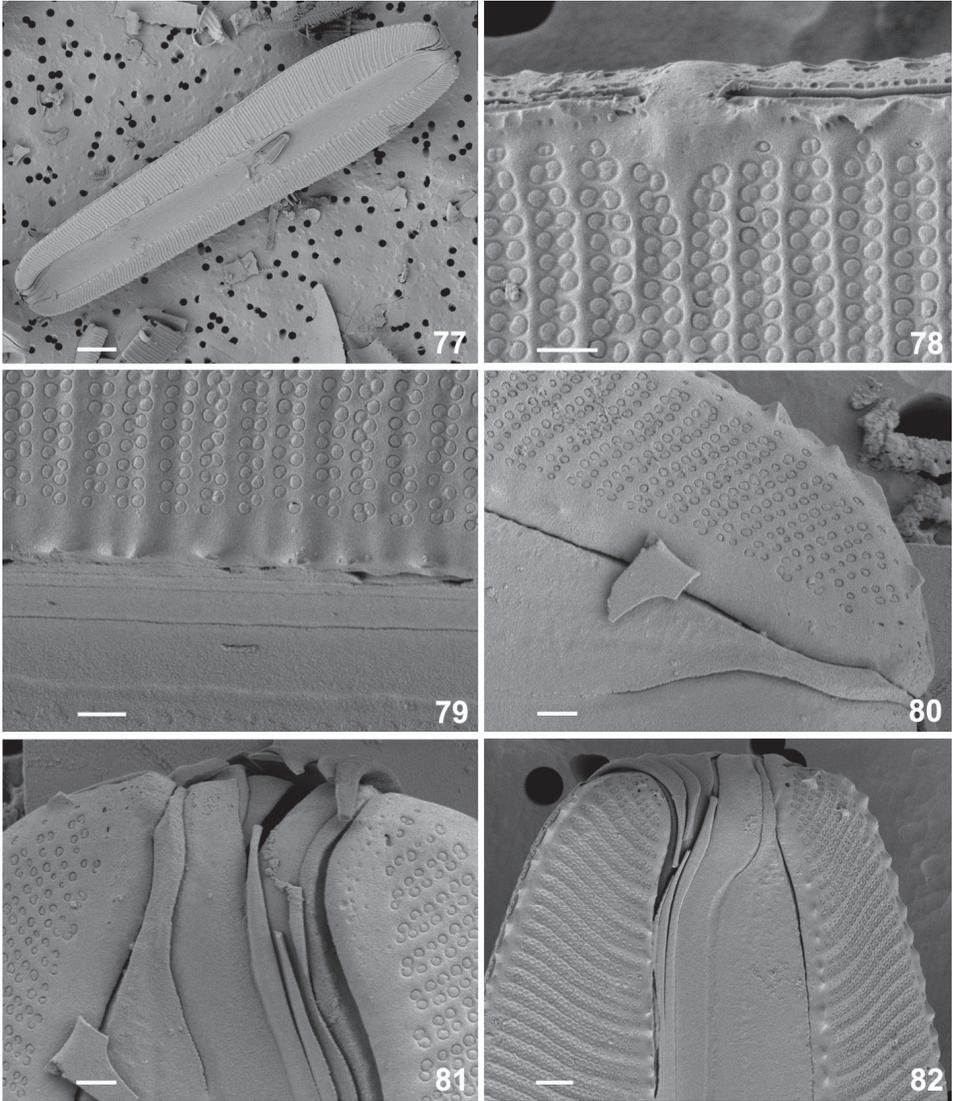
Figs 71-76. *Epithemia* (subg. *Rhopalodiella*) *hirudiniformis*. SEM, external view. Material B 52 0000038. **71.** Overview of a small valve and a part of a broken large valve. **72.** Detail of the foot pole showing the valvocopula and two girdle bands. **73.** Detail of the valve face showing the biseriate striae, the raised virgae and the flattened spines near the raphe; note the slight elevations of the valve wall at the end of the virgae and near the edge of the valve. **74.** Detail of the occluded areolae and the open valvocopula. **75.** Overview of smaller valve. **76.** Detail of the head pole with the terminal raphe endings, and the girdle bands. Scale bar = 20  $\mu\text{m}$  (Fig. 71); 10  $\mu\text{m}$  (Fig. 75); 5  $\mu\text{m}$  (Fig. 72); 2  $\mu\text{m}$  (Figs 73, 76); 1  $\mu\text{m}$  (Fig. 74).

*Name registration:* <http://phycobank.org/100100>

*Locality:* Réunion, Sainte-Rose, Anse des Cascades, (21.184056° S 55.826556° E)

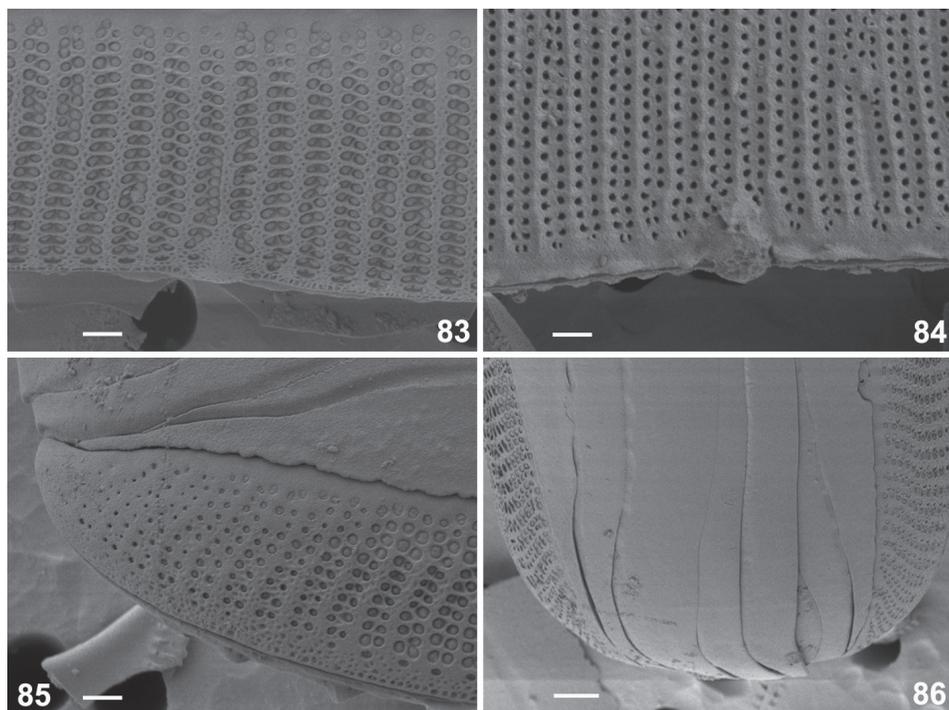
*Habitat:* Wet wall covered by mosses, behind a waterfall.

*Diagnosis:* Pervalvar axis bent, heteropolar; apical axis irregularly curved, heteropolar; transapical axis heteropolar. Length 99.4-140.7  $\mu\text{m}$ ; largest width in girdle view 29-40  $\mu\text{m}$ . Length-to-width ratio in girdle view: 3.0-4.6. Costae 4.7-5.5



Figs 77-82. *Epithemia vandevijveri* sp. nov. SEM, external view. Material BM 481. **77.** Overview of a frustule in girdle view. **78.** Detail of the striae composed of two rows of occluded areolae, and of the central raphe endings and the central area. **79.** Detail of the valve face showing the blunt spines near the edge of the valve. **80.** Detail of the valve near the foot pole; note the pyramidal spines near the raphe. **81.** Foot pole showing the girdle bands. **82.** Head pole showing the girdle bands, and the spines near the raphe and near the valve edge. Scale bar = 10  $\mu\text{m}$  (Fig. 77); 2  $\mu\text{m}$  (Fig. 82); 1  $\mu\text{m}$  (Figs 78-81).

in 10  $\mu\text{m}$ . In girdle view, the valve is wider in the valve half near the head pole, gradually becoming narrower towards the head pole. Sometimes a slight to well defined constriction is present close to the head pole (Figs 37, 38). The valve half near the foot pole is more or less parallel with nearly straight or slightly undulated



Figs 83-86. *Epithemia vandevijveri* sp. nov. SEM, external view. Material BM 481. **83-84.** Detail of the central area and the central raphe endings. **85.** Detail of the foot pole. **86.** Detail of the head pole and the girdle bands. Scale bar = 2  $\mu$ m (Fig. 86); 1  $\mu$ m (Figs 83-85).

dorsal side. Raphe strongly dorsal, the central raphe endings concurrently displaced towards the head pole.

*SEM* (Figs 77-86): External view: striae composed of a double row of complex areolae, except near the raphe where there is only one areola (Figs 78, 84, 85). Areolae occluded by flap-like occlusions mostly only opening by a crescent shaped slit, not by several slits with a flower-like aspect (Figs 78, 79); eroded areolae round (Fig. 84). Virgae only slightly raised; vimines not forming longitudinal lines parallel to the raphe (Figs 78, 83-85). Raphe straight, eccentric, not raised on a keel. Small pyramidal spines present along the raphe (Figs 80, 84). Near the edge of the valve minuscule elevations (short blunt spines) are present but not always in the prolongation of the virgae (Figs 79, 82). Central area small, formed by the absent of the last areolae of two striae (Figs 78, 84). Central raphe endings straight not expanded and not upwards on the raised part of the central nodule (Figs 78, 84). Terminal raphe endings are straight (Figs 81, 85). A small number of small poroids present near the head pole (Fig. 81). Girdle bands open (Figs 77, 81, 86). Valvocopula and the other girdle bands without any perforation or ornamentation.

*Ecology:* According to the populations found on Réunion, *Epithemia vandevijveri* is a periphytic taxon, with preference of wet wall covered with mosses in the splash zone of waterfalls. However, during our investigation no stalks were observed as cleaned samples were studied.

*Distribution*: Beside the type locality, Sainte-Rose, Anse des Cascades, and Saint-Joseph, Cascade de Grande Galet (Langevin River) on Réunion, this taxon is probably also present on Madagascar (reported as *R. hirudiniformis* in Metzeltin & Lange-Bertalot, 2002).

## DISCUSSION

According to Hustedt (1949) the systematics of the *Rhopalodia* taxa by Müller needed revision. Hustedt (1949) was convinced that *R. asymmetrica* was a sporangial state of a different species, and that *R. ascoidea* and *R. vermicularis* were closely related (belonging to the same taxon). According to Hustedt (1949) the more or less obvious corrugation of the valve margin was the only difference between *R. ascoidea* and *R. vermicularis*; he also argued that the number of undulations increased with decreasing cell sizes after the initial cell. We can consider a similar case for *R. asymmetrica*. More bizarre forms, which were sometimes strongly geniculate, can often be observed in large populations.

According to Hustedt (1949), *Rhopalodia vermicularis* was also identical to *Surirella rhopala* Ehrenb. as depicted in his Mikrogeologie (T. 33, F. I, 19 and T 35 A, F. X, 3); he decided that both taxa must be put together and named *R. rhopala*. This synonymy was overlooked by VanLandingham (1978) who only mentioned *Surirella rhopala* (and this as “invalid, poorly described, or doubtful taxonomic entry, the use of which is not recommended”).

Hustedt (1949) observed a great variability in valve length, up to 360 µm in material from Lake Kivu, and was convinced that the upper valve length limit was still not yet attained, and that the form *longa* Fricke (290 µm) had no taxonomic value. Hustedt (1949) noticed that the outline of the frustules was variable such that the heteropolarity of the apical axis can become more or less distinct. Moreover, he mentioned that in girdle view the frustules can be both strongly club-shaped or linear.

For *Rhopalodia vermicularis* Hustedt (1949) mentioned the following distribution: “very common and often present in large numbers in Kasinga Canal, Lake Eduard (common in surface plankton and on algae in the Bay of Kamanda), Lake Kivu (common on algae and in the plankton near Ngoma; Kisenyi and Keshero), Fall of Machusa, Lake Kibuga (massive attached to algae), Lake Ndalaga (rarely) and in the region of the volcans very sporadic in pools on the Karisimbi”.

Hustedt (1949) did not put *Rhopalodia hirudiniformis* and *R. vermicularis* into synonymy despite admitting that they are closely related and that it is sometimes difficult to distinguish the two taxa. The essential difference between these two taxa was in the outline of the frustules: cells with distinct broadened headpole belong to *Rhopalodia hirudiniformis* while slender club-shaped frustules belong to *R. vermicularis*.

Regarding the distribution Hustedt (1949) mentioned that they were endemic to tropical Africa. Hustedt (1949) mentioned that the *Rhopalodia hirudiniformis* var. *parva* cannot be retained because the variability of its valves fall into the description of the nominate species when they occurred *en masse*. *R. hirudiniformis* was only sporadically observed in Lake Edward, the Fall of Machusa, Lake Kibuga and Lake Ndalaga.

It should be noted that Cholnoky (1968) remarked that the morphologic variability of *Rhopalodia rhopala* led to the reporting of many spurious species and varieties which correspond with each other biogeographically as well as ecologically. He most likely meant *R. hirudiniformis* and *R. vermicularis*, which were described from tropical Africa, and the latter species made synonymous with *Rhopalodia rhopala* (Hustedt 1949). This statement can be justified by the fact that he was only given ecological information on *Rhopalodia rhopala* and not on the more commonly cited *R. hirudiniformis* and its varieties.

The description of the new species *Epithemia vandevijveri* is justified, because the biogeographical distribution and ecology of this species differ from the other morphological resembling taxa. Populations of this new taxon were found on an island in the Indian Ocean, and on a wet wall covered by mosses, behind the waterfall. The same holds true for a taxon reported from the Island Mayotte which also was found on a wet wall covered by mosses identified as *Epithemia hirudiniformis* (Rimet *et al.*, 2018). We found no indication of a wet moss substrate mentioned for any of the other taxa which were found, attached or in the plankton, in tropical African rivers and lakes. Moreover some morphologic differences with *Epithemia hirudiniformis* were observed. The shape of the frustules is different: the broadest part is at a longer distance from the head pole in *E. vandevijveri*, which has often also a slight constriction of the valves near the head pole. In SEM more differences in ultrastructure were observed: 1) the central raphe endings are not deflected upward on the raised part of the central nodule (see Figs 78, 84 versus Figs 62, 66); 2) the spines along the raphe are not flattened, but rather are pyramidal, and the ones near the head pole are not much larger than the other spines (see Fig. 80 versus Fig. 68); 3) blunt spines are present on the edge of the valve not always in the prolongation of the virgae (see Fig. 79 versus Fig. 73.); 4) the occlusion of the areolae seems to be less complex and only open by a crescent-shaped slit, in contrast to several slits with a flower-like aspect as observed in *E. hirudiniformis* (compare Figs 78, 83 versus Figs 62, 69, 70, 74); 5) the virgae are only slightly raised and the vimines do not form longitudinal lines parallel to the raphe (see Fig. 78, 80 versus Fig. 61, 69).

Recently Ruck *et al.* (2016a, b) published a new classification of the Surirellales and Rhopalodiales where both orders were combined into one (Surirellales) and where the genus *Rhopalodia* was sunk into the genus *Epithemia* because of missing morphological autapomorphies between these genera. However, all *Rhopalodia* species included in their study belong to Müller's "Sippe" *Epithemioideae*. These *Epithemioideae* taxa were, not only genetically, but also morphologically closely related to *Epithemia* s.s. Therefore, it was not surprising that they were all situated in the genus *Epithemia* Kütz. in their phylogenetic tree. No representatives of the infrageneric "Sippe" *Eurhopalodiae* which were typical components of the tropical Africa diatom flora, were included in their study. The morphology of taxa belonging to the *Eurhopalodiae* section was totally different from the species of the *Epithemioideae* section, treated here as *Epithemia* subg. *Rhopalodia*. *Epithemioideae* were reniform, falcate or clamp-shaped in valve view, elliptic to linear in girdle view and have a bilateral symmetry to the transapical axis. The *Eurhopalodiae*, treated here as *Epithemia* subg. *Rhopalodiella* on the other hand, were irregular to worm-shaped in valve view, clavate or pear-shaped in girdle view and have an asymmetry to the transapical axis. Therefore, we suspected that they also will belong to a genetically distinctive group. The justification of the taxa within *Epithemia* subg. *Rhopalodiella*, which have a large morphological variability that consequently overlaps, can only be resolved genetically. In the meantime, we recommend following the best possible morphological species concept within this section.

The conclusion by Ruck *et al.* (2016a, b) that “preserving the current generic names by restricting the definition of *Rhopalodia* to include only the freshwater clade sister to *Epithemia*, requires diagnosis of two additional genera to accommodate the grade leading to the crown clade of freshwater *Rhopalodia* and *Epithemia*” and that “it is therefore most productive to subsume *Rhopalodia* and *Tetralunata* into *Epithemia*, creating a monophyletic genus defined by fibulae that extend beyond the canal raphe and into valve face” is likely to be reconsidered when more taxa with molecular data from *Epithemia* subg. *Rhopalodiella* are included in the phylogenetic tree.

Although the species of the *Epithemia* subg. *Rhopalodiella* can be considered as tropical African taxa, their distribution seems not really be limited to tropical Africa only. The islands of Mayotte, an archipelago in the Indian Ocean between Madagascar and Mozambique, and the island Reunion in the Indian Ocean East of Madagascar are located within the tropics, the region between the Tropic and Cancer and the Tropic of Capricorn, 23.5° N and 23.5° S respectively, and can be considered more or less as belonging to the African continent. However, the material Ehrenberg (1852, 1853, 1854) studied of *Epithemia rhopala* came from Egypt; Fayyum is, located north of the Tropic of Cancer, at around 29° N and 30° N. Noteworthy is that the distribution of *Epithemia* subg. *Rhopalodiella* is restricted to the Eastern part of Africa, with the East African Great Lakes as the most western distribution (Cocquyt, unpubl.).

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