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# Morphology and Cell Division of *Saudithrix terricola* n. gen., n. sp., a Large, Stichotrich Ciliate from Saudi Arabia

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ABSTRACT. The morphology and main ontogenetic traits of a new stichotrich ciliate, *Saudithrix terricola* Foissner, AL-Rasheid and Berger n. gen., n. sp., from a terrestrial habitat in Saudi Arabia were investigated using live observation, protargol impregnation, and scanning electron microscopy. *Saudithrix terricola* is characterized by a large (200–350 × 70–150 μm), flexible body; an adoral zone formed like a three-quarter circle; a sickle-shaped buccal lip with a widened paroral forming a cyrtohymenid pattern with the endoral; 11 frontal and frontal-ventral cirral rows (including right marginal rows) and one left marginal row covering the ventral side; two buccal cirri; six to nine transverse cirri; three dorsal kineties; and two macronuclear nodules. The resting cyst is about 85 μm across, has a smooth wall, and a fluffy mucous layer. Most cirral anlagen originate within the parental rows and are arranged side by side, the proximal portion of the adoral zone of membranelles is reorganized, and some parental dorsal bristles are maintained. Neither the morphological nor the ontogenetic data reveal the systematic position of *Saudithrix* within the stichotrichs. The term multicorona is introduced and describes a frontal ciliature composed of four or more cirral bows.

**Key Words.** Morphogenesis, morphometry, multicorona, ontogenesis, resting cyst, soil ciliate, spirotrichea, taxonomy.

IN Saudi Arabia, ciliatological studies concentrated on marine sediments and saline inland ponds (AL-Rasheid 1996, 1997, 2001a; AL-Rasheid and Foissner 1999; AL-Rasheid, Nilsson, and Larsen 2001). These habitats harbored little known species, for example, *Copemetopus subsalsus*, and new taxa like *Sultanophrys arabica* (AL-Rasheid 2001b; Foissner and AL-Rasheid 1999). By contrast, nothing is known about soil ciliates from Saudi Arabia. Thus, it was not a very great surprise to find a new stichotrich spirotrich in a terrestrial habitat near Riyadh. Its morphology, including a comprehensive morphometry and some notes on cell division, are described in the present paper.

## MATERIALS AND METHODS

*Saudithrix terricola* was discovered in soil of a vegetable field from Adiriyah city (24°45′N, 46°33′E) about 20 km north of the capital Riyadh, Saudi Arabia. A culture was established in Eau de Volvic enriched with some drops of percolate from a non-flooded Petri dish raw culture and a few crushed wheat grains to stimulate growth of bacteria and prey protozoa (see Foissner, Agatha, and Berger 2002, for details on these culture methods).

Living cells were studied using a high-power oil immersion objective and differential interference contrast optics. The infraciliature and the nuclear apparatus were revealed by protargol protocols A and B and by scanning electron microscopy (SEM) as described in Foissner (1991).

In vivo measurements were conducted at magnifications of 40–1,000×. Counts and measurements on silvered specimens were performed at a magnification of 1,000× . Drawings of live specimens were based on freehand sketches and micrographs; those of impregnated cells were made with a drawing device.

Type material is deposited in the Oberösterreichische Landesmuseum in Linz (LI), Austria. The holotype specimen (accession number of slide: 2005/77) and some relevant morphostatic and dividing paratype specimens (slides 2005/78-82) are marked by a black ink circle on the coverslip.

Terminology is according to Berger (1999, 2004), Corliss (1979), and Foissner and AL-Rasheid (2006). The new term multicorona describes a frontal ciliature where the anteriormost four or more cirri of several frontal and frontal-ventral rows form four or more curved, parallel bows along the anterior body end (Fig. 1, 6, 14). For the sake of simplicity, no distinction is made between frontal-ventral rows and right marginal row(s). Possibly, all frontal-ventral rows that do not form transverse cirri are right marginal rows.

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## RESULTS

***Saudithrix terricola* Foissner, AL-Rasheid, and Berger n. gen., n. sp. (Table 1 and Fig. 1–26).** Body size 200–350 × 70–150 μm in vivo, usually near 270 × 100 μm; body flattened dorsoventrally, about 2:1; length:width ratio, about 2.7:1 for both in vivo and protargol preparations (Table 1); very flexible. Body outline elliptical to elongate elliptical or indistinctly reniform, usually slightly narrowing posteriorly; both ends broadly rounded (Fig. 1, 3, 4). Nuclear apparatus left of body midline usually comprising two macronuclear nodules and two micronuclei, specimens with three or four nodules rarely occur; individual nodules bluntly to elongate ellipsoidal, average length:width ratio of anterior nodule 2.0:1, of posterior 2.8:1 (Table 1), contain many small to moderately large, globular chromatin bodies, and often also a branched chromatin aggregate. Usually one micronucleus attached to each macronuclear nodule, globular to slightly ellipsoidal, 4–5 μm across in vivo (Fig. 1, 2, 7, 10, 12, 13, 15). Contractile vacuole near mid-body at left margin of cell, with two long, lacunar collecting canals and some satellite vacuoles along anterior cell margin (Fig. 3). Cortex very soft and flexible, does not contain specific granules. Cytoplasm colorless, contains innumerable granules, rather many lipid droplets, 1–5 μm across, and up to 50 μm-sized food vacuoles with ciliates. Movement without peculiarities, that is, swims rather rapidly on microscope slide showing great flexibility when crawling between and on soil particles.

Cirral pattern rather variable, especially the number of frontal, frontal-ventral, and left marginal rows; cirri 20–25 μm long in vivo (Table 1). Frontal ciliature of multicorona-type; frontal cirri gradually decrease in size posteriorly; leftmost frontal cirrus (= cirrus I/1) ahead of distal end of paroral. Usually two, rarely three, buccal cirri right of mid-buccal cavity. On average three frontal and eight frontal-ventral cirral rows, including right marginal row(s) (Table 1 and Fig. 1, 6, 8, 11, 13, 14, 19, 20). Leftmost frontal-ventral row usually with distinct break at level of buccal vertex, terminates on average at 41% of body length;

Table **1.** Morphometric data on *Saudithrix terricola*.

| Characteristics[a] | *x* | *M* | SD | SE | CV | Min | Max | n |
|---|---|---|---|---|---|---|---|---|
| Body, length | 241.3 | 239.0 | 34.9 | 6.5 | 14.5 | 184.0 | 312.0 | 29 |
| Body, width | 92.3 | 88.0 | 19.5 | 3.6 | 21.1 | 61.0 | 136.0 | 29 |
| Body length:width, ratio | 2.7 | 2.6 | 0.6 | 0.1 | 22.5 | 1.7 | 4.3 | 29 |
| Adoral zone of membranelles, length 1[b] | 69.4 | 69.0 | 6.1 | 1.1 | 8.8 | 58.0 | 80.0 | 29 |
| Adoral zone of membranelles, length 2[b] | 38.3 | 38.0 | 8.3 | 1.5 | 21.7 | 22.0 | 54.0 | 29 |
| Body length:length 1 of adoral zone, ratio | 3.5 | 3.5 | 0.4 | 0.1 | 11.1 | 2.8 | 4.2 | 29 |
| Widest adoral membranelle, width | 16.8 | 17.0 | 1.1 | 0.2 | 6.4 | 15.0 | 19.0 | 29 |
| Anterior body end to anterior macronuclear nodule, distance | 57.1 | 60.0 | 9.9 | 1.8 | 17.4 | 40.0 | 73.0 | 29 |
| Anterior macronuclear nodule, length | 36.0 | 32.0 | 9.7 | 1.8 | 26.8 | 24.0 | 60.0 | 29 |
| Anterior macronuclear nodule, width | 18.4 | 18.0 | 2.2 | 0.4 | 12.0 | 14.0 | 24.0 | 29 |
| Anterior macronuclear nodule, length:width ratio | 2.0 | 1.9 | 0.6 | 0.1 | 27.8 | 1.1 | 3.5 | 29 |
| Macronuclear nodules, distance in between | 38.7 | 36.0 | 13.4 | 2.5 | 34.6 | 22.0 | 80.0 | 29 |
| Posterior macronuclear nodule, length | 45.2 | 44.0 | 10.1 | 1.9 | 22.2 | 26.0 | 64.0 | 29 |
| Posterior macronuclear nodule, width | 16.6 | 16.0 | 2.9 | 0.5 | 17.7 | 10.0 | 22.0 | 29 |
| Posterior macronuclear nodule, length:width ratio | 2.8 | 2.7 | 0.8 | 0.1 | 28.0 | 1.2 | 4.9 | 29 |
| Anteriormost micronucleus, length | 3.6 | 3.5 | 0.7 | 0.2 | 20.6 | 2.5 | 5.0 | 22 |
| Anteriormost micronucleus, width | 3.2 | 3.0 | 0.6 | 0.1 | 19.4 | 2.5 | 5.0 | 22 |
| Anterior body end to paroral, distance | 19.3 | 20.0 | 3.1 | 0.6 | 15.8 | 14.0 | 25.0 | 29 |
| Anterior body end to endoral, distance | 23.6 | 24.0 | 4.8 | 0.9 | 20.2 | 17.0 | 32.0 | 28 |
| Anterior body end to anterior buccal cirrus, distance | 35.0 | 34.0 | 5.4 | 1.0 | 15.3 | 28.0 | 46.0 | 29 |
| Anterior and posterior buccal cirrus, distance in between[c] | 3.1 | 3.0 | 1.2 | 0.2 | 39.4 | 1.0 | 6.0 | 29 |
| Posterior body end to frontal-ventral row 1, distance | 99.9 | 96.5 | 29.7 | 5.6 | 29.7 | 46.0 | 170.0 | 28 |
| Posterior body end to frontal-ventral row 2, distance | 57.4 | 48.0 | 25.7 | 4.8 | 44.7 | 30.0 | 122.0 | 29 |
| Posterior body end to frontal-ventral row 3, distance | 35.4 | 30.5 | 15.7 | 3.0 | 44.4 | 18.0 | 76.0 | 28 |
| Posterior body end to frontal-ventral row 4, distance | 25.4 | 23.5 | 11.0 | 2.1 | 43.2 | 9.0 | 55.0 | 28 |
| Posterior body end to frontal-ventral row 5, distance | 17.1 | 14.5 | 8.1 | 1.5 | 47.3 | 4.0 | 36.0 | 28 |
| Posterior body end to frontal-ventral row 6, distance | 10.6 | 12.0 | 5.9 | 1.1 | 55.4 | 0.0 | 22.0 | 27 |
| Posterior body end to frontal-ventral row 7, distance | 13.9 | 8.0 | 19.8 | 4.0 | 142.8 | 0.0 | 78.0 | 25 |
| Posterior body end to frontal-ventral row 8, distance | 15.1 | 7.0 | 20.1 | 5.2 | 133.1 | 0.0 | 68.0 | 15 |
| Posterior body end to frontal-ventral row 9, distance | 2.5 | 2.5 | 2.4 | 1.2 | 95.2 | 0.0 | 5.0 | 4 |
| Posterior body end to rearmost transverse cirrus, distance | 25.3 | 24.0 | 10.5 | 1.9 | 41.3 | 10.0 | 56.0 | 29 |
| Macronuclear nodules, number[i] | 2.0 | 2.0 | 0.0 | 0.0 | 0.0 | 2.0 | 2.0 | 29 |
| Micronuclei near anterior macronuclear nodule, number | 0.7 | 1.0 | 0.7 | 0.1 | 94.2 | 0.0 | 2.0 | 25 |
| Micronuclei near posterior macronuclear nodule, number | 1.1 | 1.0 | 0.9 | 0.2 | 78.7 | 0.0 | 3.0 | 25 |
| Adoral membranelles, number | 58.5 | 59.0 | 3.3 | 0.6 | 5.7 | 53.0 | 64.0 | 29 |
| Buccal cirri, number | 2.2 | 2.0 | 9.4 | 0.1 | 17.7 | 2.0 | 3.0 | 29 |
| Frontal rows, number[f] | 3.2 | 3.0 | 0.8 | 0.2 | 25.5 | 2.0 | 5.0 | 29 |
| Frontal row 1, number of cirri[g] | 3.1 | 3.0 | 0.8 | 0.1 | 25.2 | 1.0 | 5.0 | 29 |
| Frontal row 2, number of cirri[g] | 3.7 | 4.0 | 0.8 | 0.1 | 21.0 | 2.0 | 5.0 | 29 |
| Frontal row 3, number of cirri[g] | 4.0 | 4.0 | 0.8 | 0.2 | 19.4 | 3.0 | 6.0 | 23 |
| Frontal row 4, number of cirri[g] | 4.8 | 5.0 | 1.0 | 0.3 | 20.4 | 3.0 | 6.0 | 11 |
| Frontal row 5, number of cirri[g] | 5.0 | — | — | — | — | — | — | 1 |
| Frontal-ventral rows, number | 7.9 | 8.0 | 0.7 | 0.1 | 8.5 | 7.0 | 9.0 | 29 |
| Frontal-ventral row 1, number of cirri | 26.0 | 28.0 | 6.2 | 1.1 | 23.6 | 8.0 | 35.0 | 29 |
| Frontal-ventral row 2, number of cirri | 37.6 | 37.0 | 5.0 | 0.9 | 13.3 | 28.0 | 46.0 | 28 |
| Frontal-ventral row 3, number of cirri | 45.3 | 45.0 | 5.6 | 1.1 | 12.4 | 31.0 | 58.0 | 26 |
| Frontal-ventral row 4, number of cirri | 50.9 | 51.0 | 5.3 | 1.0 | 10.5 | 41.0 | 63.0 | 27 |
| Frontal-ventral row 5, number of cirri | 52.5 | 53.0 | 5.1 | 1.0 | 9.6 | 43.0 | 64.0 | 28 |
| Frontal-ventral row 6, number of cirri | 55.0 | 54.0 | 8.1 | 1.6 | 14.8 | 43.0 | 73.0 | 27 |
| Frontal-ventral row 7, number of cirri | 55.0 | 54.0 | 10.6 | 2.0 | 19.3 | 29.0 | 73.0 | 27 |
| Frontal-ventral row 8, number of cirri | 58.1 | 60.0 | 16.2 | 3.7 | 27.8 | 21.0 | 82.0 | 19 |
| Frontal-ventral row 9, number of cirri | 62.6 | 59.0 | 10.4 | 4.6 | 16.5 | 53.0 | 76.0 | 5 |
| Transverse cirri, number[e] | 7.3 | 7.0 | 0.8 | 0.2 | 11.6 | 6.0 | 9.0 | 29 |
| Transverse cirri, total number[e] | 7.5 | 8.0 | 0.8 | 0.2 | 11.0 | 6.0 | 9.0 | 29 |
| Left marginal row, number of cirri[d] | 65.7 | 65.0 | 9.5 | 1.8 | 14.4 | 48.0 | 86.0 | 29 |
| Total number of cirri[h] | 440.6 | 454.0 | 76.2 | 14.1 | 17.3 | 159.0 | 545.0 | 29 |
| Dorsal kineties, number | 3.1 | 3.0 | 0.2 | 0.1 | 7.3 | 3.0 | 4.0 | 20 |
| Cyst, large diameter in vivo | 87.3 | 90.0 | 7.5 | 1.6 | 8.6 | 75.0 | 100.0 | 23 |
| Cyst, small diameter in vivo | 84.1 | 84.0 | 6.8 | 1.4 | 8.1 | 75.0 | 100.0 | 23 |

[a]Data based on mounted, protargol-impregnated (protocols A, B), and randomly selected specimens showing most/all features. Measurements in μm. CV, coefficient of variation in %; *M*, median; Max, maximum; Min, minimum; n, number of individuals investigated; SD, standard deviation; SE, standard error of arithmetic mean; *x*, arithmetic mean.

[b]Length 1 = distance between anterior end of cell and proximal end of adoral zone of membranelles. Length 2 = distance between anterior end of cell and distal end of adoral zone of membranelles.

[c]When three buccal cirri are present, then the distance between the anteriormost and middle cirrus was measured.

[d]Cirri right and left of main row not included.

[e]The set off cirrus (Fig. 16) not included (number), respectively, included (total number).

[f]Cirral rows, which do not extend beyond the buccal vertex (cirrus I/1 and buccal cirral row not included; Fig. 11).

[g]Anteriormost (frontal) cirrus included.

[h]Cirri of short rows left or right of main left marginal row not included.

[i]Very rarely occur specimens with three or four macronuclear nodules (Fig. 2).

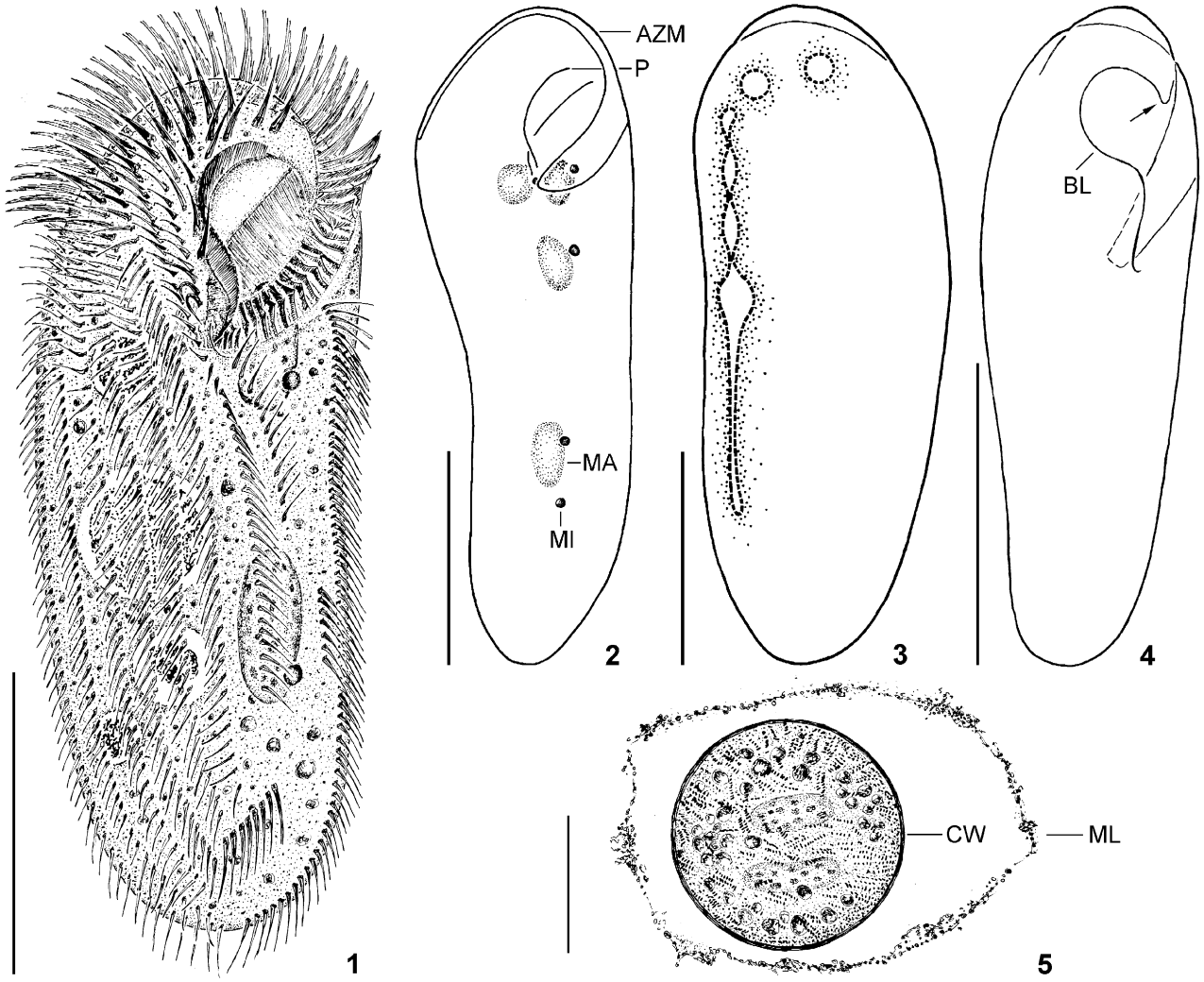



Fig. **1–5.** *Saudithrix terricola* n. gen., n. sp. from life (1, 3–5) and after protargol impregnation (2). **1.** Ventral view of a representative specimen. **2.** Ventral view of a specimen with four macronuclear nodules. **3, 4.** Shape variants in dorsal (3) and ventral (4) view showing contractile vacuole system (3) and sickle-shaped buccal lip that ends in a distinct horn distally (4; arrow). **5.** Resting cyst with mucous layer. AZM, adoral zone of membranelles; BL, sickle-shaped buccal lip; CW, cyst wall; MA, macronuclear nodule; MI, micronucleus; ML, mucous layer; P, paroral. Scale bars = 100 μm (1–4), 50 μm (5).

going rightwards, frontal-ventral rows usually gradually lengthen. Frontal-ventral rows occasionally with more or less distinct breaks and short extra rows and/or single cirri at variable positions (Fig. 6, 8). Rightmost cirral row usually extends laterally or dorso-laterally, commences near distal end of adoral zone. Left marginal row extends to cell end, anterior portion more or less distinctly curved rightwards and often with very narrowly spaced cirri; frequently, cirral row fragments and/or single cirri right and/or left of main row. Transverse cirri subterminal, not projecting beyond rear body end, slightly enlarged and arranged in oblique row with rightmost cirrus sometimes set off (Table 1 and Fig. 1, 6, 8, 16, 19).

Dorsal bristles about 4 μm long in vivo, basically arranged in three bipolar kineties, but only kinety 3 extends to rear cell end while rows 1 and 2 end subterminally. Anterior end of kinety 3 occasionally with some irregularities. Usually some scattered (parental, see ontogenesis) dikinetids between anterior half of kineties 1 and 2, rarely some pairs also in posterior half and/or between anterior portion of kineties 2 and 3. Caudal cirri lacking (Table 1 and Fig. 7, 10, 18, 21).

Adoral zone occupies 29% of body length on average, composed of an average of 59 membranelles with up to 25-μm-long cilia; bases of largest membranelles about 17 μm wide in vivo. Proximal portion of adoral zone conspicuously curved rightwards, while distal end extends so far onto right body margin that the zone becomes shaped like a three-quarter circle (Fig. 1, 6, 8, 11–13, 20). Buccal apparatus conspicuous, especially in vivo, because of the deep cavity and the sickle-shaped lip that forms a distinct process (horn) along the adoral zone. Anterior half of buccal lip semicircular and flat, posterior straight and gradually increasing in height, partially covering proximal part of adoral zone of membranelles (Fig. 1, 4, 12, 19, 20). Buccal cavity covered by an upper and lower seal, that is, delicate membranous structures recognizable only in the scanning electron microscope and described in detail by Foissner and AL-Rasheid (2006). Paroral does not extend along whole buccal lip, but only to summit of sickle-curve; rather wide, except for anterior and posterior end, because composed of short rows comprising up to four basal bodies with about 30-μm-long cilia; length of cilia gradually decreasing to about 15 μm toward ends of membrane. Endoral likely composed of a single row of dikinetids bearing about 10–15 μm long cilia, slightly curved, extends diagonally across dorsal wall of buccal cavity, optically intersecting with paroral near level of

buccal cirri, and thus forming a *Cyrtohymena*-pattern (for explanation, see Berger 1999). Pharyngeal fibers extend obliquely backwards to about 40% of body length (Fig. 1, 6, 8, 9, 11, 13, 17, 20).

Resting cysts spherical to slightly ellipsoidal, 87 μm in diameter on average, colorless. Cyst wall about 2 μm thick, homogenous, covered by an up to 40 μm thick, mucous layer easily lost when specimens are transferred onto the slide. Cyst content composed of many ellipsoidal granules (1.5 × 1.0 μm) forming stripes underneath wall; many globular and irregular, colorless lipid droplets 4–6 μm in diameter; and two macronuclear nodules (Table 1 and Fig. 5, 22).

**Notes on cell division.** Some well-prepared dividers show the following details (Fig. 23–26): (i) ontogenesis commences with the formation of an oral primordium left of the posterior portion of the leftmost frontal-ventral rows extending near to the transverse cirri (Fig. 23); (ii) the rightmost frontal-cirral rows, including right marginal row(s), and the left marginal row originate by within-row formation (Fig. 25); (iii) the cirral streaks are arranged roughly side by side (Fig. 25); the leftmost frontal cirrus originates, as is usual, from the anlage of the undulating membranes (Fig. 25, 26); (iv) the left and the posterior part of the proximal portion of the parental adoral zone are reorganized (Fig. 25); (v) the leftmost frontal-ventral row often separates into an anterior and posterior portion, while the other rows usually remain continuous (Fig. 24, 26); (vi) a very late divider and the morphometric analysis show that cirral anlage II, which forms the buccal cirri, does not produce a transverse cirrus (Fig. 24, 26); (vii) the three dorsal kineties develop within the parental rows; (viii) the scattered bristles between dorsal kineties 1 and 2 are remnants of parental rows 1 and 2; (ix) likely, dorsomarginal kineties are not formed; (x) the nuclear apparatus divides in the usual way, that is, the two macronuclear nodules fuse to a single mass in mid-dividers; later, the mass divides to the species-specific pattern.

## DISCUSSION

**Suprageneric classification.** *Saudithrix terricola* is very conspicuous owing to the large size, the high number of cirri (>440; Table 1) covering the ventral side, and the cyrtohymenid-like oral apparatus. However, we are unable to assign it to a certain suprageneric taxon because specific features are lacking, for example, the fragmenting dorsal kinety of the oxytrichids (Berger 1999) and the zigzagging cirral pairs of the urostylids (Berger 2004; Borror and Wicklow 1983; Lynn and Small 2002). This suggests that the reorganization of the adoral zone of membranelles evolved independently in *Saudithrix* (Fig. 25) and the urostylids, where this feature is very common (e.g. Eigner 2001).

The cirral pattern and some ontogenetic traits of *Saudithrix* are reminiscent of genera like *Pseudokahliella* Berger, Foissner, and Adam 1985, *Wallackia* Foissner 1976, and *Parastrongylidium* Fleury and Fryd-Versavel 1984, because the cirral anlagen are formed side by side and largely within the parental rows (e.g. Aescht and Foissner 1992; Fleury and Fryd-Versavel 1984; Foissner, Adam, and Foissner 1982; Foissner et al. 2002). However, the narrow and flat buccal cavity and the short membranes of *Pseudokahliella*, *Wallackia*, and *Parastrongylidium* are distinctly different from that of *Saudithrix*, where the buccal cavity is wide and deep and the undulating membranes are long and curved; further, the adoral zone is roughly in a *Gonostomum*-like pattern in the former three genera, while a three-quarter circle in *Saudithrix*. This suggests that *Saudithrix* is not closely related to these genera, whose suprageneric position is also in discussion (e.g. Berger et al. 1985; Eigner 1997; Lynn and Small 2002; Shi, Song, and Shi 1999; Tuffrau and Fleury 1994). Thus, we classify *Saudithrix* as genus incertae sedis in the Stichotrichia.

**The new genus *Saudithrix*.** *Saudithrix terricola* has a unique combination of features and thus represents a new genus. *Pseudokahliella* (see previous section) lacks transverse cirri and has a paroral composed of dikinetids, whereas *Saudithrix* has distinct transverse cirri and a widened paroral (Berger et al. 1985; Foissner et al. 1982; Hu and Song 2003). *Anatoliocirrus* Özbek and Foissner in Foissner et al. (2002) has, like *Saudithrix*, a widened paroral, but possesses frontoterminal and caudal cirri and a dorsomarginal kinety, and the frontal-ventral-transverse cirral anlagen originate by transverse division of long primary primordia. By contrast, *Saudithrix* lacks frontoterminal and caudal cirri and a dorsomarginal kinety, and the cirral anlagen of the proter and the opisthe originate independently from each other.

*Gigantothrix* Foissner, 1999 lacks transverse cirri (versus present in *Saudithrix*) and has a rigid body (versus flexible), a long adoral zone (46% versus 29%), and a complex dorsal ciliature (many kineties owing to dorsomarginal rows and multiple kinety fragmentation versus three bipolar kineties). The latter three features assign *Gigantothrix* to the Stylonychinae, as defined by Berger (1999).

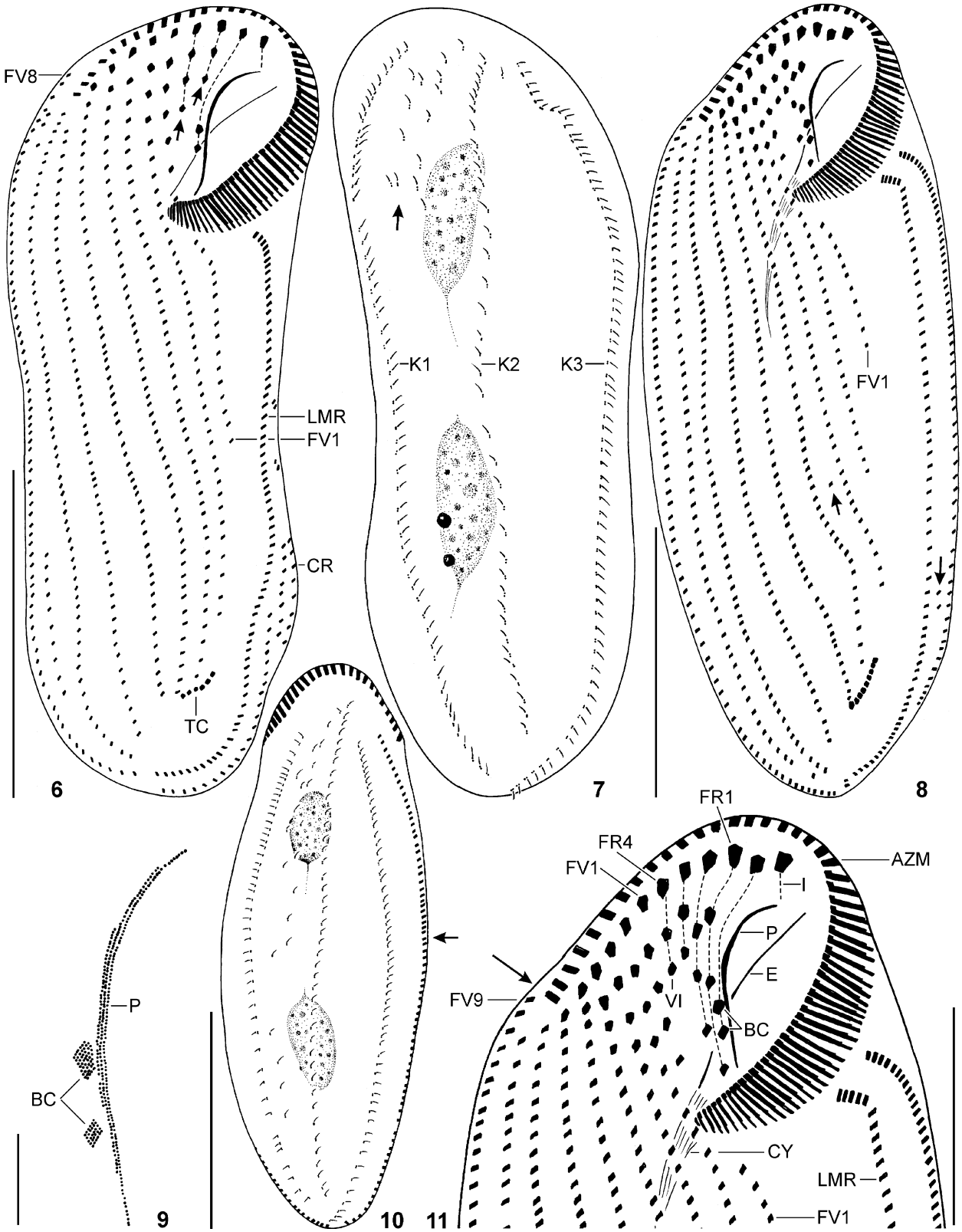
**The new species *Saudithrix terricola*.** The overall appearance of *Saudithrix terricola* is reminiscent of several large soil stichotrichs with many cirri, for example, *Eschaneustyla lugeri*, *Parakahliella binucleata*, *Anatoliocirrus capari* (Foissner et al. 2002), and *Gigantothrix herzogi* (Foissner 1999). *Eschaneustyla lugeri* has a very similar frontal ciliature, but possesses, inter alia, 60 macronuclear nodules (versus two), cortical granules (versus lacking), three frontal-ventral rows (including right marginal row versus eight), four dorsal kineties with caudal cirri (versus three without caudal cirri), but lacks transverse cirri (versus present). *Parakahliella binucleata* and *Anatoliocirrus capari* have, like *S. terricola*, two macronuclear nodules and a rather variable arrangement and number of cirral rows. However, they are distinctly smaller than *S. terricola* (body length 130–140 μm versus 270 μm), have three frontal cirri and one buccal cirrus (versus multicorona and two buccal cirri), and four dorsal kineties (including one dorsomarginal kinety) with many caudal cirri (versus three and dorsomarginal kinety and caudal cirri lacking). In addition, *Parakahliella binucleata* lacks transverse cirri (versus present in *S. terricola* and *A. capari*).

The habitus of *G. herzogi* is very similar to that of *S. terricola*, especially as concerns body size (250–400 × 120–200 μm) and cirral pattern. However, they can be easily distinguished by the nuclear apparatus (33 macronuclear nodules roughly arranged in C-shaped figure versus two), the consistency of the body (rigid versus very flexible), the length of the adoral zone (46% versus 29%), the transverse cirri (lacking versus present), and the dorsal ciliature (many kineties owing to dorsomarginal rows and multiple kinety fragmentation versus three bipolar kineties).

Some limnetic stichotrichs are reminiscent of *S. terricola*. The common *Urostyla grandis* has, inter alia, many small macronuclear nodules (versus two), conspicuous cortical granules (versus lacking), and zigzagging midventral pairs (versus absent; for description of *U. grandis* see Foissner et al. 1991 and Song and Wilbert 1989). The following species have, like *S. terricola*, only two macronuclear nodules: *Paraurostyla weissei* (for a review, see Berger 1999) can be easily distinguished from *S. terricola* by the cortical granulation (present versus lacking), details of the cirral pattern (e.g. three to four frontal cirri and one buccal cirrus versus multicorona and usually two buccal cirri) and the dorsal ciliature (caudal cirri plus six to seven rows versus caudal cirri lacking and three kineties). *Metaurostyla raikovi* and *Metaurostyla magna* from freshwater habitats in Azerbaijan are large (about 180 μm) and very large (about 500 μm), respectively, and

possess not only many left marginal rows but, more importantly, a midventral complex composed of distinctly zigzagging cirri (Alekperov 1984); by contrast, zigzagging midventral pairs are lacking in *S. terricola*.

The habitus of *Parabirojimia similis*, a marine species, is also similar to that of *S. terricola* (Hu, Song, and Warren 2002). They differ, inter alia, in the number of macronuclear nodules (three to six versus two), in the shape of the adoral zone of membranelles



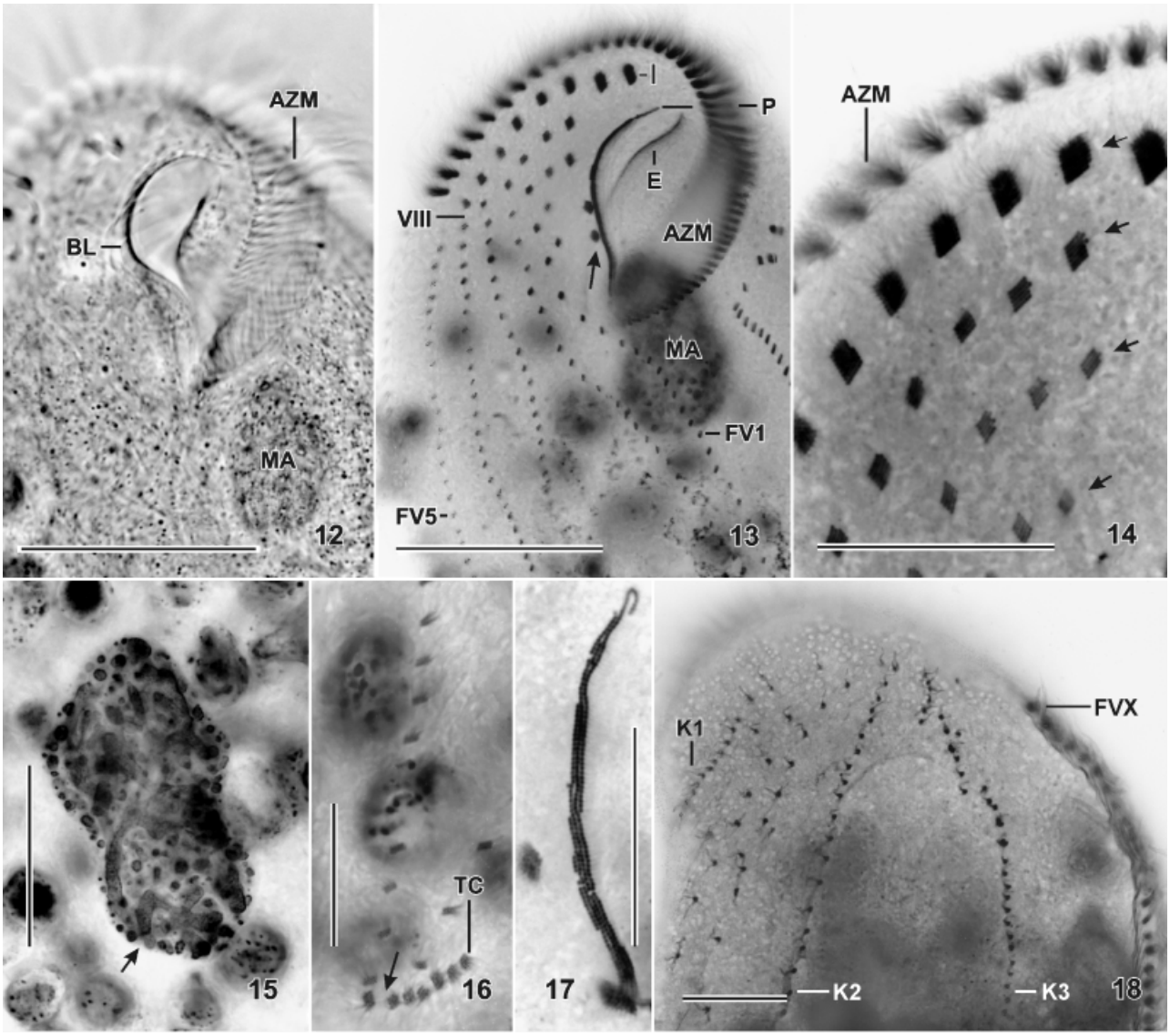



Fig. **12–18.** *Saudithrix terricola* n. gen., n. sp. from life (12) and after protargol impregnation (13–18). **12.** Oral region of a squeezed specimen showing, inter alia, the deep buccal cavity and the sickle-shaped buccal lip. **13.** Infraciliature of ventral side of anterior body third. Arrow marks buccal cirri. **14.** The anterior cirri of the frontal and frontal-ventral rows become gradually smaller posteriorly and form a multicorona, that is, four or more bows (arrows). **15.** Macronuclear nodule with globular and branched (arrow) chromatin aggregates. **16.** The rightmost transverse cirrus is sometimes slightly separated from the other transverse cirri (arrow). **17.** The middle portion of the paroral is widened and consists of several kinetofragments. **18.** Anterior portion of dorsal infraciliature showing, inter alia, the remnants of the parental kineties between kineties 1 and 2. AZM, adoral zone of membranelles; BL, buccal lip; E, endoral; FV1, 5, X, frontal-ventral rows 1, 5, X (= outermost right marginal row); K1–3, dorsal kineties; MA, macronuclear nodule; P, paroral; TC, transverse cirri; I, VIII, cirral anlagen. Scale bars = 50 μm (12, 13), 20 μm (14–18).

(bipartite versus continuous), and in details of the cirral pattern (three frontal cirri plus some zigzagging midventral cirri versus multicorona and zigzagging cirri lacking).

In vivo, *Saudithrix terricola* is best recognized by the following combination of features: body large (200–350 × 70–150 μm) and flexible; two macronuclear nodules; cortical granules lacking;

Fig. **6–11.** *Saudithrix terricola* n. gen., n. sp. after protargol impregnation. Broken lines connect cirri originating from same anlage (shown only for some rows, corresponding transverse cirri not included). **6, 7.** Infraciliature of ventral and dorsal side and nuclear apparatus of holotype specimen. Arrows in (6) denote frontal rows 1 (right arrow) and 2 (left arrow). Arrow in (7) marks scattered parental dorsal bristles between the anterior portion of kineties 1 and 2. **8, 11.** Infraciliature of ventral side of a paratype specimen. Arrows in (8) mark supernumerary cirri between frontal-ventral rows 3 and 4 and between the main left marginal row (inner row) and an additional row. Arrow in (11) denotes distal end of adoral zone. **9.** The paroral is widened in the central portion. **10.** Infraciliature of dorsal side and nuclear apparatus of a paratype specimen. Arrow marks rightmost frontal-ventral row (= outermost right marginal row). Note scattered parental bristles between kineties 1 and 2. AZM, adoral zone of membranelles; BC, buccal cirri; CR, short cirral rows; CY, cytopharynx; E, endoral; FR1, 4, frontal rows; FV1, 8, 9, frontal-ventral rows; K1–3, dorsal kineties (K1 is the left kinety); LMR, main left marginal row; P, paroral; TC, transverse cirri; I, VI, cirral anlagen I and VI. Scale bars = 100 μm (6–8, 10), 10 μm (9), 50 μm (11).

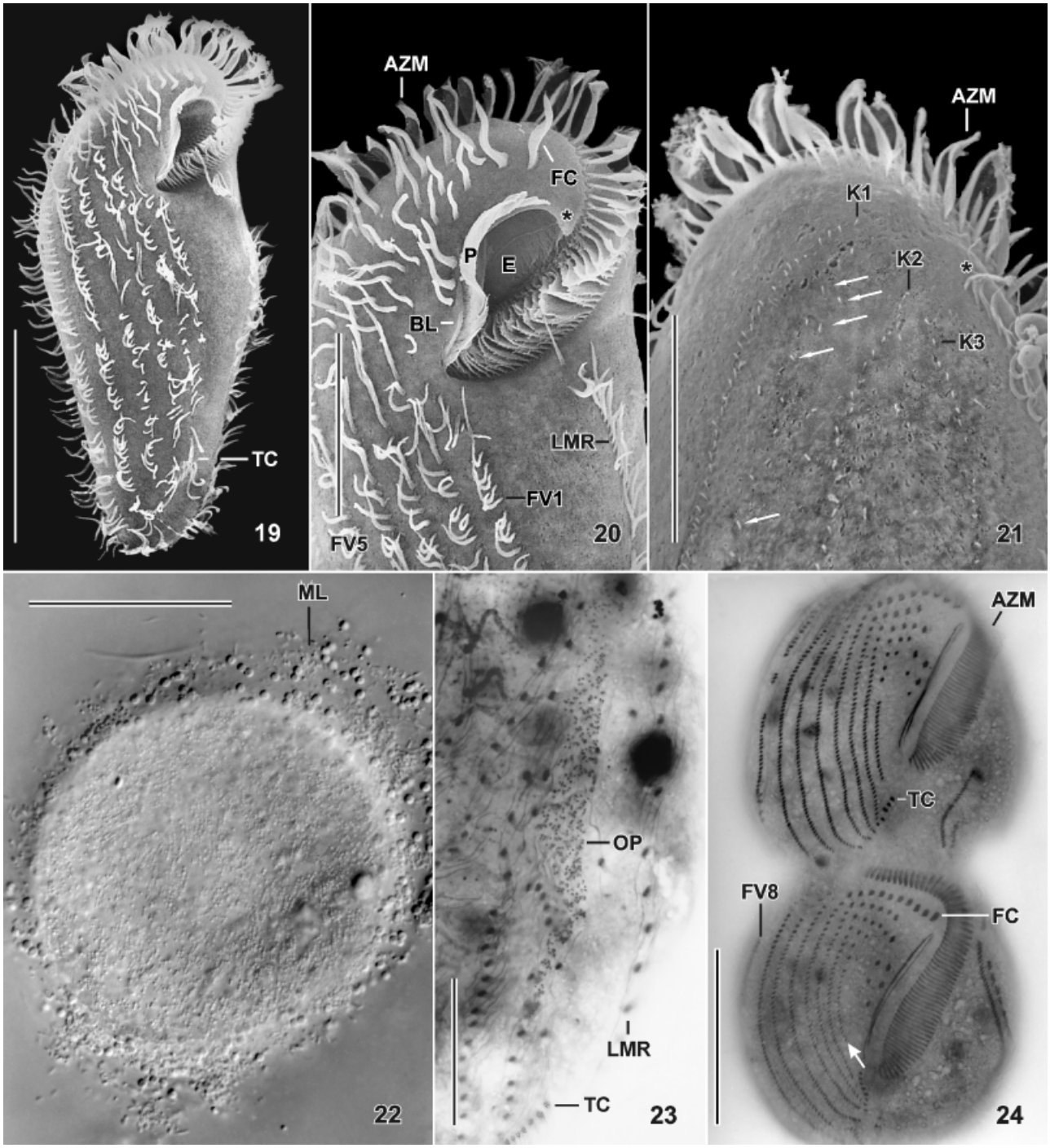



Fig. **19–24.** *Saudithrix terricola* n. gen., n. sp. in the scanning electron microscope (19–21; 19, from Foissner and AL-Rasheid 2006), from life (22), and after protargol impregnation (23, 24). **19, 20.** Overview showing the dense cirral pattern, the almost circular buccal cavity, and the sickle-shaped buccal lip containing the paroral. Note that the paroral does not extend onto the buccal horn (asterisk). **21.** Anterior portion of dorsal side showing the distal adoral membranelles inserting on the frontal scutum. Note the scattered dorsal bristles (arrows), which are remnants from the (previous) parental kineties. Asterisk marks anterior end of outermost frontal-ventral row. **22.** Resting cyst with mucous layer and stripes of ellipsoidal granules underneath cyst wall. **23.** Ontogenesis commences with the formation of an oral primordium left of the posterior portion of the leftmost frontal-ventral rows. **24.** Ventral view of very late divider (illustrated in Fig. 26). Arrow marks frontal-ventral row 1 of the opisthe. AZM, adoral zone of membranelles of proter; BL, buccal lip; E, endoral; FC, leftmost frontal cirrus (= cirrus I/1); FV1, 5, 8, frontal-ventral cirral rows; K1–3, dorsal kineties; LMR, left marginal row; ML, mucous layer; OP, oral primordium; P, paroral; TC, transverse cirri. Scale bars = 100 μm (19, 24), 50 μm (20–22), 20 μm (23).

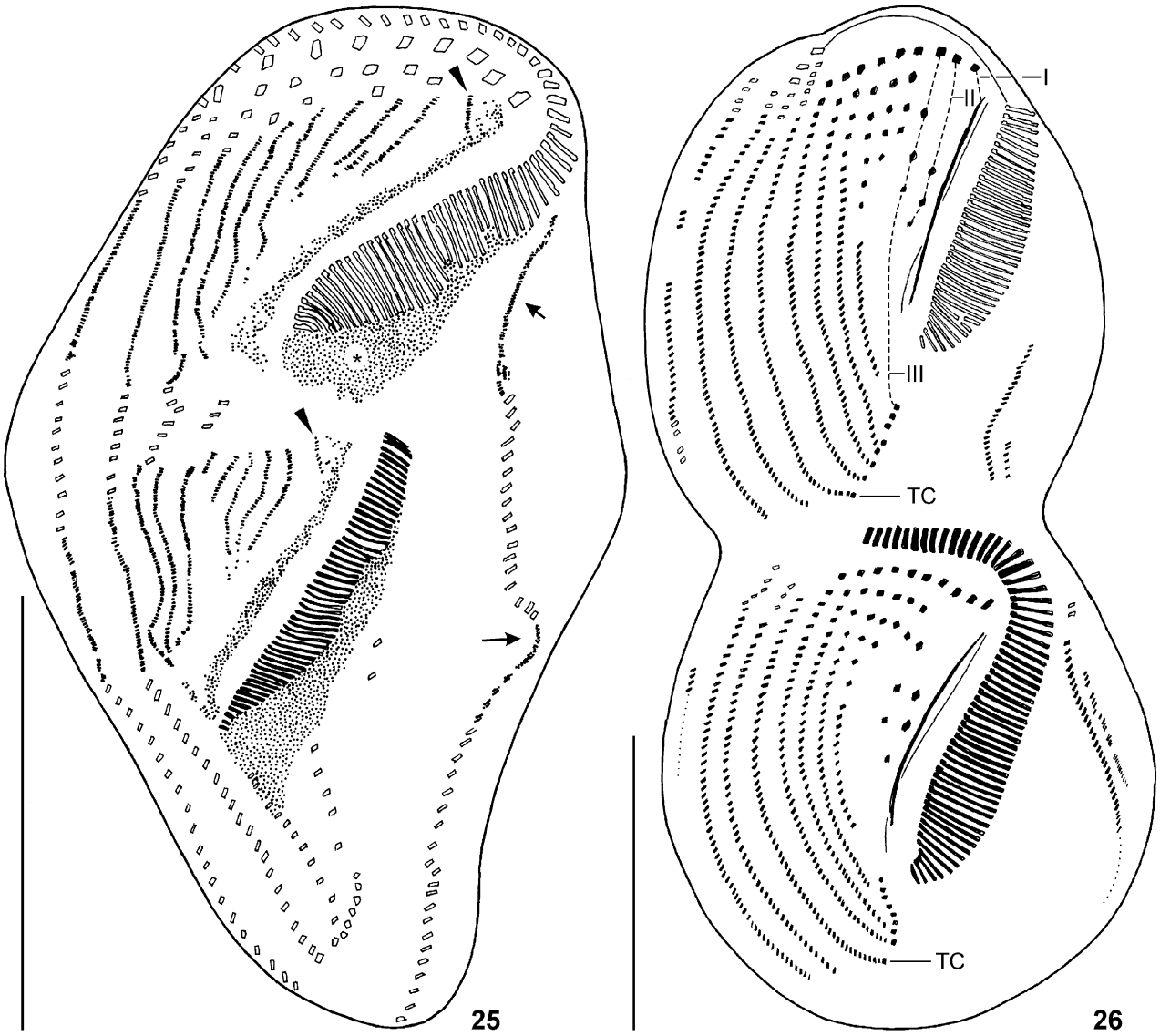



Fig. **25, 26.** *Saudithrix terricola* n. gen., n. sp. after protargol impregnation. Ventral view of a middle to late (25) and a very late divider (26; from Fig. 24). Asterisk in (25) marks the reorganizing part of the parental adoral zone of membranelles. Arrows denote left marginal row primordia, while arrowheads mark the anlage for the leftmost frontal cirrus. Broken lines (26, proter) connect cirri originating from anlagen I–III. Dotted lines mark cirral rows not clearly recognizable in the micrograph (cp. Fig. 24). Parental structures shown by contour, newly formed shaded black (except for the left-proximal part of the parental adoral zone which is reorganized). TC = rightmost transverse cirrus; I–III, leftmost cirral anlagen. Scale bars = 100 μm.

ventral side completely covered by cirri arranged in about nine rows; two buccal cirri on average; many frontal cirri arranged in a multicorona; subterminal transverse cirri; buccal cavity deep, at right bordered by a sickle-shaped lip; terrestrial.

## DIAGNOSES

### *Saudithrix* Foissner, AL-Rasheid and Berger n. gen.

*Diagnosis.* Stichotrichia with flexible body ventrally covered by cirral rows originating from intrakinetal anlagen. Oral apparatus cyrtohymenid-like with conspicuous, sickle-shaped buccal lip. Frontal ciliature multicoronar. Transverse cirri present, frontoterminal and caudal cirri absent.

*Type species.* *Saudithrix terricola* Foissner, AL-Rasheid and Berger n. sp.

*Etymology.* Composite of *Saudi* (from Saudi Arabia) and the Greek noun *thrix* (hair = ciliate s. l.), meaning ''a ciliate from Saudi Arabia.'' Feminine gender.

*Species assignable.* So far only the type species, *Saudithrix terricola*, can be assigned to the new genus.

*Remarks.* The number of marginal cirral rows, although an important feature for the characterization of supraspecific taxa (e.g. Berger 1999; Lynn and Small 2002), is not included in the diagnosis because of the problems described in the sections Materials and Methods, and morphology.

### *Saudithrix terricola* Foissner, AL-Rasheid and Berger n. sp.

*Diagnosis.* Size about 270 × 100 μm. Elongate ellipsoidal to indistinctly reniform. Two macronuclear nodules. Adoral zone forms a three-quarter circle, usually composed of 59 membranelles occupying about one-third of body length. On average two

buccal cirri, three frontal rows, eight frontal-ventral rows (including right marginal row[s]), six to nine subterminal transverse cirri, and one left marginal row. Cortical granules lacking. Three dorsal kineties and scattered parental bristles mainly between anterior portion of rows 1 and 2.

*Type locality.* Soil of a vegetable field about 20 km north of Riyadh, Saudi Arabia.

*Etymology.* The Latin *terricola* (living in soil) refers to the habitat where the species was discovered.

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