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Schmidingerothrix extraordinaria nov. gen., nov. spec., a secondarily oligomerized hypotrich (Ciliophora, Hypotricha, Schmidingerotrichidae nov. fam.) from hypersaline soils of Africa

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Abstract

Schmidingerothrix extraordinaria nov. gen., nov. spec. was discovered in hypersaline soils from Namibia and Egypt. Its morphology and ontogenesis were studied with standard methods. *Schmidingerothrix extraordinaria* is a highly flexible, slender hypotrich with an average size of 90 × 15 μm. Likely, it prefers a salinity around 100‰ and feeds mainly on bacteria. *Schmidingerothrix* is extraordinary in having a frayed buccal lip, three-rowed adoral membranelles, only one frontal cirrus, a distinct gap between frontal and ventral adoral membranelles, and a miniaturized first frontal membranelle, while a paroral membrane, dorsal bristle rows, and buccal, transverse, and caudal cirri are absent. The ontogenesis is simple: the opisthe oral apparatus and frontoventral ciliature originate de novo, while parental structures are involved in the development of the ciliature of the proter. This special organization is used to define a new family, the Schmidingerotrichidae, which is likely related to the Cladotrichidae. *Schmidingerothrix extraordinaria* is very likely a secondarily oligomerized hypotrich, and the reduction occurred possibly very long ago because no traces of the ancestral ciliature remained in the ontogenetic processes. Possibly, the simple ciliature is an adaptation to highly saline habitats, where competition is low and bacterial food abundant.

Keywords: Biodiversity; Loss of dorsal bristle rows; Loss of paroral membrane; Ontogenesis; Reduction

Introduction

Studies of the past decades have shown a fascinating diversity of undescribed hypotrich ciliates (for reviews, see Berger 1999, 2006, 2008, 2011), supporting the notion of Foissner et al. (2008) that as much as 80% of ciliate diversity is still undescribed. Few features of the hypotrichs are so stable that they are possibly not affected by evolution, for instance, the dorsal bristles, i.e., rows of dikinetids having only the anterior basal body ciliated. Thus, I was fascinated to discover a hypotrich without dorsal bristles in highly saline soils of Africa. Other very stable features of the hypotrichs include two undulating membranes (paroral and endoral) and adoral membranelles composed of four ciliary rows. The new ciliate from Africa lost the paroral and the middle ciliary row of the adoral membranelles. These and other peculiarities, e.g., lip fringes and the loss of buccal, transverse, and caudal cirri show the extraordinary vegetative morphology of the new ciliate, while its ontogenesis is comparatively simple, unfortunately telling us nothing about the ancestral cirral pattern.

Many curious hypotrichs live in saline inland habitats, e.g., *Cladotricha* Gaievskaia, 1925; *Erniella* Foissner, 1987; *Afrothrix* Foissner, 1999; *Etoschothrix* Foissner et al., 2002;

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and *Schmidingerothrix*, the new genus described here, suggesting that these are major drivers of evolution. However, few detailed studies of ciliates from saline inland biotopes are available although the above mentioned and some other studies (e.g., Borror 1972; Foissner et al. 2002; Kahl 1933; Ruinen 1938; Wilbert 1986, 1995; Wilbert and Kahan 1981, 1986) show a high number of undescribed ciliate species living there.

I shall describe *Schmidingerothrix* in great detail, not only because of its unusual morphology but also because it is likely related to the Cladotrichidae, a poorly known group of hypotrichs (Berger 2011). Unfortunately, attempts to obtain molecular sequences were unsuccessful.

Material and Methods

Material and cultivation

Schmidingerothrix extraordinaria was discovered in three hypersaline soil samples from Africa, using the non-flooded Petri dish method, as described in Foissner and Xu (2007). Briefly, this simple method involves placing 50–500 g air-dried terrestrial material (soil, leaf litter, roots, etc.) in a Petri dish (13–18 cm wide and 2–3 cm high) and saturating, but not flooding it, with distilled water. Such cultures are analysed for ciliates by inspecting about 2 ml of the run-off on days 2, 7, 14, 21 and 28. For highly saline samples (>30‰), the method usually needs to be modified. First, an ordinary, non-flooded Petri dish culture is set up with the material available. If no or very few ciliate species appear and look unhealthy after three days, the culture is flooded 5–10 times with distilled water to reduce salinity. Then, the sample is wetted as before, that is, not flooded and again inspected for ciliates after three days. If no ciliates appear, the procedure is repeated several times, i.e., until ciliates begin to grow.

Raw cultures were set up in Petri dishes, using artificial sea water with the same salinity as the soil water in the non-flooded Petri dish culture. Then, some crushed wheat or rice grains and 2 ml of soil percolate, which contained a variety of protists, were added. Usually, such "raw cultures" grow well and are sufficient for taxonomic purposes. Frequently, the target ciliates become very abundant also in the non-flooded Petri dish culture.

I first discovered *S. extraordinaria* in a soil and litter sample from the margin of Fischer's Pan in the Etosha National Park, Namibia (sample designation: Namibian site 4/2001). The sample, which was collected in January 2001 and investigated in June 2001, was composed of dark humus mixed with litter and cyanobacterial crusts. Salinity (measured with a refractometer) in the non-flooded Petri dish soil percolate was 90‰, pH 7. *Schmidingerothrix extraordinaria* appeared when the soil had been washed several times to reach a salinity of 80‰.

The second population occurred also in Namibia, viz., in the Skeletal Coast National Park near the village of Terrace Bay. The sample, which was collected in January 2001 and investigated in May 2001, was taken from the margin of a pool surrounded by small sand hills formed by sedge bushes. These hills were full of sedge roots and decomposing litter, which was collected with sand in a ratio of about 1:1. The sample had a salinity of 180‰ and pH 7.2. Ciliates appeared when the sample was washed to a salinity of 130‰.

The third population is from an island in the Nile River some kilometers south of the town of Luxor. The sample, which was collected in June 2007 and investigated in June 2008, consisted mainly of sand and had a salinity of 120‰. Ciliates appeared when it was washed to a salinity of 90‰.

Morphological methods

Living cells were studied using a high-power oil immersion objective and differential interference contrast microscopy. Protargol impregnation and scanning electron microscopy (SEM) were performed as described by Foissner and Xu (2007). Some drops of osmium acid (2%) were added to Stieve's solution to obtain well-fixed cells; in spite of this, cells became inflated (width) and shrunk (length) by about 20%.

Counts and measurements of silvered specimens were performed at a magnification of 1.000×. In vivo measurements were conducted at magnifications of 40–1.000×. Drawings of live specimens were based on free-hand sketches and micrographs; those of impregnated cells were made with a drawing device. In the ontogenetic stages, parental structures are shown by contour, while newly formed structures are shaded black. Each of the stages depicted has been seen in at least two specimens.

Terminology

For general and specific terms see Lynn (2008) and Berger (2011). Details of the oral apparatus are according to Foissner and Al-Rasheid (2006).

Results

Schmidingerotrichidae nov. fam.

Diagnosis: Amphisiellids (?) with a single short frontoventral cirral row, one frontal cirrus, one right and one left marginal row, an adoral zone of membranelles, and an endoral membrane. Paroral membrane and dorsal bristles absent. Frontoventral and oral ciliature develop independently in proter and opisthe, while marginal cirral rows and nuclear apparatus divide as usual. Frontoventral ciliature developing de novo in the opisthe, while parental ciliature is involved in the proter.

Type genus: *Schmidingerothrix* nov. gen.

Schmidingerothrix nov. gen.

Diagnosis: Schmidingerotrichidae with adoral membranelles each composed of three rows of basal bodies, a distinct gap between frontal and ventral adoral membranelles, and a fringed buccal lip. Frontal cirri 2 and 3, buccal cirrus, transverse cirri, and caudal cirri absent.

Type species: *Schmidingerothrix extraordinaria* nov. spec.

Etymology and dedication: *Schmidingerothrix* is a composite of the surname "Schmidinger", the thematic vowel "o", and the Greek noun "thrix" (hair ~ ciliate s. l.). Feminine gender. I dedicate this new genus to Univ.-Prof. Dr. Heinrich Schmidinger, Rector of Salzburg University, who granted a permanent position to Dr. Sabine Agatha, my former postdoctoral student, so that taxonomic research on ciliates can continue in Salzburg after my retirement.

Description of *Schmidingerothrix extraordinaria* nov. spec. (Figs 1–64, Table 1)

Diagnosis: Size about 90 × 15 μm in vivo. Body slender (~6:1), usually slightly widened just posterior to mid-body, with short but distinct tail. Four macronuclear nodules, forming a row near right margin in central quarters of cell; two micronuclei. Cortical granules in loose rows, colourless, about 1 μm across. Frontoventral cirral row composed of an average of three cirri. Right marginal row composed of an average of 27 cirri, left of 21. Adoral zone about 29% of body length, composed of an average of three frontal and 15 ventral membranelles. Endoral membrane 9 μm long on average.

Type locality: Highly saline (90‰) soil from Fischer's Pan in the Etosha National Park, Namibia, S 18°45′E 16°55′.

Type material: One holotype (Figs 5, 6, 23, 27) and three paratype slides (registration numbers: 2011/410; 2011/411–413) with protargol-impregnated morphostatic and dividing specimens have been deposited in the Biologiezentrum of the Oberösterreichische Landesmuseum in Linz (LI). Two voucher slides (2011/414, 415) each from soil of the Skeletal Coast in Namibia and a small island in the Nile River, Egypt have been deposited at the same repository. The holotype and other relevant specimens have been marked and labeled by black ink circles on the coverslip.

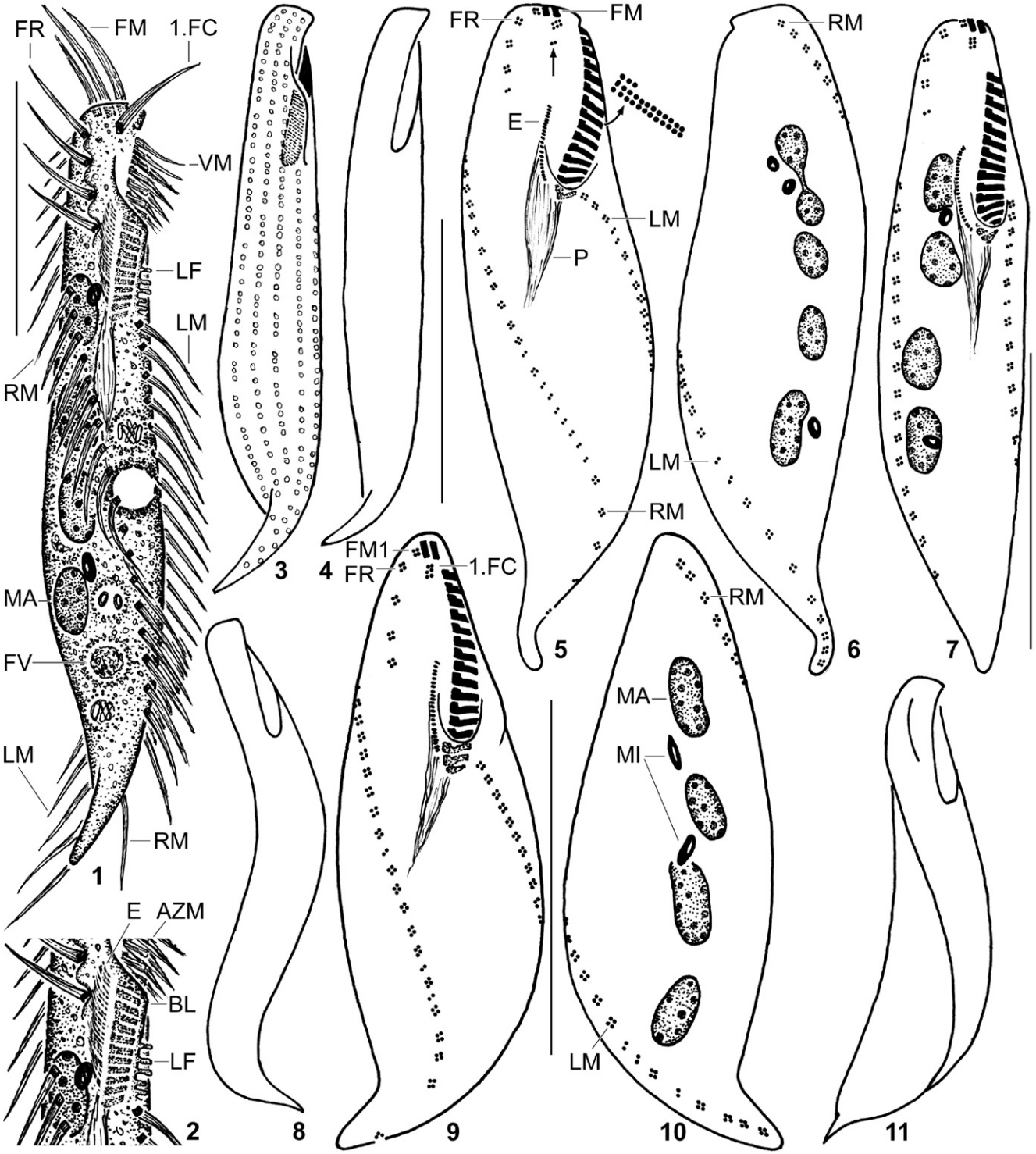
Etymology: The Latin adjective "extraordinaria" refers to the curious morphology of this ciliate.

Description (Figs 1–41, 49, 50, Table 1): The three populations studied were highly similar both in vivo and in protargol preparations. However, well prepared specimens were obtained only from Namibian site 4/2001 (type locality). Thus, all features based on protargol impregnation are from specimens of this site, while live observations include all populations because each was studied independently.

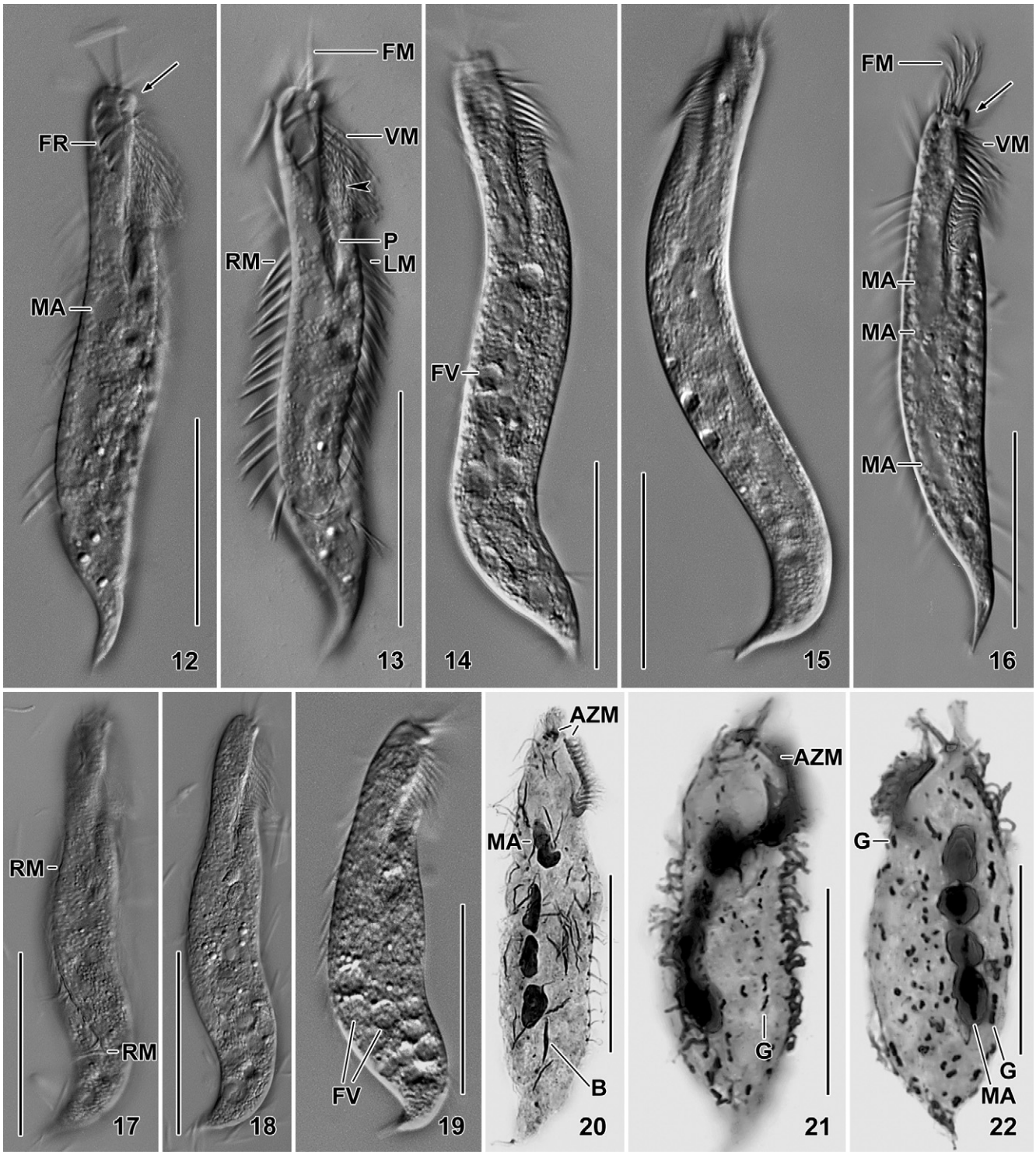
Size in vivo moderately variable, i.e., 70–100 μm × 10–20 μm, on average 90 μm × 15 μm (Table 1); in protargol preparations length shrinks by about 20%, while width is inflated by about 15% (Table 1); length: width ratio thus on average distinctly narrower in vivo (~6:1) than in protargol preparations (~4:1). Cells highly flexible, showing a variety of shapes, of which those recognizable in Figs 1, 3, 4, 12, 13, 16, 33, 50 are most common, i.e., pisciform with a slight right marginal bulge just posterior to mid-body and a short but distinct tail; cylindroidal or sigmoidal, laterally minimally flattened cells also rather common; anterior body end transverse truncate and slightly projecting ventrally (Figs 1, 8, 11, 14–16, 19, 29, 30, 49, 50); tail usually accentuated by a shallow furrow and directed right (Figs 1, 3, 4, 19, 50); cells just taken from the non-flooded Petri dish culture invariably slightly to distinctly twisted about main body axis (Figs 1, 5, 9, 17, 30, 33) and only slightly flattened laterally, rarely up to 2:1. Nuclear apparatus near right margin in central quarters of body. Three to five, usually four ellipsoidal, hyaline macronuclear nodules with minute nucleoli. One to three, usually two ellipsoidal, lenticular or narrowly ovate micronuclei along macronuclear strand, i.e., not in fixed position (Figs 1, 6, 7, 10, 16, 22–25, Table 1). Contractile vacuole in or slightly posterior to mid-body near left margin of cell, with two lacunar canals (Fig. 1). Cytopyge in base of tail, fecal mass compact and about 4 μm across. Cortex very flexible, difficult to preserve (see Material and Methods). Cortical granules distributed in entire cortex, form loose rows; individual granules colourless and about 1 μm across and thus difficult to recognize, rarely impregnate with protargol (Figs 3, 21, 22, 33, 35). Cytoplasm colourless, contains some lipid droplets 1–3 μm across and, mainly in third quarter of cell, few to many globular to ellipsoidal food vacuoles 3–15 μm in diameter. Feeds on bacteria, including spore-bearing bacilli, rarely on heterotrophic flagellates (Figs 1, 12, 14, 19, 34, 49); some cells contain rod-shaped bacteria deeply impregnating with protargol (Fig. 20). Glides slowly to rapidly on microscope slides and between soil particles, showing wriggling movements (Figs 15, 19, 33, 49, 50).

Cirri 7–10 μm long in vivo, most composed of four cilia, rarely of two or six. Cirral pattern simple, i.e., consisting of marginal and frontoventral cirri (Figs 1, 5–7, 9, 10, 12, 13, 23–33, 36, Table 1). Marginal rows wind helically, right row commences subapically on dorsal side of cell and extends obliquely posteriorly, usually ending subterminally in midline of ventral side; left row commences at level of buccal vertex and extends dorsally in posterior third of cell, ending at tip of tail. Frontoventral row commences right of first frontal adoral membranelle, slightly convex, composed of 2–6 cirri, on average of three. A single frontal cirrus in left anterior corner of cell, composed of 6–10 cilia, designated "first frontal cirrus" because of its location (if, e.g., compared with oxytrichids); rarely, a second, minute cirrus just posterior to first frontal cirrus (Figs 5, 25, 27, 32).

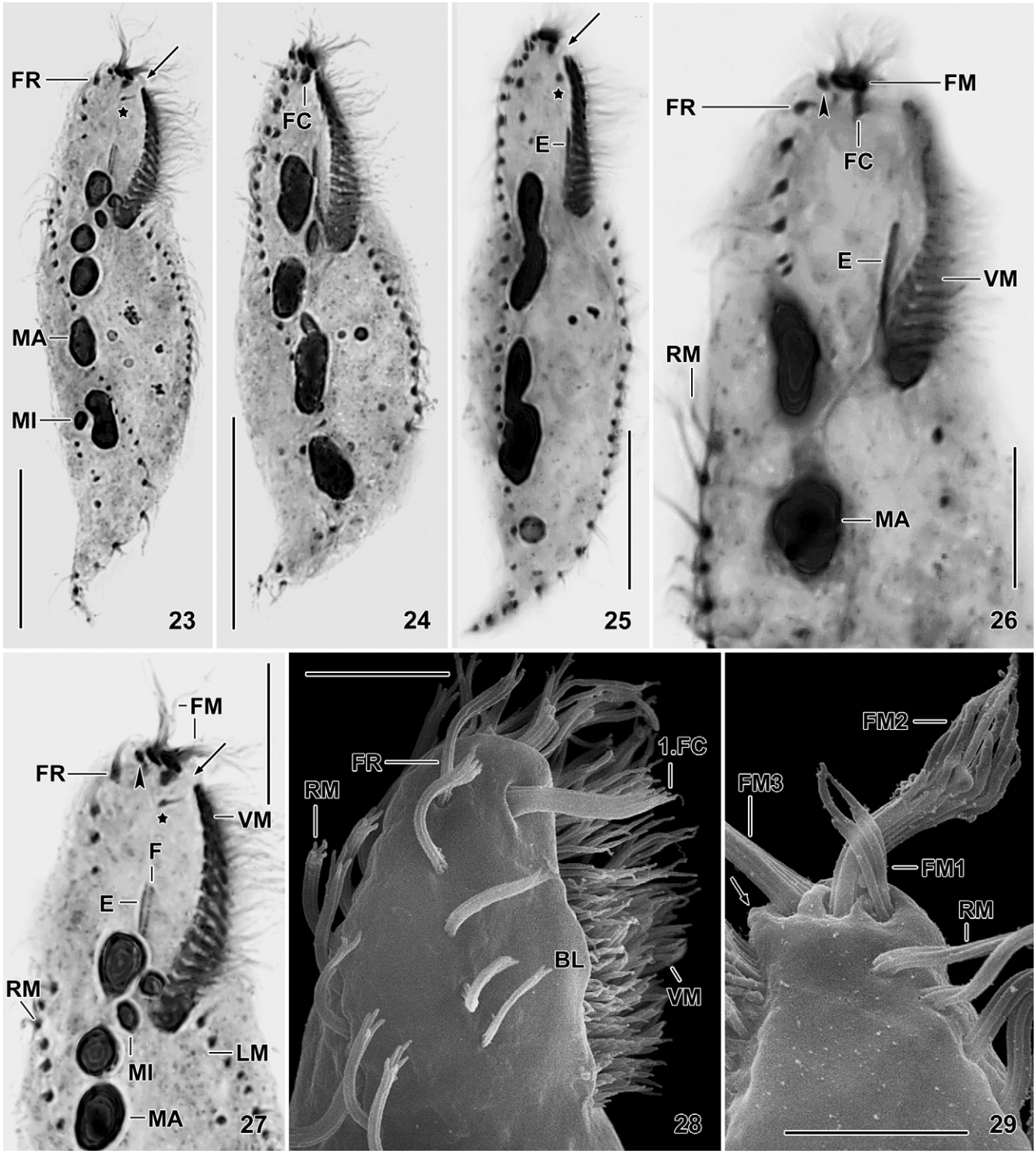
Oral apparatus in left anterior quadrant of cell, inconspicuous but full of remarkable details (Figs 1–3, 5, 7, 9, 12–16, 23–30, 32–34, 38–41, Table 1). Adoral zone of membranelles extends over 29% of body length on average, composed of three frontal and 15 ventral membranelles on average, both groups separated by a



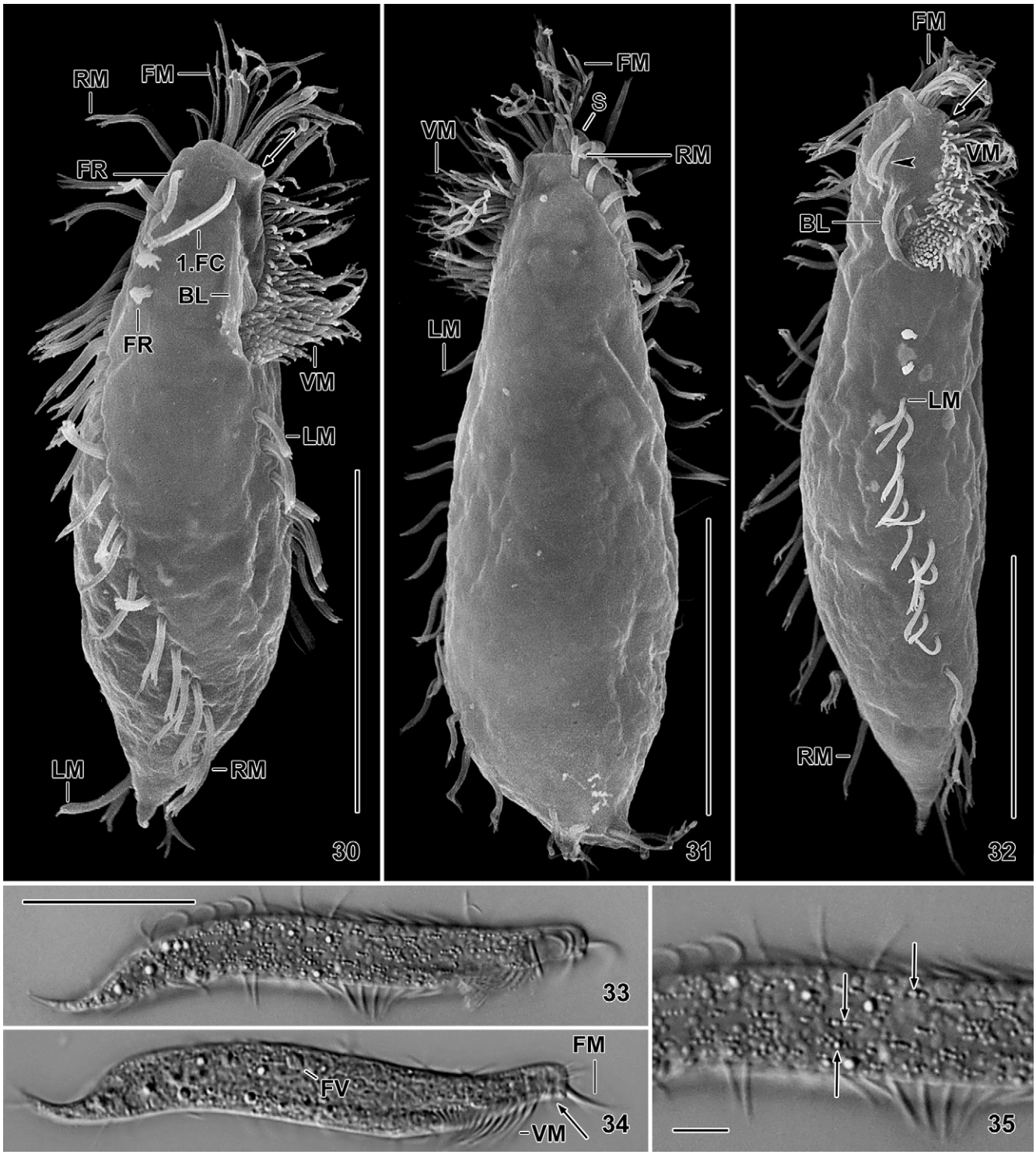
Figs 1–11. *Schmidingerothrix extraordinaria*, specimens from type population from life (1–4, 8, 11) and after protargol impregnation (5–7, 9, 10). (1, 2) Ventral view of a representative specimen, length 90 μm. Note the fringed buccal lip (2, LF). (3) The cortex contains loose rows of colourless granules. (4, 8, 11) Shape variants. (5, 6) Infraciliature of ventral and dorsal side and nuclear apparatus of holotype specimen, length 70 μm. The arrow marks a minute cirrus posterior to the first frontal cirrus. The adoral membranelles are composed of only three rows of cilia. Most cirri comprise only four cilia. (7) Ventral view of a specimen with almost straight marginal cirral rows. (9, 10) A small (52 μm) paratype specimen with helically extending marginal cirral rows. AZM – adoral zone of membranelles, BL – buccal lip, E – endoral membrane, 1.FC – first frontal cirrus, FM – frontal adoral membranelles, FM1 – frontal adoral membranelle 1, FR – frontoventral cirral row, FV – food vacuole, LF – lip fringes, LM – left marginal cirral row, MA – macronuclear nodules, MI – micronuclei, P – pharynx, RM – right marginal cirral row, VM – ventral adoral membranelles. Scale bars 30 μm.



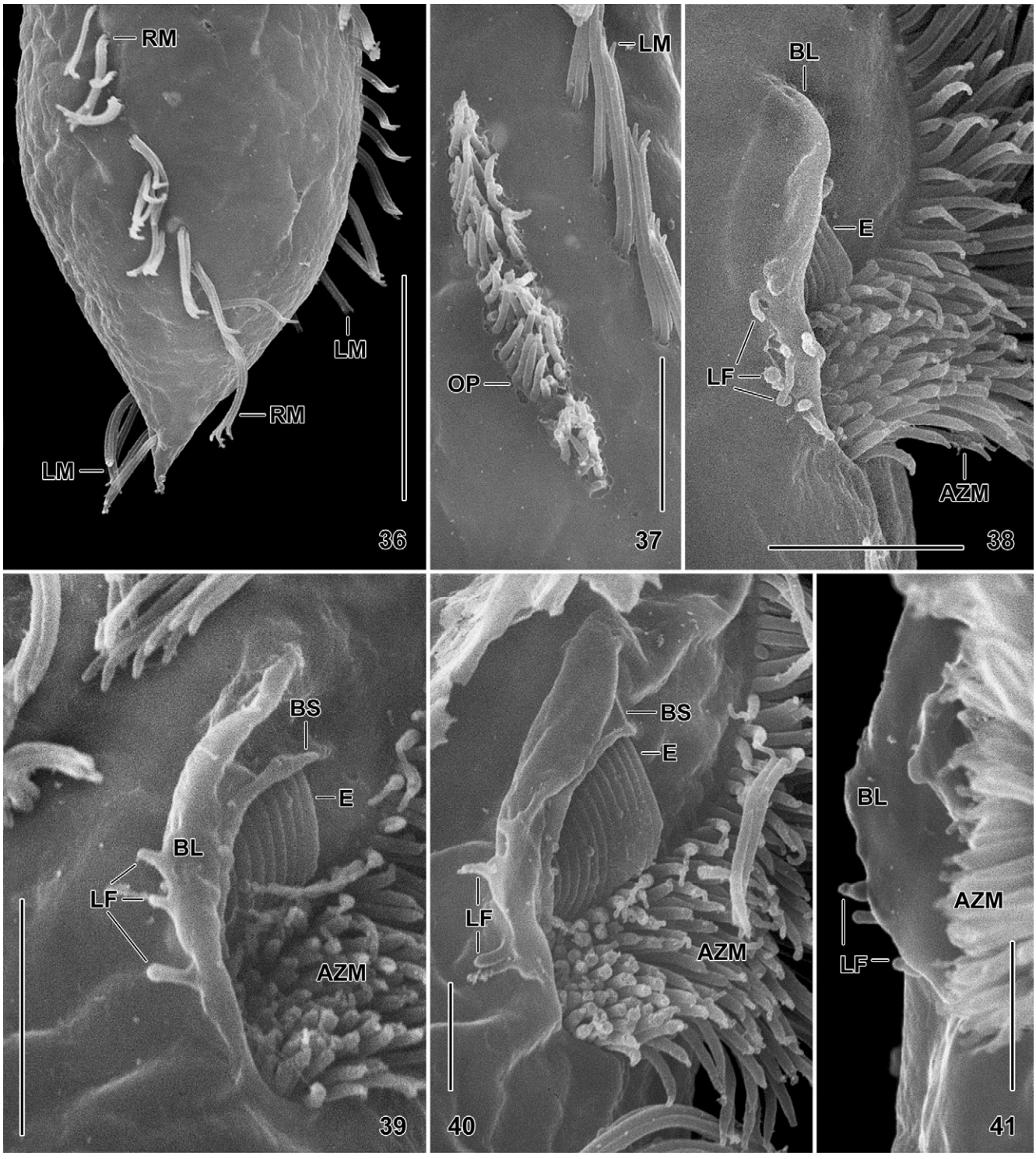
Figs 12–22. *Schmidingerothrix extraordinaria*, specimens from type population from life (12–19) and after protargol impregnation (20–22). (12–19) Shape variability and body organization of freely motile specimens. The figure pairs 12/13 and 17/18 show the same specimens at two focal planes. Note the acute tail, which is usually curved to the right; the slightly helical course of the marginal cirral rows (13, 17); the adoral zone of the membranelles, which occupies in vivo about 29% of body length and has a gap (arrows) between frontal and ventral membranelles; the buccal lip (13, arrowhead), which covers the proximal half of the adoral zone; and the row of macronuclear nodules near the right margin of the cell. (20) Some specimens are infected with long bacterial rods. (21, 22) Ventral and dorsal view, showing loose granule rows in the cortex. Note the row of macronuclear nodules near right body margin. AZM – adoral zone of membranelles, B – bacilli, FM – frontoventral adoral membranelles, FR – frontal cirral row, FV – food vacuoles, G – cortical granules, LM – left marginal cirral row, MA – macronuclear nodules, P – pharynx, RM – right marginal cirral row, VM – ventral adoral membranelles. Scale bars 30 μm.



Figs 23–29. *Schmidingerothrix extraordinaria*, infraciliature of specimens from type population after protargol impregnation (23–27) and in the SEM (28, 29). Arrows mark gap between frontal and ventral adoral membranelles; arrowheads denote the minute first frontal membranelle; asterisks mark a minute cirrus posterior of the first frontal cirrus. (23, 27) Ventral view of holotype specimen, showing the organization of the infraciliature and the nuclear apparatus. (24–26) Ventral views of paratype specimens. (28). Ventral view of oral portion, showing that the buccal cavity and part of the adoral zone are covered by the buccal lip. (29) Dorsal view of anterior body end, showing the frontal adoral membranelles, of which membranelle 1 consists of only four distinctly shortened cilia. BL – buccal lip, E – endoral membrane, F – fibres originating from the basal bodies of the endoral membrane, FC(1) – first frontal cirrus, FM1–3 – frontal adoral membranelles, FR – frontoventral cirral row, LM – left marginal cirral row, MA – macronuclear nodules, MI – micronuclei, RM – right marginal cirral row, VM – ventral adoral membranelles. Scale bars 5 μm (28, 29), 10 μm (26, 27), and 20 μm (23–25).



Figs 30–35. *Schmidingerothrix extraordinaria*, specimens from type population (30–32) and Egypt (33–35) in the SEM (30–32) and from life (33–35). The SEM specimens widened distinctly due to the preparation procedures (cp. Figs 12–19). (30) Ventral view, showing the helically extending marginal cirral rows and the sparse frontal ciliature. The arrow marks the gap between frontal and ventral adoral membranelles. (31) Dorsal view, showing the absence of dorsal bristles, a main feature of the new family. (32) Left marginal view, showing the location of the oral structures. The arrowhead denotes a thin cirrus posterior to the frontal cirrus. The arrow marks the gap between frontal and ventral adoral membranelles. (33, 35) Surface views, showing the loose cortical granulation (arrows). (34) Same specimen as in (33) but focused on cell centre to show the wide gap between frontal and ventral adoral membranelles (arrow). BL – buccal lip, 1.FC – first frontal cirrus, FM – frontal adoral membranelles, FR – frontal cirral row, FV – food vacuole, LM – left marginal cirral row, RM – right marginal cirral row, S – scutum, VM – ventral adoral membranelles. Scale bars 30 μm (30–34) and 5 μm (35).



Figs 36–41. *Schmidingerothrix extraordinaria*, specimens from type population in the SEM. (36) Posterior body portion, showing the acute posterior end and the helically extending marginal cirral rows. (37) The oral primordium develops apokinetally near the left marginal row, whose cirri are composed of 2–4 cilia. (38–41) Oral apparatus, showing the posterior third of the adoral zone of membranelles, whose cilia increase in length from right to left; the buccal seal that is partially destroyed, exposing the cilia of the endoral membrane; and the buccal lip which has minute processes, the lip fringes, in the lower half, a unique feature not described in any other hypotrich. AZM – adoral zone of membranelles, BL – buccal lip, BS – buccal seal, E – endoral membrane, LF – lip fringes, LM – left marginal cirral row, OP – oral primordium, RM – right marginal cirral row. Scale bars 2 μm (40, 41), 4 μm (37–39), and 10 μm (36).

Table 1. Morphometric data on *Schmidingerothrix extraordinaria*.

Characteristics[a]	$\bar{x}$	*M*	SD	SE	CV	Min	Max	*n*
Body, length	70.1	70.0	7.8	1.7	11.2	52.0	86.0	21
Body, width	18.0	18.0	2.9	0.6	15.9	14.0	24.0	21
Body, length: width ratio	4.0	4.1	0.6	0.1	15.7	2.9	5.5	21
Body, length in vivo[b]	87.0	90.0	8.5	2.6	9.8	70.0	100.0	11
Body, width in vivo[b]	15.6	15.0	3.4	1.0	21.9	10.0	20.0	11
Body, length: width ratio in vivo[b]	5.8	5.3	1.4	0.4	23.5	4.5	8.0	11
Body, length: width ratio in vivo (from micrographs)	6.6	6.8	1.1	0.3	17.3	3.9	8.3	12
Anterior body end to end of adoral zone, distance	20.6	21.0	1.8	0.4	8.6	18.0	25.0	21
Anterior body end to end of frontoventral cirral row, distance	11.4	11.0	2.0	0.4	17.9	8.0	16.0	21
Anterior body end to begin of macronuclear figure, distance	15.0	15.0	2.5	0.6	16.9	9.0	20.0	21
Anterior body end to end of macronuclear figure, distance	48.3	49.0	5.6	1.2	11.5	33.0	57.0	21
Macronuclear figure, length	34.2	34.0	3.1	0.7	9.0	28.0	40.0	21
Macronuclear nodule 3, length	6.9	7.0	1.0	0.2	14.8	5.0	9.0	21
Macronuclear nodule 3, width	3.4	3.0	0.6	0.1	16.8	3.0	5.0	21
Macronuclear nodules, number	4.0	4.0	0.3	0.1	7.9	3.0	5.0	21
Micronuclei, length	3.0	3.0	1.0	0.2	32.0	2.0	5.0	21
Micronuclei, width	1.8	1.8	0.3	0.1	15.4	1.2	2.0	21
Micronuclei, number	1.8	2.0	0.6	0.1	33.3	1.0	3.0	21
Anterior body end to begin of endoral membrane, distance	10.4	10.0	1.5	0.3	14.1	8.0	14.0	21
Endoral membrane, length	8.7	9.0	1.2	0.3	13.3	7.0	10.0	21
Posterior body end to right marginal row, distance	8.0	8.0	4.1	0.9	52.1	0.0	15.0	21
Adoral membranelles, total number	18.3	19.0	1.0	0.2	5.2	17.0	20.0	21
Frontal adoral membranelles, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
Ventral adoral membranelles, number	15.3	16.0	1.0	0.2	6.3	14.0	17.0	21
Frontal and ventral adoral membranelles, distance	2.1	2.0	0.7	0.2	31.4	1.0	4.0	21
Largest ventral adoral membranelle, length	3.2	3.0	0.3	0.1	7.8	3.0	3.5	21
Right marginal row, number of cirri	26.7	26.0	2.7	0.6	10.0	22.0	35.0	21
Left marginal row, number of cirri	20.5	21.0	3.1	0.7	15.2	16.0	28.0	21
Frontoventral row, number of cirri	3.4	3.0	0.9	0.2	25.4	2.0	6.0	21
Frontal cirri, number	1.2	1.0	–	–	–	1.0	2.0	21

[a] Data based, if not stated otherwise, on mounted, protargol-impregnated, and randomly selected specimens from a raw culture of the type population. Measurements in μm. CV, coefficient of variation in %; *M*, median; Max, maximum; Min, minimum; *n*, number of specimens investigated; SD, standard deviation; SE, standard error of arithmetic mean; $\bar{x}$, arithmetic mean.

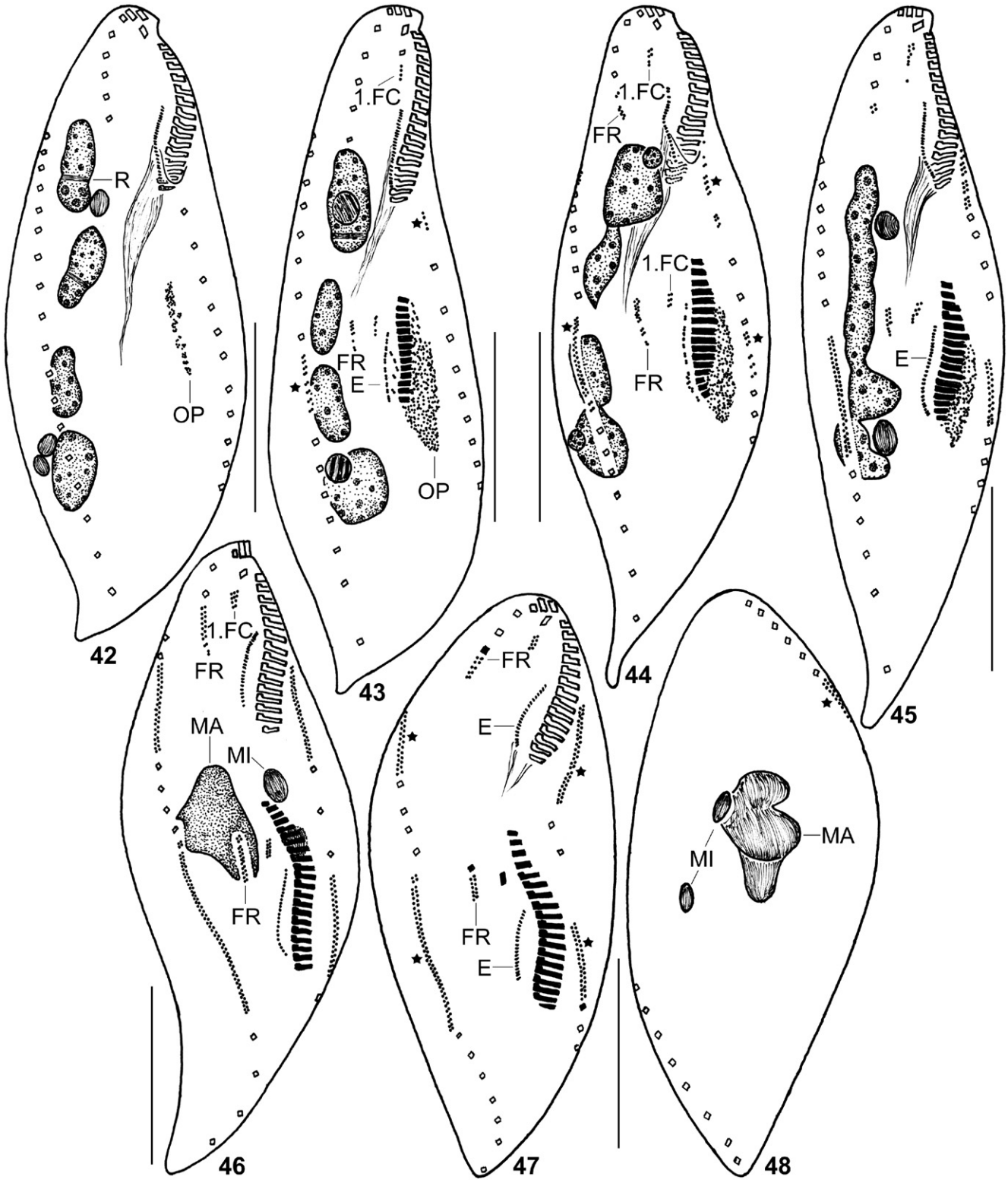
[b] From three populations.

gap about 2 μm wide in protargol preparations; individual membranelles composed of only two long and one very short row of up to 10 μm long cilia the length of which distinctly decreases in proximal quarter of zone and from left to right, except in frontal membranelles (Figs 28, 30, 38, 40); intermembranellar ridges minute, recognizable only at left margin of zone; lateral membranellar cilia and membranellar bolsters absent; first frontal membranelle composed of only 4–6 distinctly shortened cilia, and thus easily confused with cirri of frontoventral row. Frontal scutum very small, almost exposing frontal membranelles (Figs 28, 29). Buccal cavity flat and narrow in vivo (Figs 1, 13, 16, 33, 34) and in SEM preparations (Figs 30, 32, 38–40), often widened in protargol preparations (Figs 5, 23, 27). Buccal lip inconspicuous, covers posterior half of oral apparatus, fringed in posterior half, a unique feature not yet reported in any other hypotrich; fringes 1–2 μm long in vivo, delicate and thus poorly preserved in SEM preparations (Figs 1, 2, 38–41). Paroral membrane lacking, as shown by the absence of cilia on the buccal lip and the ontogenetic inactivity of the single membrane present, i.e., the endoral; endoral membrane entirely covered by buccal lip and buccal seal, composed of about twenty 4 μm long cilia, gives rise to rather distinct pharyngeal fibres (Figs 1, 2, 5, 7, 9, 13, 23–28, 38, 39).

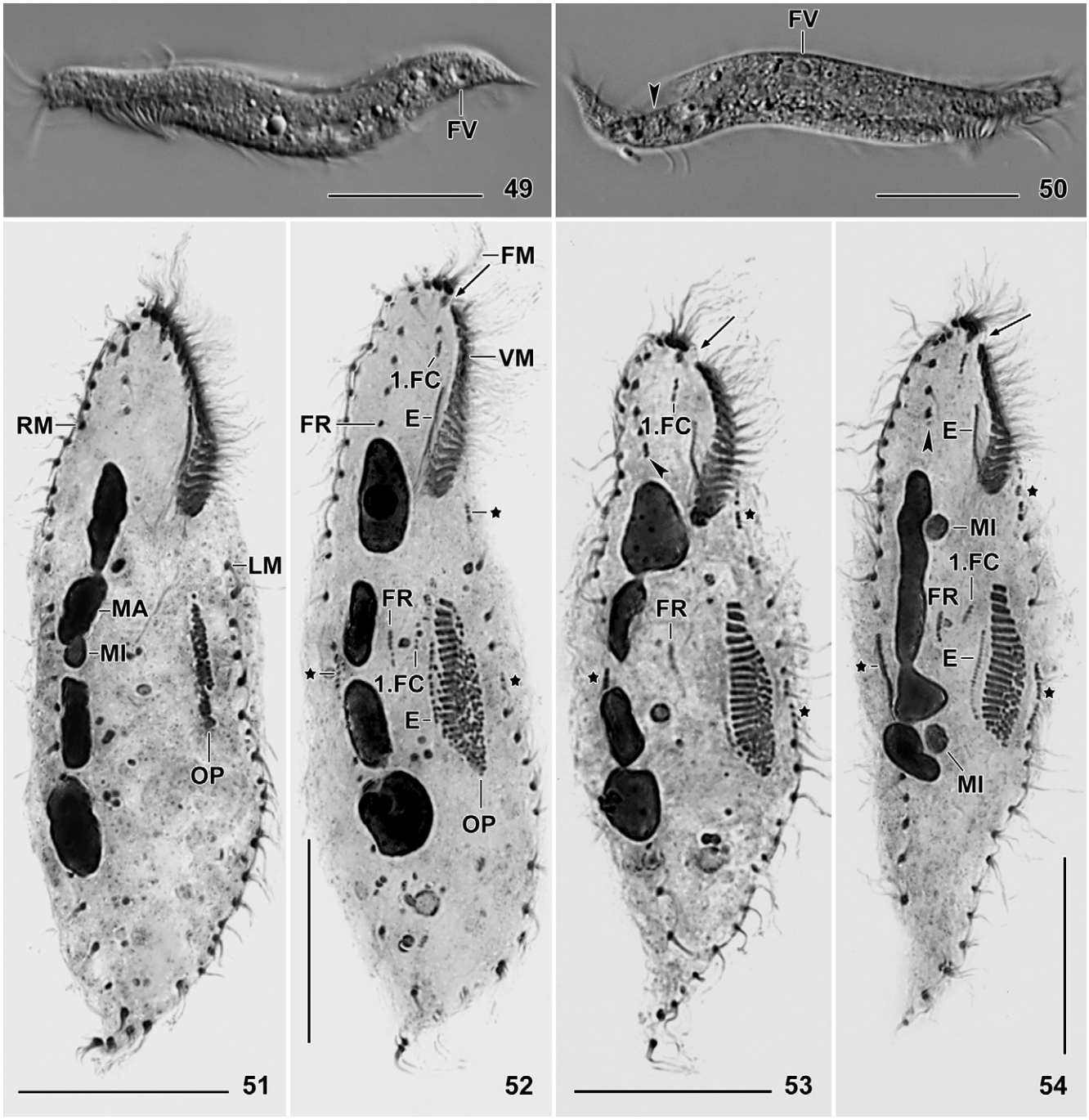
Occurrence and ecology: As described in the Material and Methods Section, *S. extraordinaria* has been found in highly saline soils from Namibia and Egypt; likely, the preferred salt concentration is around 100‰. It did not occur in many similar habitats of Australia and South America, indicating restricted distribution. The preferred food are small (<5 μm) bacterial rods; bacilli spores remain undigested.

Ontogenesis of *S. extraordinaria* (Figs 37, 42–48, 51–64)

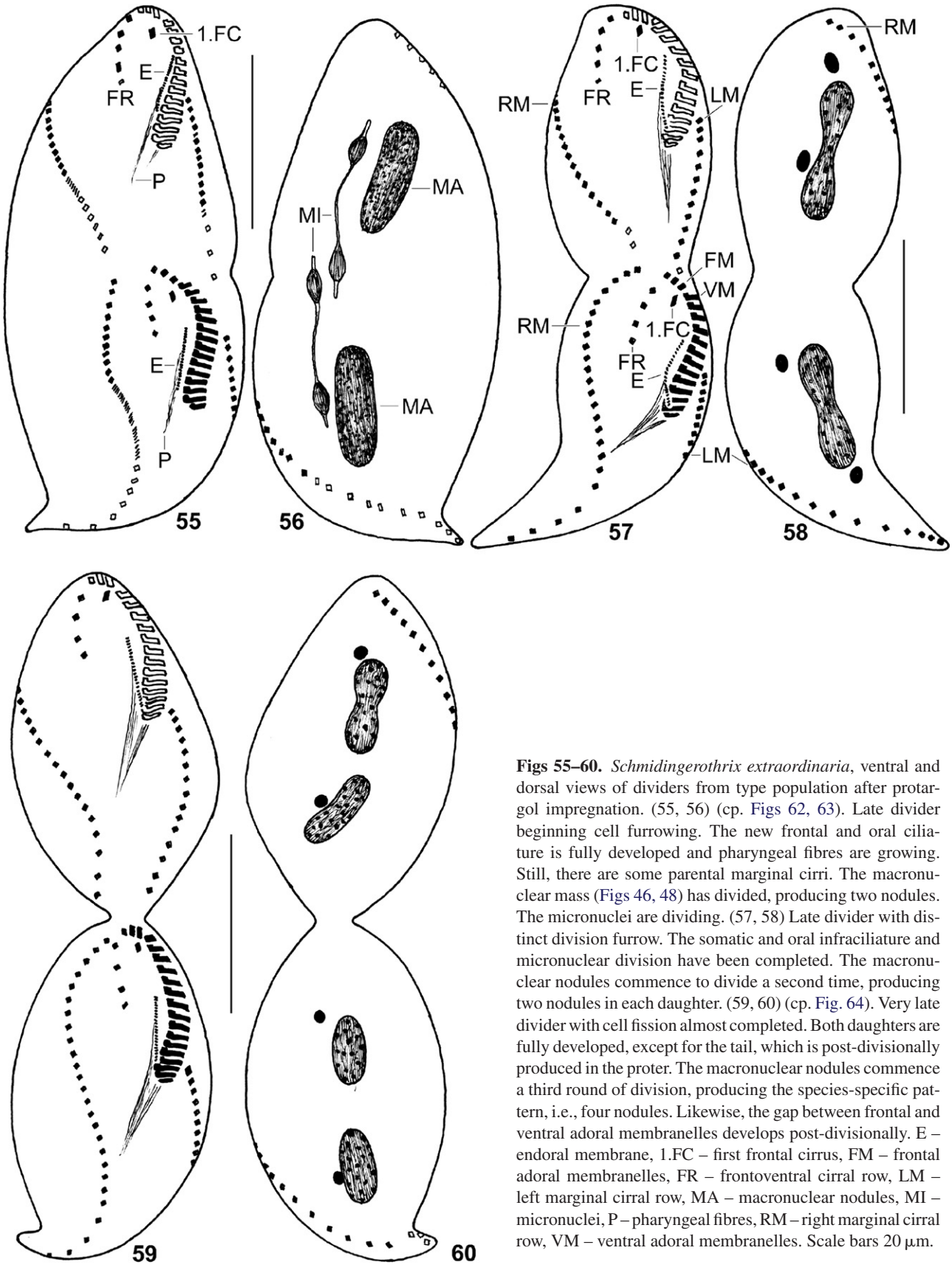
General: The ontogenesis of *S. extraordinaria* is comparatively simple due to the highly reduced ciliature. It confirms the curious vegetative morphology, viz., the three-rowed adoral membranelles, the minuteness of the first frontal membranelle, and the presence of only one frontal cirrus; further,



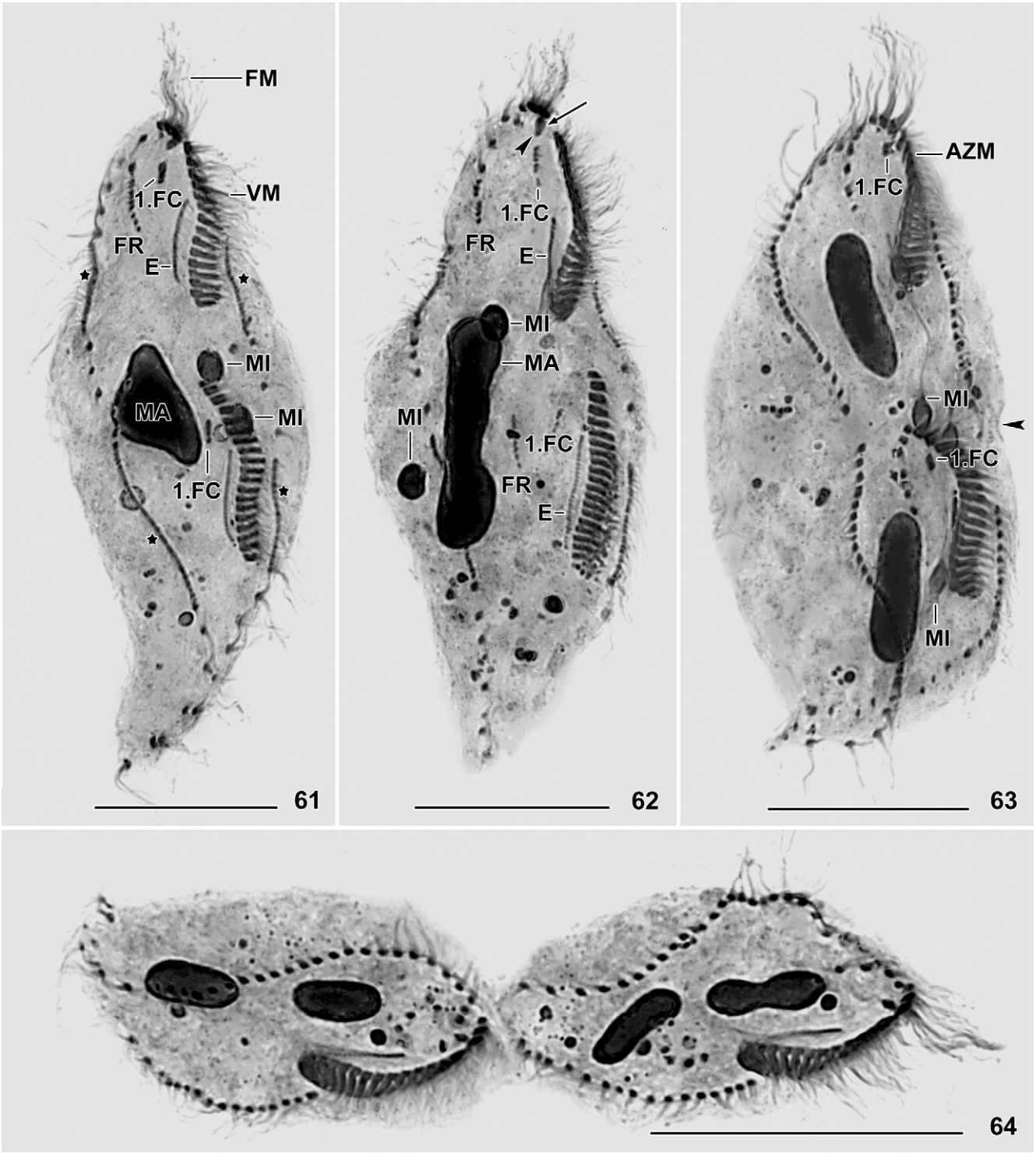
Figs 42–48. *Schmidingerothrix extraordinaria*, ventral view of dividers from type population after protargol impregnation. Asterisks mark anlagen within marginal cirral rows. (42) Very early divider with oral primordium. (43, 44) Early dividers, showing the opisthe ciliature developing de novo. The new endoral membrane consists of dikinetids. (45) Early mid-divider with fusing macronuclear nodules. The endoral now consists of monokinetids. (46–48) Mid-dividers with fused macronuclear nodules. New cirri develop in the anlagen. E – endoral membrane, 1.FC – anlage of first frontal cirrus, FR – frontal cirral row, MA – macronucleus, MI – micronuclei, OP – oral primordium, R – reorganization band. Scale bars 20 μm.



Figs 49–54. *Schmidingerothrix extraordinaria*, dividing specimens from type population (51–54) and vegetative Egyptian (49, 50) specimens from life (49, 50) and after protargol impregnation (51–54). Arrows mark gap between frontal and ventral adoral membranelles. Asterisks denote anlagen in the marginal cirral rows. (49, 50) Typical specimens, showing body shape and the transverse truncate anterior body end. The arrowhead marks the furrow at base of tail. (51) Very early divider, showing the oral primordium developing apokinetally in mid-body near the left marginal cirral row. (52, 53) Early dividers, showing that proter and opisthe develop independently and the opisthe's frontal and oral ciliature originates de novo. In the proter, the last cirrus of the frontal row becomes an anlage (arrowhead), while the anlage for the frontal cirrus develops posterior to the parental one. (54) Early mid-divider with fusing macronuclear nodules and inflated micronuclei. Arrowhead marks the last cirrus of the frontal row, which transforms into an anlage. E – endoral membrane, 1.FC – anlage of first frontal cirrus, FM – frontal adoral membranelles, FR – anlage of frontoventral cirral row, FV – food vacuoles, LM – left marginal cirral row, MA – macronuclear nodules, MI – micronuclei, OP – oral primordium, RM – right marginal cirral row, VM – ventral adoral membranelles. Scale bars 20 μm.



Figs 55–60. *Schmidingerothrix extraordinaria*, ventral and dorsal views of dividers from type population after protargol impregnation. (55, 56) (cp. Figs 62, 63). Late divider beginning cell furrowing. The new frontal and oral ciliature is fully developed and pharyngeal fibres are growing. Still, there are some parental marginal cirri. The macronuclear mass (Figs 46, 48) has divided, producing two nodules. The micronuclei are dividing. (57, 58) Late divider with distinct division furrow. The somatic and oral infraciliature and micronuclear division have been completed. The macronuclear nodules commence to divide a second time, producing two nodules in each daughter. (59, 60) (cp. Fig. 64). Very late divider with cell fission almost completed. Both daughters are fully developed, except for the tail, which is post-divisionally produced in the proter. The macronuclear nodules commence a third round of division, producing the species-specific pattern, i.e., four nodules. Likewise, the gap between frontal and ventral adoral membranelles develops post-divisionally. E – endoral membrane, 1.FC – first frontal cirrus, FM – frontal adoral membranelles, FR – frontoventral cirral row, LM – left marginal cirral row, MA – macronuclear nodules, MI – micronuclei, P – pharyngeal fibres, RM – right marginal cirral row, VM – ventral adoral membranelles. Scale bars 20 μm.



Figs 61–64. *Schmidingerothrix extraordinaria*, ventral views of dividers from type population after protargol impregnation. (61) (cp. Fig. 46). Mid-divider with fully developed cirral anlagen and fused macronuclear nodules. The asterisks denote the anlagen within the marginal cirral rows. (62) Late divider with dividing macronuclear mass. Cirri develop in the anlagen. The parental frontal cirrus is dissolving (arrowhead). Arrow marks gap between frontal and ventral adoral membranelles. (63) (cp. Figs 55, 56). Late divider, showing begin of cell furrowing (arrowhead). The parental (proter) frontal cirrus has been replaced by a new one. The macronuclear mass has divided once. (64) (cp. Figs 59, 60) Very late divider with proter and opisthe almost separated. Both daughters are complete, except for the proter tail and the gap between the frontal and ventral adoral membranelles; these develop post-divisionally. AZM – adoral zone of membranelles, E – endoral membrane, 1.FC – first frontal cirrus, FM – frontal adoral membranelles, FR – frontoventral cirral row, MA – macronucleus, MI – micronuclei, VM – ventral adoral membranelles. Scale bars 20 μm (61–63) and 30 μm (64).

it emphasizes the absence of a paroral membrane; of buccal, transverse, and caudal cirri; and of dorsal bristle rows. No vestiges of these structures appear during the ontogenetic processes.

The division of the marginal cirral rows, the nuclear apparatus, and cell fission occur in the manner typical of hypotrichs (Figs 42–48, 51–64; Berger 1999). The tail of the proter and the gap between frontal and ventral adoral membranelles are completed in post-dividers.

Oral apparatus: The oral primordium of the opisthe, i.e., an anarchic field of basal bodies with minute cilia, develops in mid-body right of the left marginal row (Figs 37, 42, 51). Next, the anarchic field increases in size and splits in a narrow right and a wide left portion: the right field becomes a dikinetidal row, i.e., the endoral membrane, while the left field produces two-rowed adoral membranelles from anterior to posterior and from right to the left (Figs 43, 44, 52, 53). These processes proceed: the dikinetids of the right row disassociate into equally spaced monokinetids and a minute third row of basal bodies is added to the ventral adoral membranelles. Concomitantly, the parental buccal field flattens and the pharyngeal fibres disappear (Figs 45–47, 54, 61, 62). When cell fission commences, both the proter and opisthe oral apparatus develop pharyngeal fibres and the fourth adoral membranelle ventralizes by resorption of basal bodies in the upper row (Figs 55, 57, 63). When cell separation commences, frontal membranelles 2 and 3 elongate slightly, while membranelle 1 remains minute (Figs 59, 64). When cell fission is complete, the oral apparatus of proter and opisthe are mature (Figs 59, 64).

Frontoventral ciliature: The single frontal cirrus and the short frontoventral cirral row develop de novo in the opisthe, while parental structures are likely involved in the proter genesis. The primordium of the frontal cirrus develops rather far posterior to the parental cirrus, which is resorbed in late dividers (Figs 43–47, 52–55, 61–63). Thus, the proter's frontal cirrus possibly develops de novo, as in the opisthe. The proter's frontoventral cirral row forms an anlage at posterior end, including one or two parental cirri. This anlage grows, while the anterior cirri of the parental row are resorbed (Figs 44–47, 55, 61–63).

Discussion

Schmidingerothrix: a living fossil or secondarily oligomerized?

The simple organization and ontogenesis of *S. extraordinaria* could be interpreted as an indication of a very ancient state, especially the lack of dorsal bristles and of a paroral membrane, two highly stable features in the evolution of hypotrichs. However, I consider these features as highly apomorphic and propose *Schmidingerothrix* as a secondarily oligomerized hypotrich for four reasons: the typical adoral zone of membranelles, although highly modified; the typical marginal cirral rows and their ontogenesis; the nuclear apparatus with reorganization band and fusing macronuclear nodules during division; and the extreme habitat. In this context it is important that both, the absence of dorsal bristles and of a paroral membrane are very likely not caused by simple spatial constraints because, e.g., *Circinella* spp., which are much more slender than *Schmidingerothrix*, have both (Berger 2011). Further, it is known that highly saline habitats often produce highly modified organisms (Remmert 1992).

Classification of *Schmidingerothrix*

The following discussion is based on the assumption that *Schmidingerothrix* is a highly reduced hypotrich (see chapter above). The revision of Berger (2011) provides descriptions of all taxa mentioned.

Considering the cirral pattern, *Schmidingerothrix* has similarities with the Gonostomatidae Small and Lynn, 1985, Trachelostylidae Small and Lynn, 1985, and Cladotrichidae Small and Lynn, 1985. Of the genera and species included by Small and Lynn (1985) and Berger (2011), *Circinella* Foissner, 1994 is possibly most similar to *Schmidingerothrix* because both have a single, short frontoventral cirral row, a bipartite adoral zone of membranelles, and lack transverse and caudal cirri. On the other hand, *Circinella* has three frontal cirri (only one in *Schmidingerothrix*), a paroral membrane (lacking in *Schmidingerothrix*), and at least one row of dorsal bristles (bristles absent in *Schmidingerothrix* at all). Furthermore, ontogenesis is different: the proter frontoventral cirral row originates de novo (from parental cirri in *Schmidingerothrix*) and the proter paroral is involved in anlagen formation (absent in *Schmidingerothrix*). Thus, *Circinella* and *Schmidingerothrix* possibly belong to different families. None of the genera and species presently included in the three families mentioned above has lost the dorsal bristles and the paroral membrane (Berger 2011). Unfortunately, the organization of *Cladotricha koltzowii*, type of the genus *Cladotricha* Gaievskaia, 1925, is insufficiently known with regard to the dorsal bristles. However, Ruinen (1938) mentions dorsal bristles in *C. sagittata*, a species rather similar to *C. koltzowii*, and several other supposed *Cladotricha* species have three rows of dorsal bristles, a paroral membrane, and a different ontogenesis from that of *Schmidingerothrix* (Berger, 2011). Furthermore, I found a *Cladotricha*, possibly even *C. koltzowii*, in hypersaline coastal soil from Costa Rica. This species has both, a paroral membrane and three rows of dorsal bristles, showing the uniqueness of *Schmidingerothrix*.

The dorsal bristles and the paroral membrane are both highly characteristic features present in all hypotrichs investigated so far. Thus, *Schmidingerothrix* is a remarkable exception deserving at least family rank. Indeed, the morphological distance of *Schmidingerothrix* to the Gonostomatidae, Trachelostylidae, and Cladotrichidae is much larger than

those among these families, supporting the family rank for *Schmidingerothrix*.

Schmidingerothrix extraordinaria

I did not find any ciliate in the literature that could be identical with *S. extraordinaria*. However, body shape and size are very similar to several *Cladotricha* species, all having one or two long frontoventral cirral rows left of the right marginal row (Berger, 2011).

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