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SURIRELLA ENGLERI O. MÜLLER—A STUDY OF ITS ORIGINAL INFRASPECIFIC TYPES, VARIABILITY AND DISTRIBUTION

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***SURIRELLA ENGLERI* O. MÜLLER – A STUDY OF ITS ORIGINAL INFRASPECIFIC TYPES, VARIABILITY AND DISTRIBUTION**

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Surirella engleri, including its four original infraspecific taxa, was studied and typified using historical East African material from which Otto Müller described more than 100 new diatom taxa at the beginning of the 20th century. Considerable outline variation was found, in agreement with the results of experimental cultures carried out in the late 1980's on material from the northern basin of Lake Tanganyika. This variation supported the abandonment of taxonomic recognition of the four infraspecific taxa proposed by Müller. SEM analyses of this taxon from the original Lake Malombe material and from the recent Lake Tanganyika material showed some minor differences. The past and current distribution of this taxon which is endemic to Tropical Africa was summarized.

INTRODUCTION

In the first half of the 20th century a number of tropical African *Surirella* species were described from Lakes Malawi, Tanganyika and Malombe by Otto Müller (Müller 1903, 1904; for a compilation see Jahn 2002), West (1907) and Hustedt (e.g. 1904, pl. 245 figs 7, 9, 10, 15–18 and pl. 246 figs 1, 2, 9, 11) in Schmidt 1874–1959 and in Huber-Pestalozzi 1942).

The renewed attention to the diatom flora of East Africa (i.e. Cocquyt *et al.* 1993, Cocquyt 1998) and the conviction that species of micro-algae are not as ubiquitous and cosmopolitan as earlier assumed, has initiated our reinvestigation of Müller's taxa (Cocquyt & Jahn 2005, Cocquyt & Jahn 2007). As the original slides were lost during the Second World War, new permanent diatom slides were made from the material used by Otto Müller in describing many new East African diatom taxa (Jahn 1996, 2002). The present publication deals with *Surirella engleri* and its variety and formae. *Surirella engleri* and its infraspecific taxa are lectotypified, their German descriptions are translated, LM- and SEM- photographs of the original material are provided, and historical as well as recent biogeographical references are included.

As *Surirella engleri* is also common in Lake Tanganyika and regularly observed in Lake Victoria, material from these two lakes was also studied and its variability is presented in a PCA plot. In addition to this publication, the information on the discussed taxa will also be made available via the AlgaTerra Information System (Jahn & Kusber 2006).

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MATERIAL AND METHODS

From the original samples – dried material in their original bottles available in the Botanical Museum Berlin-Dahlem (B) – new permanent slides were made to be used for lectotypification. Since all taxa have one syntype locality where they all should occur together, we studied this sample, B 2.0039, intensively and used it for the designation of the lectotypes. The following samples were also investigated for the present paper: B 2.0032, B 2.0037, B 2.0038, B 2.0040, B 2.0041, and B 2.0053. The complete collection information on all the studied samples, translated from German, is given in Table 1. Another sample from the same expedition to East Africa and studied by Otto Müller (his no. 16) was never found.

Table 1. List of samples studied in this paper with collection information (translated from German) and current names of the localities in square brackets. The sample numbers correspond to Müller's numbers; the modern numbers in the collection at the Botanical Museum Berlin-Dahlem (B) are put in parenthesis. The information on the sample labels is in accord with the list of collectors and collecting localities and details published by Müller (1903).

39	(B 2.0039): Lake Malombe after discharge of Lake Nyassa [Lake Malawi, Malawi]; collected by Fülleborn on 7 February 1900; label has extra word "Diatoms".
32	(B 2.0032): River Baka, Konde-Land [Tanzania]; plankton; collected by Fülleborn in December 1898. B 2.0036: River Songwe, about 1 hour from discharge into Lake Nyassa [Lake Malawi, Tanzania].
37	(B 2.0037): Lake Malombe after discharge of Lake Nyassa [Lake Malawi, Malawi]; collected by Fülleborn on 1 February 1900.
38	(B. 2.0038): Lake Malombe after discharge of Lake Nyassa [Lake Malawi, Malawi]; collected by Fülleborn on 3 February 1900.
40	(B 2.0040): Lake Malombe after discharge of Lake Nyassa [Lake Malawi, Malawi]; plankton; collected by Fülleborn on 3 February 1900; label has extra words "Polycystis, Aphanotheca".
41	(B 2.0041): Lake Malombe after discharge of Lake Nyassa [Lake Malawi, Malawi]; plankton; collected by Fülleborn on 3 February 1900; label has extra word "Plankton".
53	(B 2.0053): In a watercourse near the hot springs of Utengule [Tanzania]; collected by Fülleborn on 6 November 1899.

Additionally, we studied samples from Lake Tanganyika collected at Bujumbura by Dr A. Caljon between 1980 and 1990 (Cocquyt 1998) and deposited at the National Botanic Garden of Belgium. To analyze the variability of *Surirella engleri*, data from an experiment performed in the 1980s by G. Ntirushize (a student of A. Caljon, the late husband of the first author) is also included in this paper. Original material was taken from Lake Tanganyika at Bujumbura near the "Cercle Nautique", the same location as the monthly sampling station in 1986 and 1987 (Cocquyt 1998). Single cells of *Surirella engleri* were cultivated in different culture media (Watanabe 1, Watanabe 2 and Chu 16 (Stein 1973) added to sterilized Lake Tanganyika water) and subjected to several light intensities (1000, 2000, 2500 and 2800 lux during 12 h days; see also Ntirushize 1991).

Some samples from the Mwanza Bay in Lake Victoria collected by Van den Heuvel in 1983 and put at our disposal by Van den Heuvel and Dr W. F. Prud'homme van Reine (National Herbarium Nederland, University of Leiden, The Netherlands) were also studied.

Results of LM morphometric studies of material from Lakes Malombe, Tanganyika and Victoria were analysed with the program CANOCO (Ter Braak 2002) using a Principal Component Analysis with log transformation of the data.

The samples were oxidized using peroxide, rinsed and then embedded in Naphrax to obtain microscopic slides. Investigations were done both at the Botanical Museum Berlin-Dahlem (Germany) and at the laboratory of Protistology and Aquatic Ecology, Ghent University (Belgium), with a Zeiss Axioplan and a Leitz Diaplan microscope, respectively. Most of the micrographs were taken with Nomarski differential interference contrast (DIC) with 40×, 63× (oil immersion) and 100× objectives. Light microscopic photographs of the culture material were taken with an Olympus BH2 microscope, equipped with a Wild camera, at the University of Burundi. Scanning electron microscopy was done at the Botanical Museum Berlin-Dahlem (Germany) using a Philips 515 operating at 30 KV.

RESULTS

Surirella engleri O. Müller in Bot. Jahrb. Syst. 34: 28, pl. 1, fig. 4. 1903.

Synonyms:

Surirella engleri f. *genuina*, f. *recta* O. Müller in Bot. Jahrb. Syst. 34: 28, pl. 1, fig. 4. 1903. nom. inval.

Surirella engleri f. *angustior* O. Müller in Bot. Jahrb. Syst. 34: 28, pl. 1, fig. 5. 1903.

Surirella engleri f. *subconstricta* O. Müller in Bot. Jahrb. Syst. 34: 28-29, pl. 1, fig. 6. 1903.

Surirella engleri var. *constricta* O. Müller in Bot. Jahrb. Syst. 34: 29, pl. 1, figs 7, 8. 1903.

Surirella engleri [var. *constricta*] f. *sublaevis* O. Müller in Bot. Jahrb. Syst. 34: 29 pl. 1, fig. 9. 1903.

Translated from German, Müller's description reads (from his forma *genuina* 1903: 28): "Valves linear with cuneate (apex subtruncatis) or somewhat protracted (apex subrostratis) poles. Costae weakly developed, sometimes stronger, 1.5–1.7 in 10 µm, straight in the middle, divergent near the poles, reaching the pseudoraphe, building stronger alar canals near the margins, with indistinct wing projection. Pseudoraphe a continuous line. Pleura long linear with blunt poles and rounded angles, wings straight, fenestrae broader than supports. Length: 150–250 µm, width: 27–40 µm. Width-to-length ratio 1:4.5–6.2. – Lives in the plankton of Lake Nyassa at 80–90 m depth (16), in Lake Malombe (37, 39), in the plankton of the river Baka (32), Konde-land, and in the river Songwe (36)."

Lectotype: (designated here): slide B 400 040 240 (the valve representing the lectotype is here illustrated, Fig. 1).

Type locality: Lake Malombe after discharge of Lake Nyassa (Lake Malawi), Malawi.

The valve fits very well the description given by O. Müller: length: 165 µm, width: 34.5 µm, width-to-length ratio 1:4.8; 1.6 costae in 10 µm.

Habitat: plankton.

Distribution (including all infraspecific taxa listed above as synonyms): Besides Lake Malawi, Lake Malombe, River Baka, River Mbasi, River Songwe, near a hot spring of Utengule (Tanzania) (O. Müller 1903), this species was also reported from Congo (Zaire) (Zanon 1938, Woodhead & Tweed 1958a), Ethiopia (Gasse 1986), Ghana (Foged 1966, Ross 1983), Kenya (Bachmann 1938, Gasse 1986), Nigeria (Woodhead & Tweed 1958b, Ross 1983), Sierra Leone (Bachmann 1938, Woodhead & Tweed 1958b, Mölder 1962,

Ross 1983), Tanzania (Zanon 1938), Uganda (Hustedt 1949), Lake Albert (Van Meel 1954, Ross 1983), Lake Edward (Hustedt 1949, Ross 1983, Gasse 1986), Lake Kivu (Hustedt 1949, Ross 1983), Lake Malawi (Ross 1983), Lake Tanganyika (Van Meel 1954, Ross 1983, Mpawenayo 1996, Caljon & Cocquyt 1992, Cocquyt 1998) and Lake Victoria (Wołoszyńska 1914, Van Meel 1954, Thomasson 1955, Gasse 1986).

Müller's infraspecific taxa

Although *Surirella engleri* f. *angustior*, f. *subconstricta*, var. *constricta*, and var. *constricta* f. *sublaevis* are here treated as taxonomic synonyms, for nomenclatural reasons they are here lectotypified.

***Surirella engleri* f. *angustior* O. Müller** in Bot. Jahrb. Syst. 34: 28, pl. 1, fig. 5. 1903 (also published in A. Schmidt's Atlas Diatomaceenkunde, pl. 245, fig. 14. 1904).

Translated from German, Müller's description reads (1903: 28): "Valves as nominate forma but more slender and with more acutely rounded poles. Costae and alar canals weak, sometimes stronger, 2 in 10 μm . Length: 173–290 μm , width: 30–36 μm . Width-to-length ratio 1:5.8–8.5. – Lives in the plankton of Lake Nyassa near Langenburg at 40–90 m depth (14, 16), in the plankton of Lake Malombe (40), in Lake Malombe (37, 39), in a watercourse near the hot spring of Utengule (53), in the river Songwe (36)."

Lectotype (designated here): slide B 400 040 241 (the valve representing the lectotype is here illustrated, Fig. 2).

Type locality: Lake Malombe after discharge of Lake Nyassa (Lake Malawi), Malawi.

The lectotype valve, resembling most Müller's picture (1903), fits the valve shape given by Müller, although the valve is larger and wider, 462 μm and 67 μm , and the number of valve undulations (costae) in 100 μm is smaller (1.2 in 10 μm). The fewer undulations are probably related to the great length of the valve. The width-to-length ratio 1:6.6 falls within the ratio given by Müller.

Forma *angustior* is somewhat more slender than the nominate form. Müller described that the valve undulations (costae) and marginal alar canals should be weaker than in the typical form, but this is not very pronounced in the designated valve. O. Müller (1903: 28) remarks that "these slender individuals are hard to distinguish from the larger *Surirella linearis* W. Smith f. *linearis*, which consequently are very closely related to *S. engleri*". From the same samples, Müller (1903, p. 29, 30) gave the following dimensions for *S. linearis*: length: 75–180 μm , width: 14–33 μm , width-to-length ratio: 1:4–5.7 and 2.2–2.5 costae in 10 μm .

***Surirella engleri* f. *subconstricta* O. Müller** in Bot. Jahrb. Syst. 34: 28–29, pl. 1, fig. 6. 1903 (also published in A. Schmidt's Atlas Diatomaceenkunde, pl. 245, fig. 15. 1904).

Translated from German, Müller's description reads (1903: 28–29): "Valves and girdle as the nominate form, the margins only slightly constricted. Costae and alar canals weaker, sometimes stronger, 1.5–1.6 in 10 μm . Length: 220–360 μm , width: 32–45 μm . Width-to-length ratio 1:6.4–8.5. – Lives in the plankton of Lake Nyassa at 80–90m depth (16), in Lake Malombe (37, 39), in a river near the hot spring of Utengule (53)."

Lectotype (designated here): slide B 400 040 239 (the valve representing the lectotype is here illustrated, Fig. 3).

Type locality: Lake Malombe after discharge of Lake Nyassa (Lake Malawi), Malawi.

The valve chosen in the lectotype fits the description given by O. Müller: length: 228 µm and width: 34.5 µm and the width-to-length ratio 1:6.5. Only the number of valve undulations (costae) is a little higher with 1.8 in 10 µm. The form of the valve is more slender than other valves observed in the same material and the poles are also somewhat more acutely rounded. The valve of *S. engleri* var. *constricta* has more cuneate, protracted poles.

***Surirella engleri* var. *constricta* O. Müller** in Bot. Jahrb. Syst. 34: 29, pl. 1, figs 7, 8. 1903 (also published in A. Schmidt's Atlas Diatomaceenkunde, pl. 245, figs 16, 17. 1904).

Translated from German, Müller's description reads (1903: 29): "Valves linear, margins more or less constricted, with cuneate (apex cuneatis) or somewhat protracted (apex subrostratis) poles. Costae stronger, sometimes weaker, 1.6 in 10 µm, straight in the middle, divergent near the poles, reaching the pseudoraphe. Alar canals with more or less distinct wing projection. Pseudoraphe a continuous line. Girdle linear with obtuse poles and rounded angles, margins bent to the inner side. Wings half high, fenestrae broader than their supports. Length: 180–346 µm, width: 33–47 µm. Width-to-length ratio 1:5.3–8. – Lives in the river Mbasi near Nyassa, Konde-land (35), in Lake Malombe (39) and its plankton (40, 41)."

Lectotype (designated here): slide B 400 040 238 (the valve representing the lectotype is here illustrated, Fig. 4).

Type locality: Lake Malombe after discharge of Lake Nyassa (Lake Malawi), Malawi.

The length of the valve, 295 µm, its width, 44 µm, the width-to-length ratio of 1:6.7, the more cuneate valve shape and the somewhat protracted poles, fit the description given by O. Müller. Only the number of valve undulations (costae) in 10 µm is a little higher (1.8).

Surirella engleri* [var. *constricta*] f. *sublaevis in Bot. Jahrb. Syst. 34: 29, pl. 1, fig. 9. 1903 (also published in A. Schmidt's Atlas Diatomaceenkunde, pl. 245, fig. 18. 1904).

Translated from German, Müller's description reads (1903: 29): "As var. *constricta*, poles cuneate (apex cuneatis). Costae 1.6 in 10 µm, very weak, near the margins alar canals without wing projection. Length: 128–346 µm, width: 30–47 µm. Width-to-length ratio 1:4.3–8.5. – Lives in Lake Malombe (39) and its plankton (40, 41)."

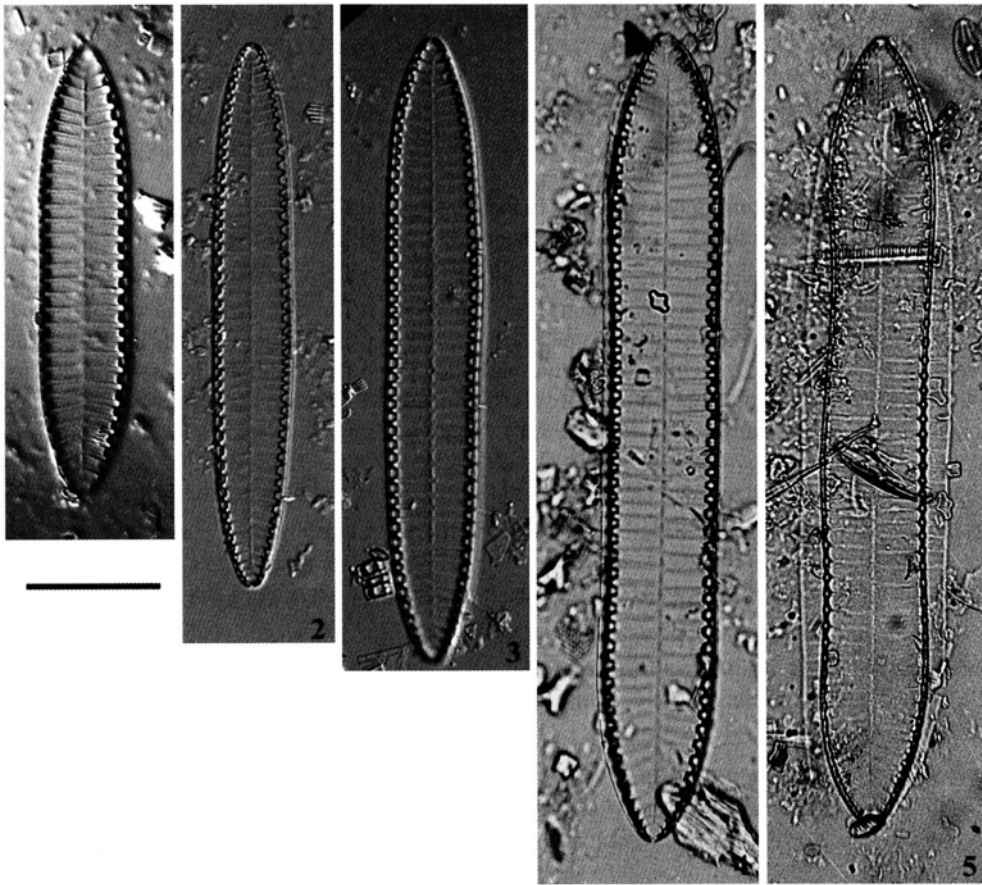
Lectotype (designated here): slide B 400 040 238 (the valve representing the lectotype is here illustrated, Fig. 5).

Type locality: Lake Malombe after discharge of Lake Nyassa (Lake Malawi), Malawi.

The valve fits the description given by O. Müller, length: 288µm, width: 40 µm, width-to-length ratio: 1:7.2. The number of valve undulations (costae) in 10 µm is somewhat higher, viz. 1.7 in 10 µm.

SEM features of *Surirella engleri* as found in the original material from Lake Malombe

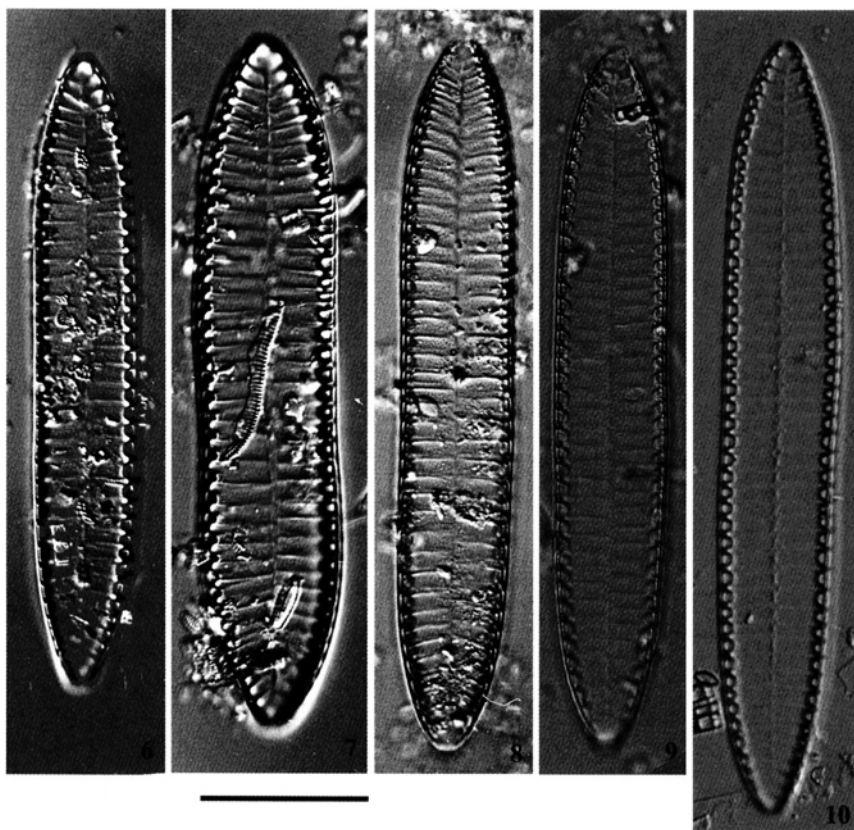
The external valve face is gradually elevated towards the axial area. Axial area (pseudoraphe) is without a siliceous ridge (Fig. 17). The valve face is ornamented by small scattered siliceous granules in the depressions of the valve undulations (Fig. 17). These granules can be rounded or become more irregular, especially near the poles. Raphe canals are elevated above the valve face on well developed wings (alae) with barred fenestrae, (6) 7–9 (11) bars per fenestra, about 30–35 bars in 10 µm (Fig. 18). The external raphe fissures are bent towards the mantle side (Fig. 24).



Figs 1–5. *Surirella engleri* O. Müller, original material from Lake Malombe, LM. **Fig. 1.** Lectotype of *S. engleri* [var. *engleri*] f. *engleri*, slide B 400 040 240. **Fig. 2.** Lectotype of *S. engleri* f. *angustior*, slide B 400 040 241. **Fig. 3.** Lectotype of *S. engleri* f. *subconstricta*, slide B 400 040 239. **Fig. 4.** Lectotype of *S. engleri* var. *constricta*, slide B 400 040 238. **Fig. 5.** Lectotype of *S. engleri* [var. *constricta*] f. *sublaevis*, slide B 400 040 238. Scale bars: 50 µm (Figs 1, 3, 4, 5); 100 µm (Fig. 2).

The top of the valve undulations, lying in the prolongations of the alar canals, are always smaller than the depressions (Fig. 17). These undulations always reach the axial area, forming a right angle except near the poles where the top of the undulations becomes somewhat radiate. There are 24–26 alar canals in 100 µm, becoming somewhat denser near the poles (Fig. 16). The uniseriate striae, about (44) 50–70 in 10 µm, are composed of round poroids, 50–70 (74) in 10 µm, which are visible on the top and in the depression of the transapical undulations (Fig. 17). The valve mantle is smooth (Fig. 18); oval swellings of about 1 µm length and 0.5 µm width are present at the outer edge (Fig. 24).

On the internal valve face, the striation is distinct (Figs 22, 23) and poroids are also present on the axial area. The alae have a single row of portulae (Fig. 23). The portulae are smaller than the space between the portulae, (1.9) 2.0–2.4 µm and 2.5–3.5 (4.1) µm respectively (Fig. 23). The striation continues into the alar canals, 30 (35) in 10 µm and is composed of two rows of areolae. At one pole the raphe is continuous (Fig. 20) while at the opposite pole the raphe is discontinuous (Fig. 21).



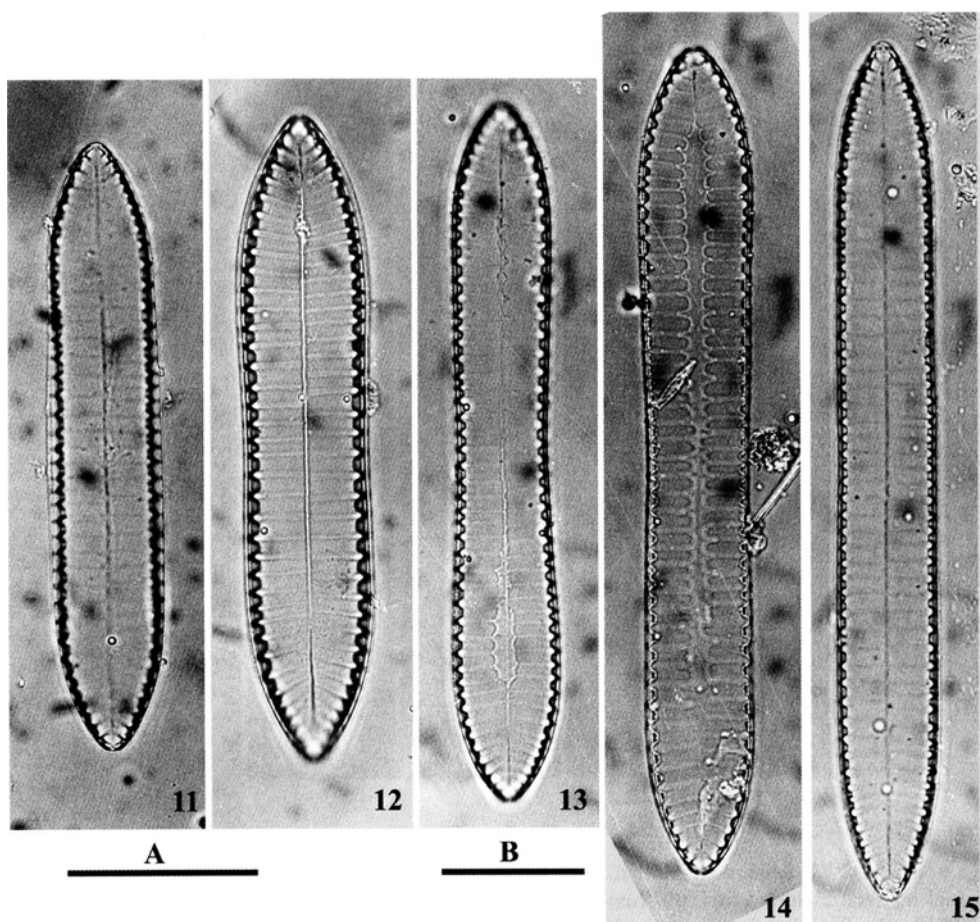
Figs 6–10. *Surirella engleri* O. Müller, LM. Valves with different outlines and sizes observed in the original material collected in 1900 from Lake Malombe, East Africa. **Figs 6, 7.** Valves from material B 2.0038. **Fig. 8.** Valve from material B 2.0035. **Figs 9, 10.** Valves from material B 2.0039. Scale bar = 50 μm .

Additional and divergent SEM features of *Surirella engleri* in material from Lake Tanganyika

External valve face has well developed transapical undulations, reaching the axial area. The axial area bears a strong siliceous ridge (Figs 24, 25) in contrast to the Malombe material. This ridge is sometimes interrupted (Fig. 27). No spines are present on the valve face or on the ridge. Alae with barred fenestrae, 5 to 8 bars per fenestra, and about 30 fenestral bars in 10 μm (Figs 27, 28). In the material of Lake Malombe the number of fenestral bars is generally higher, 7 to 9 and even 11, and only exceptionally were 6 bars observed. The valve mantle is not smooth but has siliceous granules while in the material from Lake Malombe it is smooth.

The external and internal valve face have a distinct striation, 36–40 uniseriate striae in 10 μm , composed of rimmed areolae, 60–70 in 10 μm (Fig. 30). The striation densities are lower than for the Malombe material, 50 and 70 in 10 μm , exceptionally 44.

A broad girdle band is present around almost the entire frustule (Fig. 28), but opens near the middle of the side (not shown). A smaller girdle band, present between the large band and the valve mantle (Fig. 28), has an extension (6–7 μm broad, 11 μm long) (Fig. 31) that fits into the opening of the broad band.

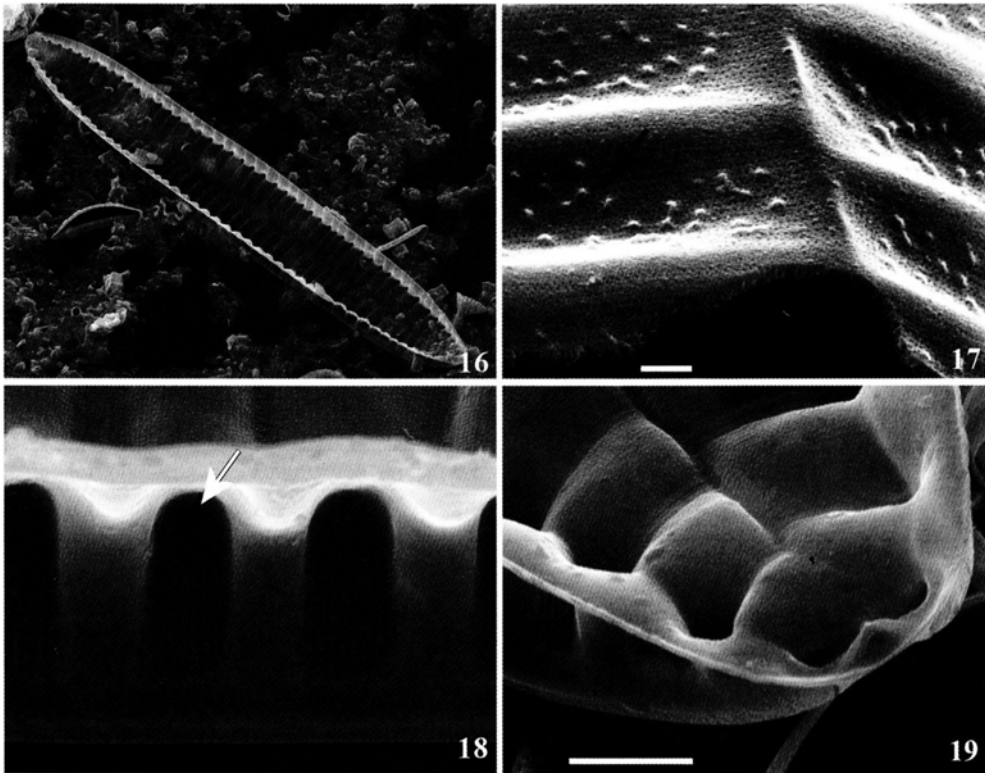


Figs 11–15. *Surirella engleri* O. Müller, LM. Valves of a clone culture of material from the northernmost part of Lake Tanganyika, collected in 1989. Scale bar A: 50 µm (Figs 11, 12); scale bar B: 50 µm (Figs 13–15).

Cultured Lake Tanganyika cells

As summarized by Ntirushize (1991) *Surirella engleri* cells could only be cultivated on Watanabe 2 and Chu 16 media. The best results were obtained using the Watanabe 2 medium under 2500 lux, where the highest number of living cells (mean of 20 cells in 0.1 ml) were observed on the 21st day, afterwards the culture started to decline very rapidly (only a mean of 4 frustules in 0,1 ml on the 28th day).

Another important result of this experimental work, but not included in Ntirushize (1991) was the variability observed within a clone (personal observations). Valves with straight margins (like the “genuina” form) as well as slightly constricted margins (like f. *subconstricta* and var. *constricta*) were present in one culture, starting from a frustule with straight margins. The morphometric results of valves measurements (length, width, number of alar canals and length-to-width ratio) (similar to Figs 11–15) in the culture deriving from a single clone culture are summarized in Table 2.



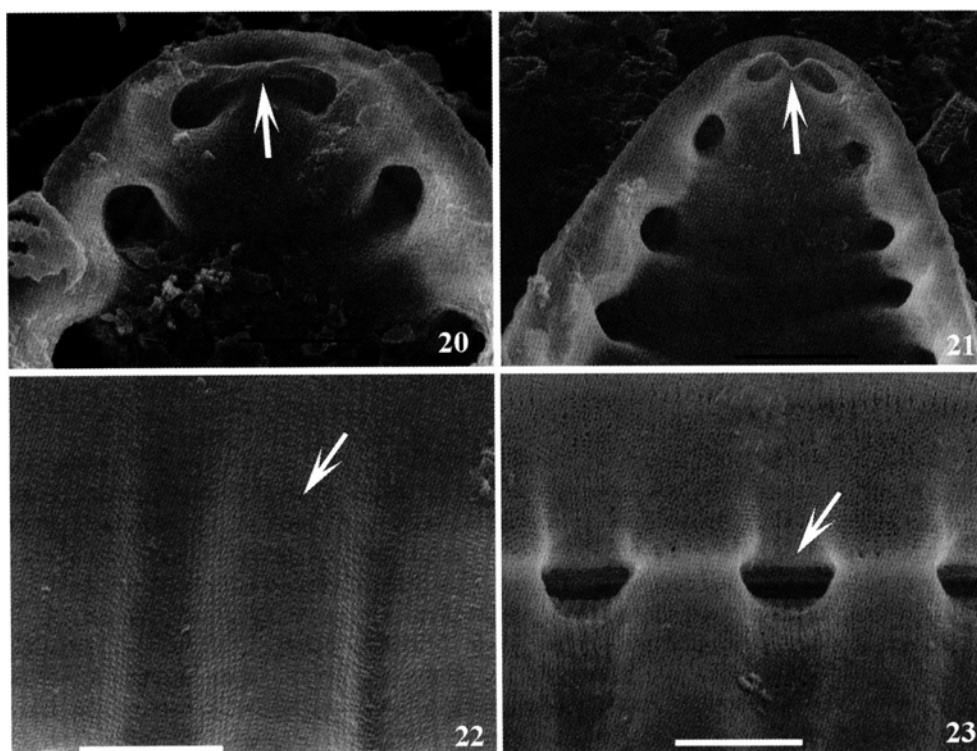
Figs 16–19. *Surirella engleri* O. Müller, SEM. Original material from Lake Malombe (B 2.0039). **Fig. 16.** Internal valve view. **Fig. 17.** External valve face showing uniseriate striae, and scattered siliceous granules (arrow) in the depressions of the valve undulations. **Fig. 18.** External valve mantle view showing barred fenestrae (arrow). **Fig. 19.** Internal view of the valve at one pole. Scale bars: 1 μm (Fig. 17); 4 μm (Figs 18, 19); 60 μm (Fig. 16).

Results of the PCA analysis

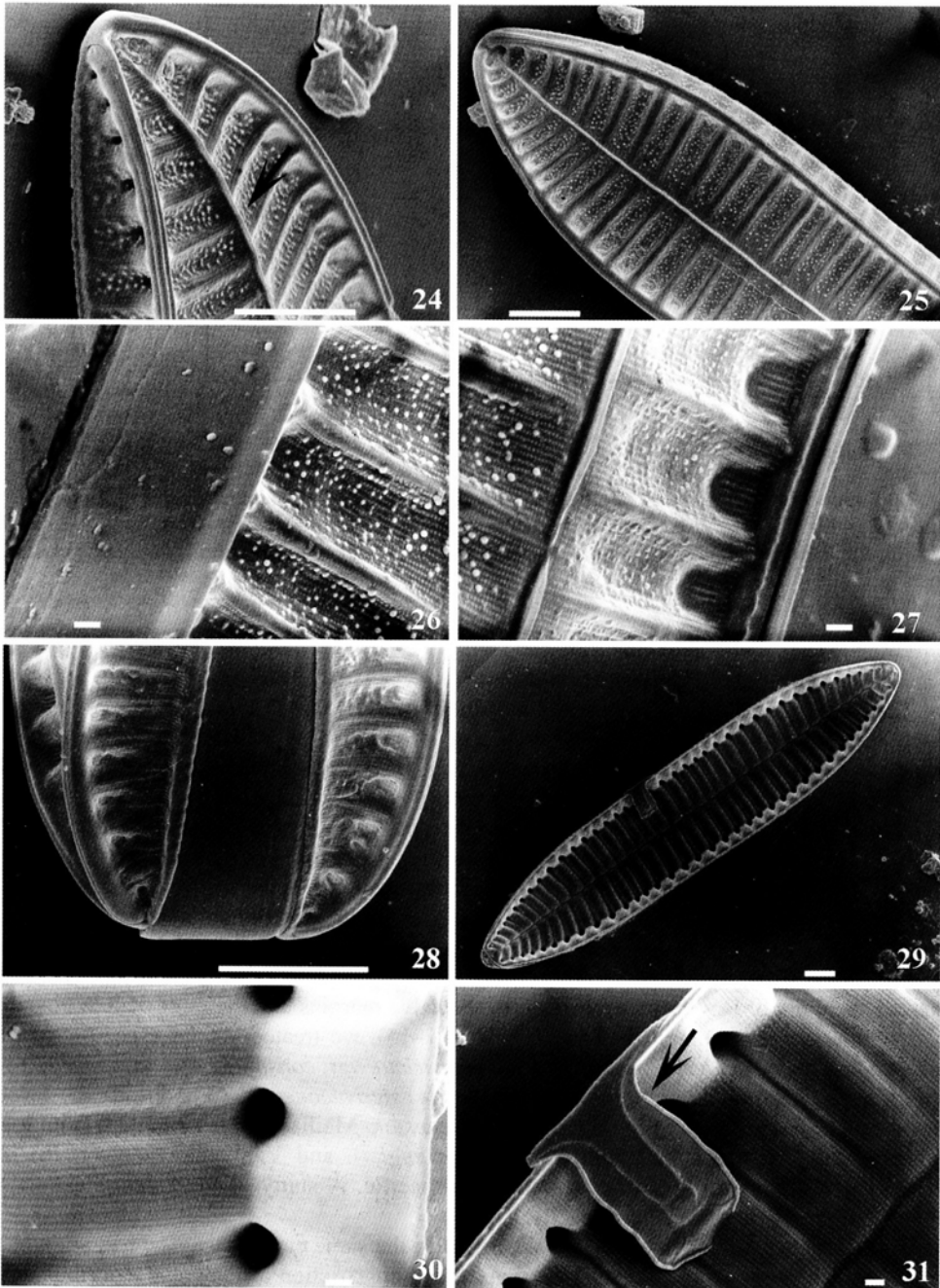
The results of the morphometric measurements of length, maximal width, width mid-valve, length to maximal width ratio, length or mid-valve width ratio and number of alar canals in 10 μm of thirty-two valves were used in the PCA. Of these valves, 14 belong to the historical material of Lake Malombe, 15 to samples of Lake Tanganyika and 3 to samples of Lake Victoria. The first and second axes of the PCA (Fig. 32) (eigenvalue of 0.619 and 0.370 for the first and second axis respectively, these axes explain 98.9% of the variance in the morphometric data) show that there is no clear difference between the valves from Lake Malombe, Lake Tanganyika and Lake Victoria. Moreover, all valves are scattered over the graph, giving no differentiation between the formae described by Müller or between the lakes. There was only one valve that is separated clearly from the other valves along the first and second PCA axis. This separation is due to length and length-to-width ratio respectively (Fig. 32): this valve belongs to *S. linearis* W. Smith, a closely related taxon, from Lake Tanganyika.

Table 2. Measurements of *Surirella engleri* valves of one clone culture, from material of the northernmost part of Lake Tanganyika.

Valve	Length	Width	Width midvalve	Length to width ratio	Length to width (midvalve) ratio	Number of alar canals in 10 μm
1	157	32	32.5	4.9	4.8	2
2	158	33.4	29.5	4.7	5.4	2
3	188	37	36.2	5.1	5.2	1.8
4	189	37.5	35.8	5.0	5.3	1.8
5	202	31.5	26.6	6.4	7.6	2
6	239	32.5	30	7.4	8.0	2
7	248	29.9	29	8.3	8.6	2.2
8	276	52	52	5.3	5.3	1.4
9	302	52	48	5.8	6.3	1.3



Figs 20–23. *Surirella engleri* O. Müller, SEM. Original material from Lake Malombe (B 2.0039). **Fig. 20.** Internal valve view near one pole showing a continuous raphe slit (arrow). **Fig. 21.** Internal valve view of the opposite pole of the same valve showing a discontinuous raphe slit (arrow). **Fig. 22.** Internal valve view with uniseriate striae, composed of rimmed areolae (arrow). **Fig. 23.** Internal valve view of the single portula (arrow). Scale bars: 3 μm (Figs 20, 22, 23); 6 μm (Fig. 21).



Figs 24–31. *Surirella engleri* O. Müller, SEM. Lake Tanganyika material, collected 1987. **Figs 24–28.** External views. **Figs 24, 25.** Valve face near the poles, showing the siliceous ridge (arrow) on the axial area and siliceous granules present in the depressions of the valve undulations. **Fig. 27.** Valve face showing barred fenestrae. **Fig. 28.** Girdle view showing barred fenestrae on the valve mantle and girdle bands near one pole. **Figs 29–31.** Internal valve views. **Fig. 30.** Uniseriate striae continuing into the portulae. **Fig. 31.** Lip-like extension (arrow) of a girdle band. Scale bars: 1 μm (Figs 26, 27, 30, 31); 10 μm (Figs 24, 25, 28, 29).

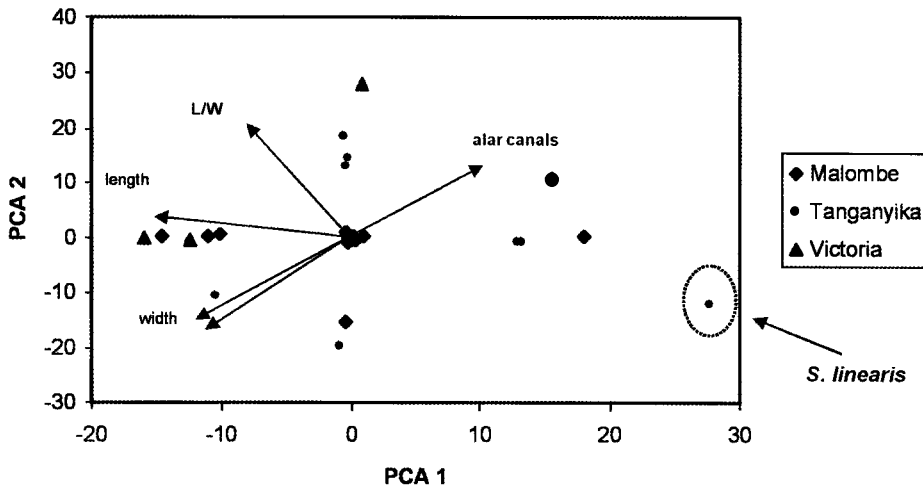


Fig. 32. Biplot (PCA axis 1 and 2) of *Surirella engleri* taxa from Lakes Malombe (large black rhombus), Tanganyika (black dots), Victoria (large black triangular) and *Surirella linearis* from Lake Tanganyika based on some morphological data (e.g. valve length, width, length-to-width ratio (L/W), number of alar canals in 10 μm).

DISCUSSION

The description of *Surirella engleri* by Müller (1903) started with the “forma genuina”, which in Müller’s nomenclatural understanding was the form, containing the type of the species (a superfluous name of the autonyms “var. respectively f. *engleri*”). Müller (1903) also added “f. *recta*” (1903, p. 28) probably wanting to illustrate that the typical *S. engleri* had straight valve margins in contrast to the four constricted formae and variety that he described at the same time from the same material. According to Greuter *et al.* (2000) these formae “genuina, recta” are not validly published; but this does not affect the validity of the specific name.

However, we believe that in Müller’s taxon concept, his formae are only illustrating the extreme ends of the variability within a taxon not necessarily signifying a genetically different taxon (Cocquyt & Jahn 2005; on his taxon concept see also Jahn 2002). Since we consider the more or less deep constriction of the valve margins and the more acutely rounded poles within the morphological variability (Figs 1–15), we treated the infraspecific taxa of *Surirella engleri*, *S. engleri* f. *angustior*, f. *subconstricta*, var. *constricta*, and var. *constricta* f. *sublaevis*, as taxonomic synonyms. The forma *sierraleonensis* Woodhead & Tweed (Woodhead & Tweed 1958b) and the forma *densecostata* Maillard (Maillard 1977) from Mali probably also fall in the variability of *Surirella engleri*, and VanLandingham (1978) has already considered forma *sierraleonensis* as conspecific. A study of the types, however, is needed to be sure that they are conspecific.

Results of the Tanganyika cultures show that in the same clone *S. engleri* had straight as well as slightly constricted valves. This proves that a constriction of the valve margin is not a good characteristic for distinguishing different taxa within *Surirella engleri* and supports Gasse (1986) who already assumed that the variety and formae of *S. engleri* were to be regarded as synonyms of the nominate variety and forma as they are connected to each other through a series of transitional forms. Also Hustedt (1949, p. 154) remarked that the larger valves observed in material from Lake Edward were always slightly constricted and that intermediate valves between f. *subconstricta* and var. *constricta* were present.

Besides the outline, Müller put a lot of emphasis on the wing projection and robustness of the alar canals, but he was not very clear in his description of this feature. For the f. *sublaevis*, for instance, he mentioned that there was “no wing projection” whereas in the nominate forma “genuina” he wrote that the wing projection was “indistinct”; for all the formae he described, the undulations (costae) are weakly developed on the valve face and the alar canals are more strongly built near the margins, except for the var. *constricta* where it is “stronger, and sometimes weaker”. But in all the material we studied, no real difference was observed. Because neither the outline nor the characteristics of the wing projection nor the strongness of the alar canals are good features for distinguishing entities within *S. engleri*, we therefore decided to abandon Müller’s infraspecific taxa.

This synonymization of Müller’s variety (there is only one variety but several forms) is in contrast to our earlier statement (Cocquyt & Jahn 2005) that his varieties are generally separate taxonomic entities which we today would define as species. We would restrict this statement now to those cases where he described African varieties of European species; i.e. where he connected new African taxa to established European taxa. However, in the case of *S. engleri*, where he described a number of African infraspecific variation within an African taxon, we think that his variety as well as his formae are only the extreme ends of the variability within this species.

A close relationship with *Surirella linearis* W. Smith, which has been reported from European as well as from African waters, was already mentioned by Müller (1903) as a note after his description of *S. engleri* f. *angustior*. Also Cocquyt (1998) found that the number of alar canals in 10 µm (2.7–3.5) was higher but on the upper limit of *S. engleri* (1.3–2.8 in 10 µm). This may point to a possible relationship between the two species. Table 3 gives an overview of LM features of *Surirella engleri* and *S. linearis* from Müller’s material from Lake Malombe, first author’s material from Lake Tanganyika, and data from the literature. Note the Krammer & Lange-Bertalot (1997) data are only from European material. Although there is some overlap in the LM features within the African material, the habitat of both taxa is different: *S. engleri* being a planktonic species, while *S. linearis* is benthic. And the PCA result (Fig. 32) shows that the one included valve of *S. linearis* separated clearly from the *S. engleri* valves. However, more morphometric data on *Surirella linearis* are needed to state the statistic validity of this separation. This is an additional argument that these two species are separate taxa, but that they might be closely related and might have derived from a common ancestor, but as long as the *S. linearis* type has not been reinvestigated, no conclusion can be drawn.

A possible synonymy of *Surirella africana-orientalis* Cocquyt & R. Jahn (replaced name for *Surirella constricta* var. *africana* O. Müller) with *S. engleri* as suggested by Hustedt (1911; as *S. engleri* var. *constricta* f. *africana* (O. Müller) Hustedt) is incorrect. *Surirella africana-orientalis* has a sole-shaped valve with more broadly rounded cuneate poles which are never protracted. An emended description of this taxon with the depicted lectotype and epitype is given in Cocquyt & Jahn (2005).

An infraspecific relationship between *S. engleri*, *S. malombae* O. Müller and *S. nyassae* O. Müller was suggested by Müller (in Ostenfeld 1909) because in Lake Victoria, mainly intermediate forms between the three species were supposedly found and the typical valves were seldom observed, whereas in Lakes Malawi and Malombe, on the other hand, the three species *S. nyassae*, *S. malombae* and *S. engleri* were sharply delimited. Results of an ordination analysis of some LM morphometric features on material from the three lakes, however, showed a distinct separation between all four species: the specimens from Lake Malawi were corresponding to *S. nyassae*, the specimens from Lake Malombe to *S. malombae*, the specimens from Lake Tanganyika to *S. chepurnovii* Cocquyt & R. Jahn, and the valves named *S. engleri* from Lakes Tanganyika and Malombe grouped together and separated clearly from the other three (Cocquyt & Jahn 2007).

Table 3. Comparison of LM features, habitat and distribution of *Surirella engleri* with *S. linearis* from our own measurements of East African material and from literature.

	<i>Surirella engleri</i> O.Müller	<i>Surirella linearis</i> W. Sm. (Hustedt 1942)	<i>Surirella linearis</i> W. Sm. (Cocquyt 1998)	<i>Surirella linearis</i> W. Sm. (Krammer & Lange Bertalot 1997)
Length [μm]	(103.5) 115–360	20–125	45–57 (62.5)	20–120
Width [μm]	17.2–60	9–25	12–20 (23.5)	9–25
Alar canals [in 10 μm]	1.3–2.8 (3.2)	2.0–3.0	2.7–3.5	2.0–3.0
Valve shape	linear to lanceolate	elliptical to linear -elliptical	elliptical to linear -elliptical	linear to linear lanceolate to lanceolate
Poles	more or less cuneiform	bluntly rounded		cuneiform
Distribution	Tropical Africa	Cosmopolitan	Cosmopolitan	Cosmopolitan
African distribution	Lakes Malawi, Malombe, Tanganyika, Victoria	Lake Malawi	Lake Tanganyika	
Habitat	planktonic	benthic, sometimes planktonic	littoral	

Small differences in SEM features were observed between *S. engleri* populations collected in 1900 in Lake Malombe, the type locality, and collected about 90 years later in Lake Tanganyika. The higher number of striae and areolae in 10 μm and the higher number of fenestral bars in 10 μm in the population of Lake Malombe can be an indication that this taxon is radiating and in the process of speciation in the African Great Rift area as was suggested for *Surirella nyassae*, *S. malombae* and *S. chepurnovii* (Cocquyt & Jahn 2007).

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