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Updating the Trachelocercids (Ciliophora, Karyorelictea). VI. A Detailed Description of *Sultanophrys arabica* nov. gen., nov. spec. (Sultanophryidae nov. fam.)

W. Foissner[1]* and K. A. S. AL-Rasheid[2]

[1]Universität Salzburg, Institut für Zoologie, Hellbrunnerstrasse 34, A - 5020 Salzburg, Austria
[2]King Saud University, Zoology Department, P.O. Box 2455, Riyadh 11451, Saudi Arabia

Summary

***Sultanophrys arabica* nov. gen., nov. spec. was discovered in the mud of a saline coastal pond at the Arabian Gulf coast. Its morphology and infraciliature were studied in live and silver-impregnated specimens as well as in the scanning electron microscope. *Sultanophrys arabica* has two unique features warranting separation from other trachelocercids at genus and family level: (1) the anterior secant system is at the right side of the glabrous stripe, (2) there is a special "lateral kinety" between the left branch of the bristle kinety and the first ordinary somatic ciliary row. All other (five) genera, whose type species were reinvestigated, have the anterior secant system at the left side of the glabrous stripe and lack a lateral kinety. The lateral kinety is very likely homologous to the dorsolateral kinety of loxodid karyorelictids because both have the same location and conspicuous fibres extending into the cytoplasm. It is thus argued that trachelocercids evolved from loxodids and *S. arabica* is an ancient species being near the node where loxodid and trachelocercid karyorelictids separated from a common ancestor. At species level, *S. arabica* is distinct by its size (about 800 × 70 µm); a glabrous stripe almost as wide as the cell; conspicuous, brilliant brown cortical granules; and the number of macronuclear nodules (13–47, 31 on average) and ciliary rows (31–40, 34 on average).**

Key words: Arabian Gulf; Infraciliature; *Kovalevaia*; Loxodids; Mesopsammon.

Introduction

The new generic classification of trachelocercid karyorelictids is based entirely on their oral structures because of the great similarity of the somatic infraciliature [14, 17]. Typically, the right side is ciliated, while the left bears a more or less wide glabrous (unciliated) stripe framed by a special (bristle) kinety. The somatic ciliary rows extend parallel to the bristle kinety on the right side of the glabrous stripe, while they are gradually shortened along its left anterior side, forming the anterior secant system [16]. This pattern has been found in 13 thoroughly studied species (out of about 70 described so far [3]) belonging to five genera [7, 13, 14, 16, 17]. It was thus a great surprise to find a species in which this pattern is quite different and which has, like loxodid karyorelictids [11, 12, 18, 20], a special (lateral) kinety along the left branch of the bristle kinety. The detailed description of this species is given in the present paper. Its morphogenesis will be analysed in a forthcoming study.

Materials and Methods, Terminology

Sultanophrys arabica was discovered in a large (about 200 × 200 m, max. depth 4 m), brackish (~ 12–28‰) pool at Safwa village in the Al Qatif oasis (50°06' E, 26°39' N), about 15 km north of Dammam (Saudi Arabia) and about 2 km inshore from the Saudi Arabian Gulf coast. The pool is surrounded by the salt-tolerant tall reed *(Phragmites communis)* and black mangrove *(Avicennia marina)* and connected with the Gulf via the water table. *Sultanophrys arabica* was collected at the margin of the pool, where the muddy sediment is mixed with some sand. During the hot season, when the water level decreases, the sediment becomes microaerobic or anaerobic. When *S. arabica* was collected, the pool contained a typical marine ciliate fauna.

Sultanophrys arabica was cultivated as described in [1] and studied in vivo using a high-power oil immersion objective and differential interference contrast [10]. Scanning electron microscopy (SEM) was performed as described in [10].

*corresponding author

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All trials to reveal the infraciliature with conventional protargol methods failed, mainly because of the dense cortical granulation, which impregnated intensively. Finally, we were successful with a combination of Wilbert's protargol and Fernandez-Galiano's silver carbonate method. The combined technique provided excellent results but is, unfortunately, hardly reproducible, that is, later trials failed more or less completely. Thus, we provide only a brief protocol: Fix specimens as described in [16] and perform Wilbert's protargol method to stage 5, as described in [10], that is, do not develop specimens; rinse cells three times in distilled water; put specimens on a slide and perform the silver carbonate method, as described in [10] (start with fixing the cells in formalin!); fix impregnated specimens in sodium thiosulfate for 1 min; rinse cells 10 times in distilled water; place specimens on an albumised slide and proceed as usual (stages 10–12 in Wilbert's protocol, as described in [10]) to obtain permanent slides.

Terminology is according to [4, 11, 16] because ontogenetic data (manuscript submitted) and live observations on feeding cells [1] proved that trachelocercids have a true, functional, apical oral apparatus. Type slides of other trachelocercids were obtained from the type slide collection in the Oberösterreichische Landesmuseum in Linz (LI).

Results

Sultanophryidae nov. fam.

Diagnosis: Trachelocercida with anterior secant system at right side of glabrous stripe and a specialised ciliary row (lateral kinety) between left branch of bristle kinety and first ordinary somatic kinety.

Type genus: *Sultanophrys* nov. gen.

Sultanophrys nov. gen.

Diagnosis: Same as family.

Type species: *Sultanophrys arabica* nov. spec.

Dedication and etymology: We dedicate this new genus to His Royal Highness Prince Sultan bin Abdul Aziz Al-Saud, Second Deputy Premier, Minister of Defense and Aviation of Saudi Arabia, for his great personal interest and support for researchers on wildlife biodiversity and protection. The name is a composite of the Anglo-French word Sultan (Prince, Sovereign) and

Table 1. Morphometric data from *Sultanophrys arabica*.

Character[1]	x̄	M	SD	CV	Min	Max	n
Body, length in vivo	784.5	780	74.7	9.5	670	900	11
Body, maximum width in vivo	75.0	70	14.1	18.9	50	100	11
Body, length[2]	408.9	390	102.0	24.9	270	630	18
Body, maximum width[2]	162.1	158	24.0	14.8	120	205	18
Body, width at head	43.8	43	5.5	12.6	35	54	18
Glabrous stripe, width in mid-body[2]	133.3	133	19.0	14.2	95	170	18
Anterior end to nuclear apparatus, distance[2]	75.3	72	13.9	18.5	55	105	18
Nuclear figure, length	259.2	262	52.0	20.0	160	390	18
Macronuclear nodules, length	9.6	10	1.1	12.0	8	11	18
Macronuclear nodules, width	9.1	9	1.1	12.2	7	11	18
Macronuclear nodules, number	30.8	31	9.0	29.1	13	47	18
Micronuclei, number	11.7	12	3.5	30.3	6	19	18
Micronuclei, length	4.1	4	–	–	3	5	18
Micronuclei, width	3.9	4	–	–	3	5	18
Somatic kineties on head, number	33.7	34	2.3	6.8	31	37	18
Somatic kineties, maximum number on trunk	34.9	34	2.5	7.1	31	40	18
Neck dikinetids, number in 10 µm	6.9	7	1.2	17.8	4	8	18
Trunk dikinetids, number in 10 µm	8.9	9	1.2	13.1	7	10	18
Brosse kineties, number	2.9	3	0.9	32.3	1	5	18
Anterior brosse kinety, length[3]	2.7	3	0.5	20.3	2	4	18
Anterior brosse kinety, number of kinetids[3]	4.9	5	1.5	31.2	3	7	18
Middle brosse kinety, length[3]	3.6	4	0.8	22.6	2	5	18
Middle brosse kinety, number of kinetids[3]	6.2	6	1.7	27.2	3	8	18
Posterior brosse kinety, length[3]	3.3	3	1.0	31.2	1	5	18
Posterior brosse kinety, number of kinetids[3]	6.3	6	2.2	35.7	3	10	18

[1] Data based, if not stated otherwise, on silver-impregnated and mounted morphostatic specimens from cultures as described in [1]. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of specimens investigated, SD – standard deviation, x̄ – arithmetic mean.

[2] Data of very limited value because specimens strongly contract when fixed for preparation and the trunk often becomes inflated due to the preparation procedures.

[3] Mostly from specimens with three kineties.

the Greek noun phrya (eyelash ~ cilium ~ ciliate sensu lato), meaning "the Prince's ciliate". Feminine gender.

Description of *Sultanophrys arabica*

Diagnosis: Extended cells *in vivo* about 780 × 70 µm and flattened ribbon-like, contract slowly to about half of body length. Head, neck, and tail indistinctly set off from trunk. 31 macronuclear nodules and 12 micronuclei on average form distinct strand in middle third of body. On average 35 ciliary rows on right side of cell; left unciliated, except for bristle kinety, glabrous stripe thus as wide as trunk and tuberculate in fully contracted specimens. Head dark due to accumulation of cytoplasmic inclusions and brilliant brown cortical granules in oral bulge and bowl-shaped oral cavity; circumoral kinety interrupted by indistinct cleft containing 3 brosse kineties on average. Cells dark and punctate due to two types of cortical granules (extrusomes?): large granules about 2 µm across, brilliant brown, in single row between each two kineties and irregularly distributed in cortex of glabrous stripe; small granules about 0.2 µm across, citrine, densely and irregularly arranged.

Type location: Brackish coastal pond at Safwa village (50°06' E, 26°39' N), Saudi Arabian Gulf coast.

Type slides: 1 holotype slide and 2 paratype slides with protargol-silver carbonate impregnated specimens have been deposited in the Oberösterreichische Landesmuseum in Linz (LI), Austria. Relevant specimens are marked by a black ink circle on the cover glass.

Etymology: Named after the region found.

Description: Morphometric data shown in Table 1 are repeated in this section only as needed for clarity. Many characters are highly variable (coefficient of variation > 20%), as is usual in trachelocercids [17].

Fully extended specimens *in vivo* about 670–900 × 50–100 µm, on average 780 × 70 µm (Tab. 1), length : width ratio 8:1–16:1, usually 11:1, that is, stouter than many other large trachelocercids; flattened ribbon-like (2–3:1), including oral area (Fig. 1, 6, 14, 16, 18–20). Very flexible and thus usually curved and spirally twisted along main body axis, producing bright stripe under transmitted light; occasionally even coiled up (Fig. 7, 16). Glides and winds moderately fast on and between organic debris. Body of almost same width in anterior three quarters of cell, head and neck thus indistinctly set off from trunk; posterior quarter gradually narrowed forming short, blunt tail curved to left when cell is viewed from right side. Head indistinctly set off from broad neck, dark due to accumulation of cytoplasmic granules (Fig. 1, 21), not fragile; head margins at left side of cell thickened due to encroaching somatic kineties of right side, produce distinct postoral depression appearing, under transmitted light, as bright patch between brosse and bulging glabrous stripe (Fig. 5, 6, 19, 49, 62). Oral bulge conspicuous, although not projecting above body proper, because packed with brilliant brown granules described below, interrupted at brosse site. Specimens dark and opaque in dissecting microscope, punctate under transmitted light at low magnification (≤ × 100) due to large, brown cortical granules (Fig. 18–20, 44, 46).

Contracts slowly and not very extensively, that is, up to half of body length, prepared specimens thus about 400 µm long (Tab. 1). Fully contracted cells banana-shaped, convex glabrous side distinctly protruding and often conspicuously tuberculate (Fig. 4, 23); frequently partially contracted for long periods and then easily mistaken as extended (Fig. 2). Postdividers about half as long as morphostatic specimens, flask-shaped with rear end narrowly to broadly rounded.

Macronuclear nodules globular to slightly ellipsoidal, number highly variable (Tab. 1), form long strand in middle third of cell (Fig. 1, 26); occasionally some nodules scattered throughout body or, if many are present, arranged side by side producing two indistinct rows (Fig. 29). Nodules not connected or clustered, stand out as bright blisters from opaque cytoplasm under transmitted light (Fig. 1, 26), each surrounded by distinct membrane and containing many minute nucleoli (Fig. 17, 22). Micronuclei globular to slightly ellipsoidal, near and between macronuclear nodules. No contractile vacuole.

Cortex very flexible and thin, not gelatinous, tuberculate in contracted cells (Fig. 2–4, 15, 23, 43–45), contains two size- and colour-types of granules, which are not extruded when cells are pressed or treated with methyl green-pyronin; both granule types coloured and thus easily recognisable in living cells (Fig. 44, 46), impregnate heavily with protargol (Fig. 24, 25, 38, 45), large type makes cell's periphery knobby in the light and scanning electron microscope (Fig. 44). Large granules 0.8–2.5 µm, usually 2 µm across, brilliant brown, composed of thick membrane (?) surrounding bright centre (Fig. 50), sometimes containing conical structure after silver impregnation (Fig. 13, 38), surface smooth in the scanning electron microscope (Fig. 51), release brownish fluid and become lighter and wrinkled in dying and dead cells, form complex pattern in cortex (Fig. 8, 9, 24, 25, 44–46, 50, 57, 58): (1) a single, loose row of these granules is between each two somatic kineties, except for the neck, where they are lacking; (2) in the cortex of the glabrous stripe and oral cavity, they are irregularly arranged; (3) a single row of narrowly spaced granules surrounds the glabrous stripe; and (4) one or two rows are in the oral bulge, which is thus black at low magnification (≤ × 100). Small cortical granules about 0.2 µm across, citrine, stain lilac with methyl green-pyronin, very numerous and irregularly arranged, form citrine

(dark in micrographs, Fig. 44) transverse lines between kineties in contracted specimens, very likely extrusive because cortex of prepared specimens sometimes studded with minute holes (Fig. 51, 63).

Cytoplasm colourless or yellowish, contains rather many 2–20 µm sized golden and colourless fat globules, small and large food vacuoles, and three types of crystal-like inclusions: type 1 numerous, about 3 × 1–2 µm, ellipsoidal and moderately refractile, occasionally impregnated with protargol (Fig. 12, 28); type 2 mainly in head, 3–4 × 2–3 µm, irregularly shaped and highly refractile (Fig. 10, 27, 28); type 3 scattered throughout cytoplasm, 3–4 µm across, spherical, composed of concentric layers and thus lithosome-like (Fig. 11, 27). Some specimens contained many about 4 µm long rods, some with a minute constriction in mid-body, very likely bacteria.

Omnivorous, feeds on filamentous cyanobacteria, up to 1 mm long nematodes, rotifers, small nauplii, and various ciliates and flagellates. The prey is ingested through the apical end, which is very flexible and can open widely. See [1] for details on feeding process.

Somatic infraciliature (Fig. 1, 14, 23–26, 29–43): *Sultanophrys arabica* has only the right surface ciliated, the left is occupied by the glabrous stripe bordered by the bristle kinety. Cilia are about 10 µm long and arranged in longitudinal rows, which are distinctly separate from the circumoral kinety and extend between flat cortical crests. The anterior end of the ciliary rows is distinctly curved to the right and composed of condensed, that is, more narrowly spaced dikinetids. Usually, the curvature and condensation are inconspicuous or even lacking in some kineties. At the right margin of the glabrous stripe are two to four ciliary rows gradually shortened anteriorly and about 20 rows posteriorly (Fig. 23, 29, 30, 32, 33, 38). In other words, an anterior and posterior secant system are formed at the right margin of the cell, where some ciliary rows abut to the bristle kinety. Thus, the head, neck and tail have slightly fewer kineties than the trunk (Tab. 1). The ciliary rows left of the glabrous stripe are unshortened anteriorly and posteriorly (Fig. 30, 54).

There is a special ciliary row, the lateral kinety, between the left branch of the bristle kinety and the first ordinary somatic ciliary row. The lateral kinety shows the following specialisations (Fig. 30–32, 35, 39–43): (1) the dikinetids have ciliated only the anterior basal body and are usually lighter impregnated than those from ordinary ciliary rows; (2) the kinetids are more narrowly spaced than in the ordinary ciliary rows, except for the posterior quarter, and less obliquely arranged; (3) the subkinetal fibres are lacking; (4) the ciliated anterior basal body of the dikinetids bears a conspicuous (modified subkinetal?) fibre, which is short and close to the kinety axis in the anterior three quarters of the kinety and gradually increases in length posteriorly, where the fibres of several kinetids unite to up to 50 µm long, subcortical bundles (Fig. 31); and (5) the cortical tubercles between the bristle and lateral kinety have a particular, conical shape (Fig. 43).

The entire infraciliature consists of ciliated dikinetids, except for the following regions, where only the anterior basal body is ciliated: (1) the curved anterior end of the kineties, (2) the tail, (3) the posterior portion of the secant kineties, and (4) the dikinetids of the lateral kinety (Fig. 8, 9, 35, 37, 39, 43, 52). The dikinetids are associated with a short, sharply impregnated subkinetal fibre extending slightly beyond the next dikinetid, and a long postciliary fibre forming a distinct postciliodesma right of the kineties (Fig. 34). No oralised somatic dikinetids and no myonemes were recognisable. Whether they are lacking or did not impregnate needs transmission electron microscopic investigations.

The glabrous stripe extends along the whole body length and width, except for the head region, where it gradually narrows and deepens to form the postoral depression (Fig. 5, 6, 14, 19, 23, 25, 26, 29, 30, 33, 46, 53, 55, 56). It is bordered by the bristle kinety, which consists of dikinetids having about 15 µm long, rather stiff cilia (Fig. 14, 29, 30, 33, 35–41, 43, 53–56, 59, 61, 63). The bristle kinety is easily distinguished from ordinary ciliary rows and the lateral kinety because its dikinetids are more widely spaced, except in the anterior region, and more irregularly arranged, frequently forming short fragments consisting of 2–5 bristles; furthermore the kinetids either lack or have very inconspicuous postciliary fibres, too small to be recognised with the light microscope. The subkinetal fibres, in contrast, are well developed and unite to a distinct fibre underneath the left branch of the kinety, while those of the right branch extend straight into the cell (Fig. 35–37). The ciliation of the bristle dikinetids, interspersed by rather many unciliated granules, is as in other trachelocercids [17], that is, those along the right margin of the glabrous stripe have ciliated posterior basal bodies, whereas the dikinetids along the left stripe margin have ciliated anterior basal bodies; thus, the ciliation of the bristle kinetids is opposed by about 180° where the ends of the kinety abut, that is, subapically at the right margin of the glabrous stripe (Fig. 53).

Oral infraciliature (Fig. 5, 29, 30, 47–49, 52, 53, 55, 56–63): The oral infraciliature of *S. arabica* consists of a circumoral kinety and a minute brosse, difficult to recognise in living specimens. The circumoral kinety extends in the flat groove separating the oral bulge from the head and is interrupted at the brosse site with ends sometimes indistinctly curved posteriorly. It is composed of a single row of obliquely oriented, very narrowly spaced dikinetids, which have 15 µm long cilia and 10–35 µm long nematodesmata associated with the

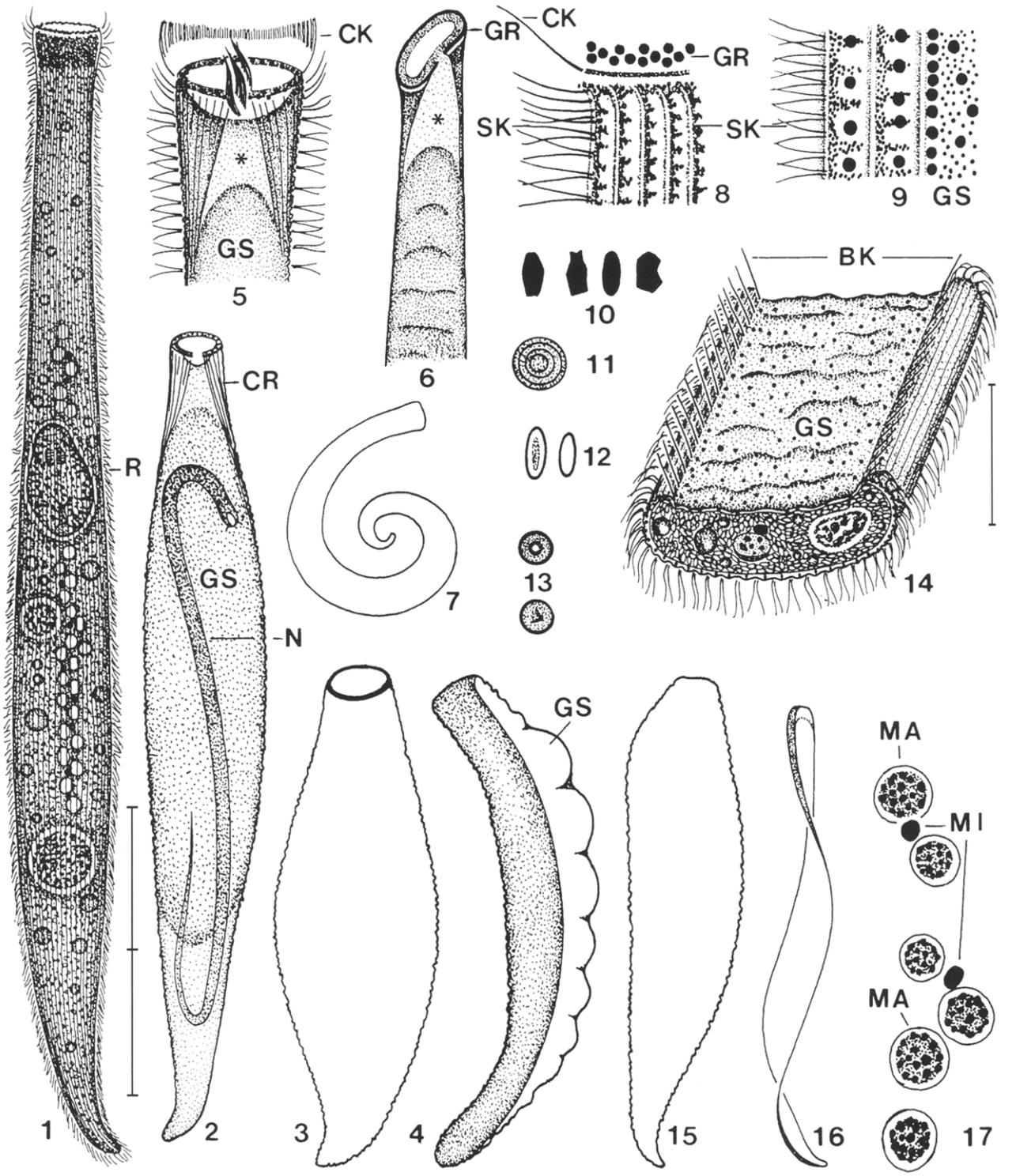

Fig. 1–17. *Sultanophrys arabica* from life (1–12, 14–16) and after silver impregnation (13, 17). **1.** Right side view of a fully extended, representative specimen. **2.** Left side view of a slightly contracted specimen. **3, 4.** Left side and lateral view of a fully contracted specimen. **5, 6.** Left side views of anterior body portion showing organisation of oral apparatus and postoral depression (asterisks). **7, 15, 16.** Curled, fully contracted, and leaf-like flattened specimen. **8, 9.** Arrangement of cortical granules in oral area and mid-body. **10–12.** Three types of crystal-like inclusions occur in head and trunk. **13.** Large cortical granules. **14.** Transverse section of trunk. **17.** Part of nuclear apparatus. BK – bristle kinety, CK – circumoral kinety, GR – granule ring in oral bulge, GS – glabrous stripe, MA – macronuclear nodules, MI – micronuclei, N – ingested nematode, R – ingested rotifer, SK – right side somatic kineties. Bar division 100 µm (Fig. 1–4) and 40 µm (Fig. 14).

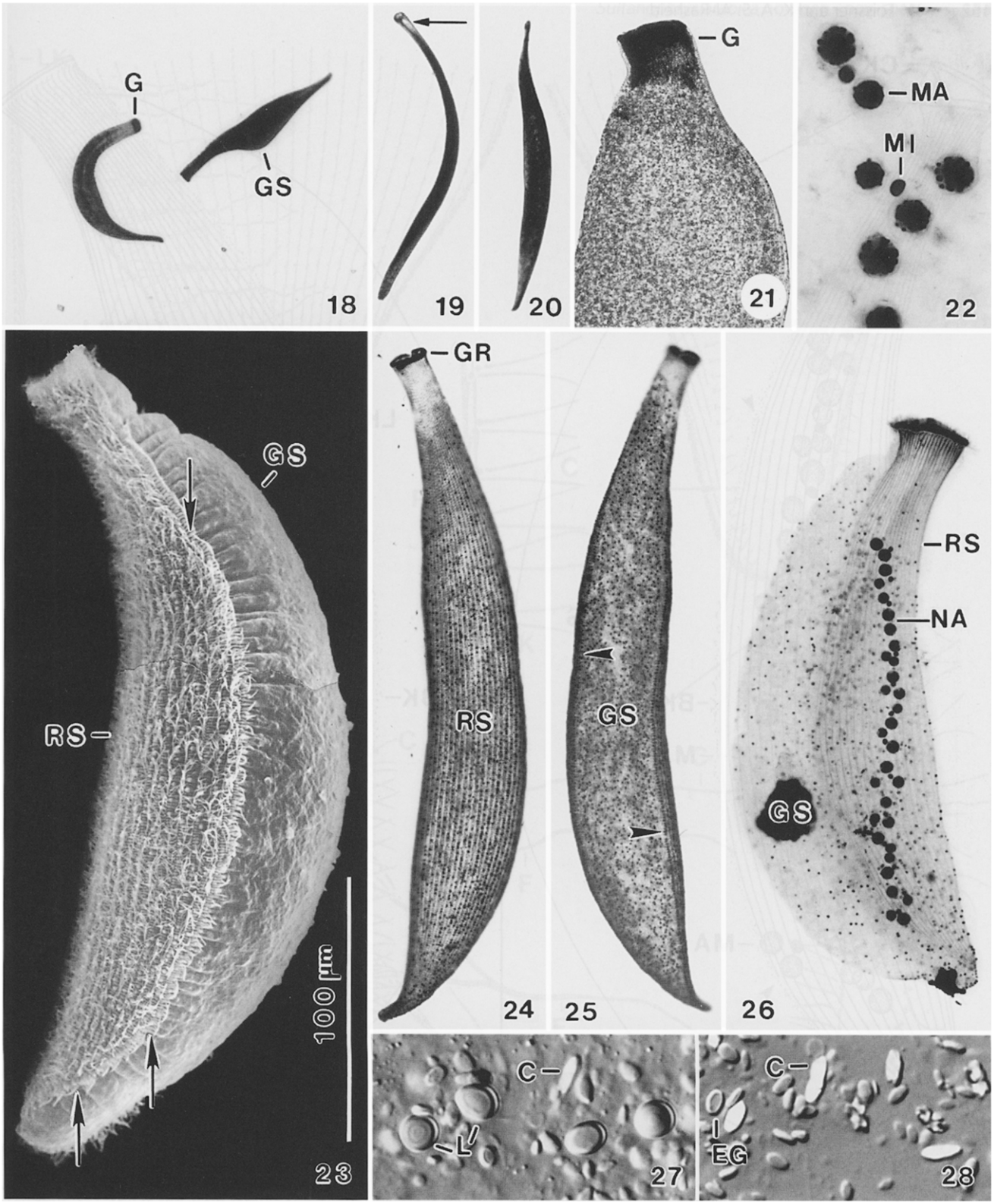

Fig. 18–28. *Sultanophrys arabica* from life (18–21, 27, 28), after silver impregnation (22, 24–26), and in the SEM (23). **18–21, 27, 28.** Freely motile specimens and cytoplasmic inclusions, which form a dark accumulation in the head (18, 19, 21). Arrow marks bright postoral depression. **23, 24, 25.** Lateral, right side, and left side view. Arrows mark secant system. The right side ciliary rows extend slightly onto the left side (arrowheads). **22, 26.** Nuclear apparatus. C – crystal-like inclusions, EG – ellipsoidal granules, G – granule accumulation, GS – glabrous stripe, L – lithosome-like inclusions, MA – macronuclear nodule, MI – micronucleus, NA – nuclear apparatus, RS – ciliated right side.

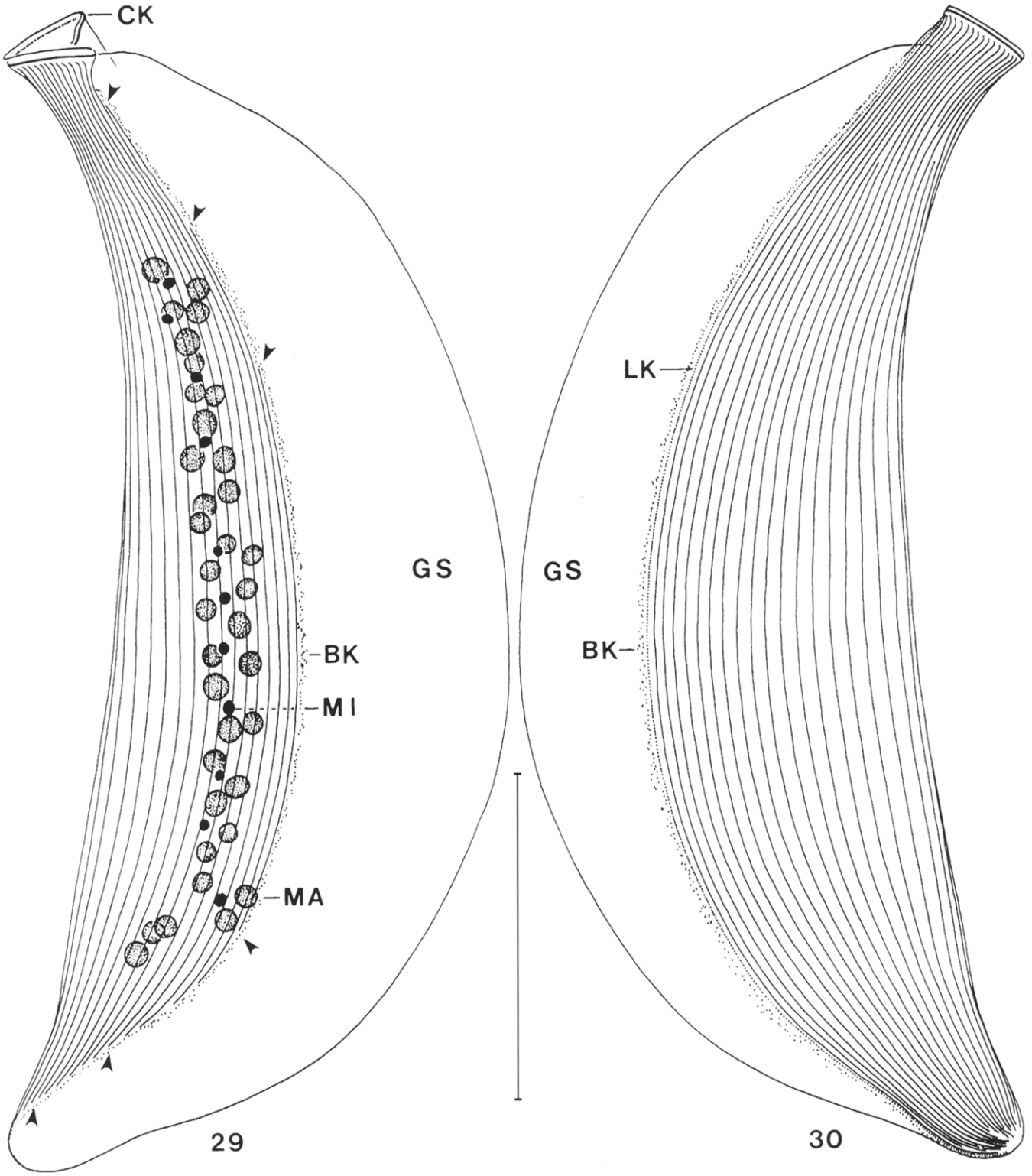

Fig. 29, 30. *Sultanophrys arabica*, general organisation of the infraciliature after protargol-silver carbonate impregnation. For details, see following figures. Arrowheads mark the anterior and posterior secant system produced by shortened ciliary rows. Only *S. arabica* has an anterior secant system at the right margin of the glabrous stripe. No secant system occurs at the left side of the glabrous stripe, where a special (lateral) kinety, the main family character, extends. BK – bristle kinety, CK–circumoral kinety, GS – glabrous stripe, LK – lateral kinety, MA – macronuclear nodule, MI – micronucleus. Bar 100 µm.

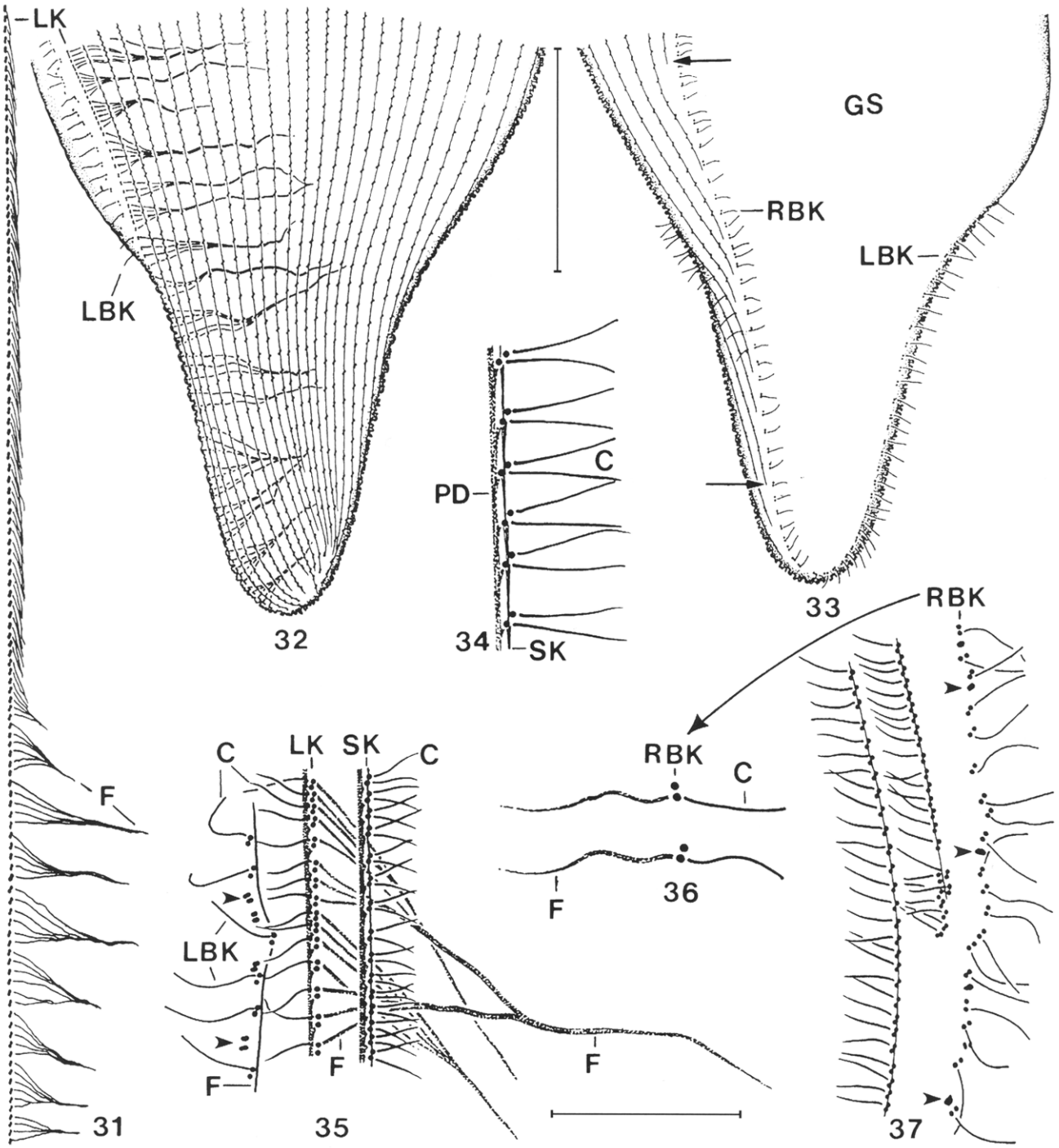

Fig. 31–37. *Sultanophrys arabica*, details of the somatic infraciliature after protargol-silver carbonate impregnation. **31, 35.** A special "lateral kinety" (LK) extends between the left branch of the bristle kinety and the first ordinary somatic ciliary row (cp. Fig. 30). The lateral kinety (schematised in Fig. 31) possesses long fibres, possibly specialised subkinetal microtubule ribbons (cp. Fig. 34), and is the main family and genus character because it is lacking in all other trachelocercids studied so far. Only the anterior basal body of the dikinetids is ciliated in the lateral kinety (LK) and the bristle kinety (LBK), which is accompanied by a longitudinal fibre. Arrowheads mark unciliated granules. **32, 33.** Right and left side view of posterior body portion. The fibres of the lateral kinety form conspicuous bundles. Arrows mark posterior secant system at right margin of glabrous stripe. **34.** Somatic fibrillar system. **36, 37.** Details from right branch of bristle kinety (RBK). Note that only the posterior basal body, associated also with a long (subkinetal?) fibre extending into the cell, of the bristle kinetids is ciliated. Arrowheads mark unciliated granules. C – cilia, F – fibres, GS – glabrous stripe, LBK – left branch of bristle kinety, LK – lateral kinety, PD – postciliodesma, RBK – right branch of bristle kinety, SK – somatic kinety. Bars 50 µm (Fig. 32, 33) and 20 µm (Fig. 35).

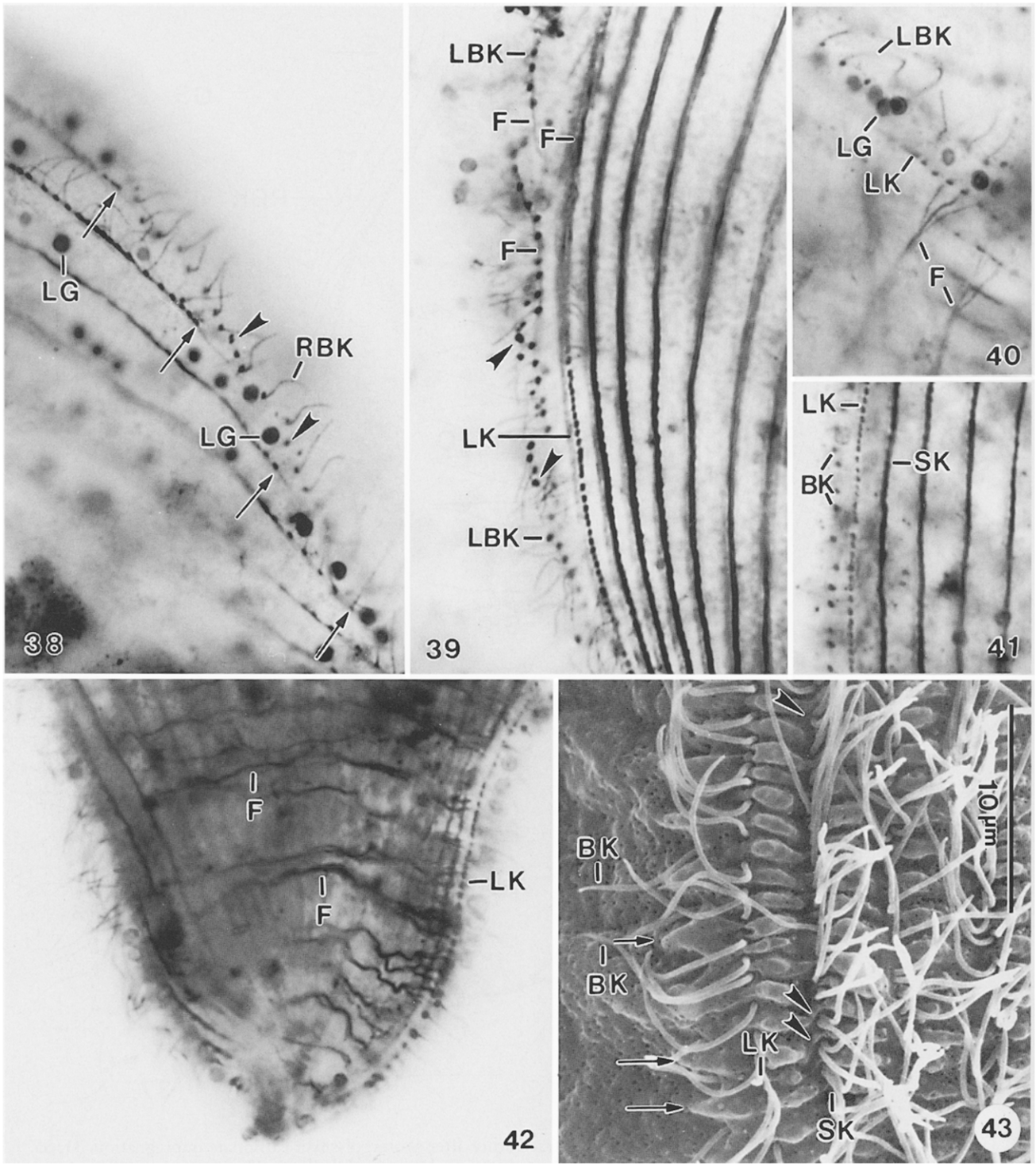

Fig. 38–43. *Sultanophrys arabica*, somatic infraciliature after silver impregnation (38–42) and in the SEM (43). **38.** Right posterior area showing shortened ciliary rows (arrows), which form the posterior secant system. Arrowheads mark unciliated granules within the bristle kinety, where only the posterior basal body of the dikinetids is ciliated. **39–42.** Left margin of glabrous stripe showing the lateral kinety (LK), from which conspicuous fibres originate. Arrowheads mark unciliated granules within the bristle kinety. **43.** Left margin of glabrous stripe showing bristle kinety with widely spaced, single cilia, lateral kinety with narrowly spaced, single cilia, and ordinary somatic ciliary rows with double cilia (arrowheads). Arrows mark particular, conical cortical tubercles between bristle and lateral kinety. BK – bristle kinety, F – fibres, GS – glabrous stripe, LBK – left branch of bristle kinety, LG – large cortical granules, LK – lateral kinety, RBK – right branch of bristle kinety, SK – ordinary somatic kinety.

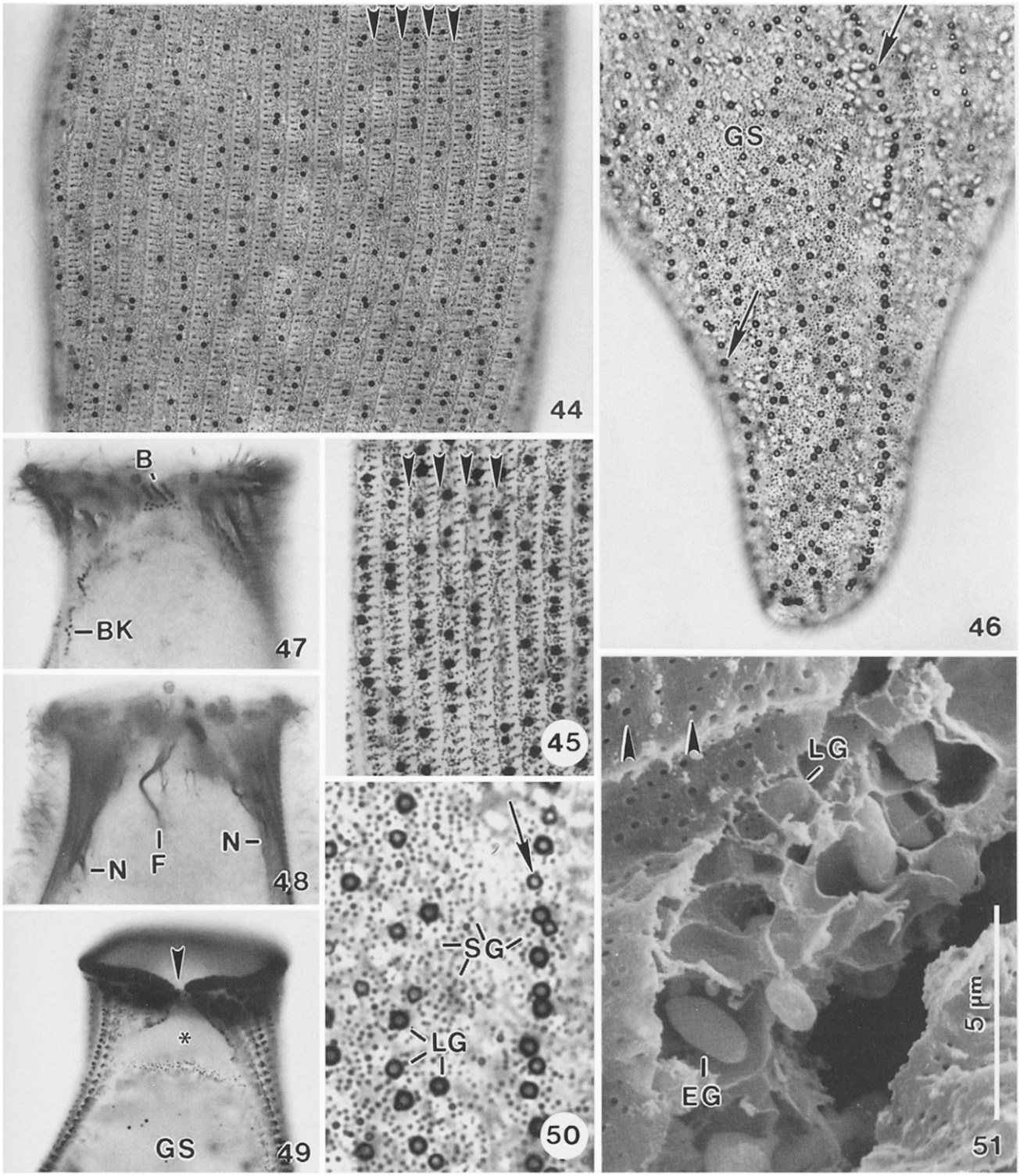

Fig. 44–51. *Sultanophrys arabica* from life (44, 46, 50), after silver impregnation (45, 47–49), and in the SEM (51). **44, 45.** Between each two ciliary rows (arrowheads) are a single row of large and innumerable small cortical granules. **46, 50.** The glabrous left side is framed by a row (arrows) of narrowly spaced, large cortical granules. **47, 48, 49.** Left anterior end. A conspicuous bundle of fibres originates from the brosse kineties. The circumoral kinety is open at the brosse site (arrowhead). Asterisk marks postoral depression. **51.** Broken specimen showing many minute openings (arrowheads) in the cortex, probably from extruded small cortical granules (cp. Fig. 63). Note large, ellipsoidal cytoplasmic inclusions (EG) in individual vacuoles. B – brosse, BK – bristle kinety, F – fibres, EG – ellipsoidal inclusions, GS – glabrous stripe, LG – large cortical granules, N – nematodesmata, SG – small cortical granules.

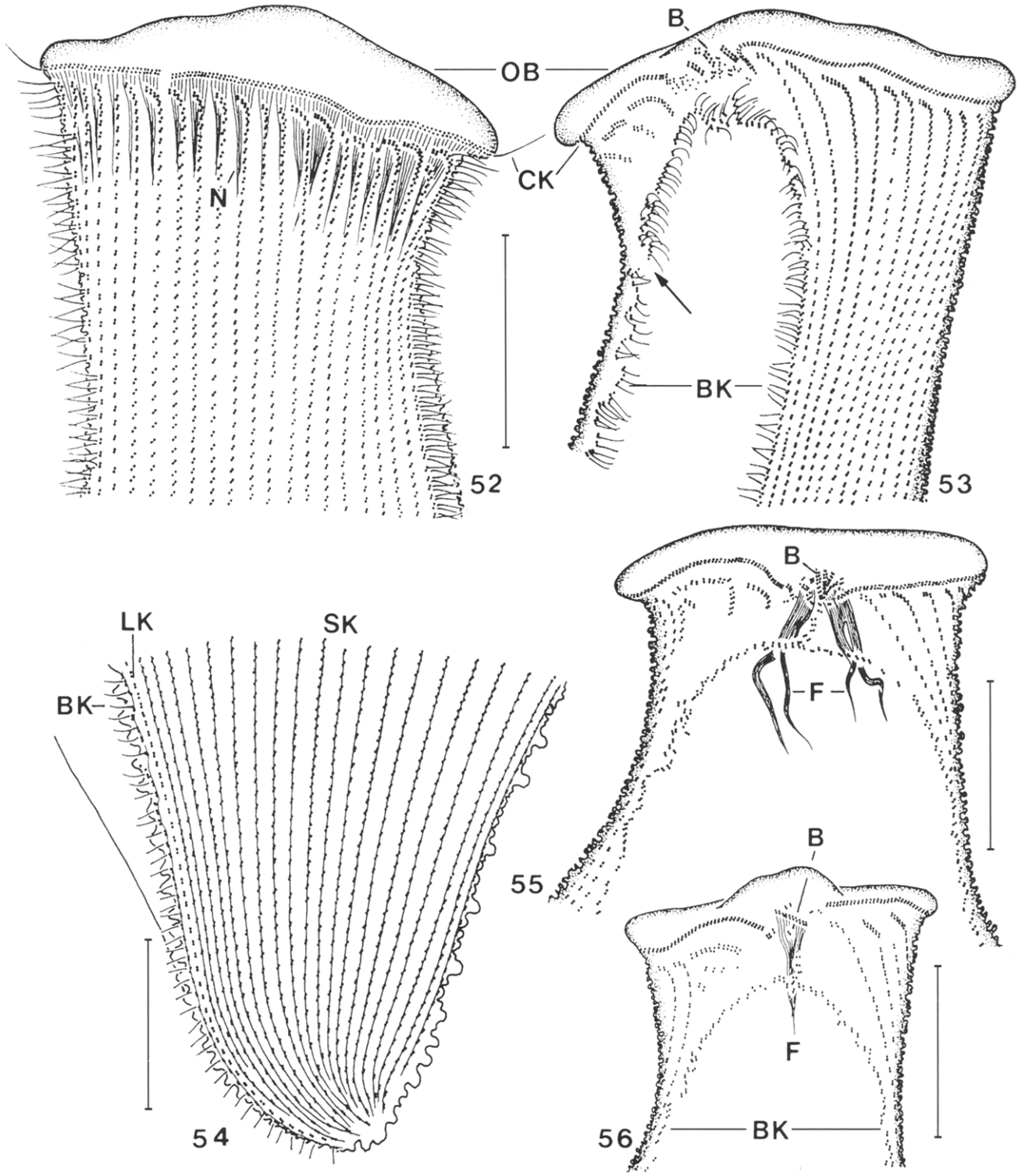

Fig. 52–56. *Sultanophrys arabica*, infraciliature at anterior and posterior end after protargol-silver carbonate impregnation. **52, 53.** Right and left side view of anterior end of same specimen, showing details of the oral and somatic infraciliature. Note that dikinetids at anterior end of somatic kineties have ciliated only the anterior basal body. Nematodesmata omitted in (53) for clarity. Arrow marks site where ends of bristle kinety abut and ciliation of dikinetids is opposed by 180°. **54.** Left lateral view of posterior body portion. The lateral kinety (LK) extends to the body end and lacks the subkinetal fibre present in the ordinary somatic kineties (cp. Fig. 34). **55, 56.** Oral structures at left anterior end. Note brosse variability (cp. Fig. 53). B – brosse, BK – bristle kinety, CK – circumoral kinety, F – fibres, LK – lateral kinety, N – nematodesmata, OB – oral bulge, SK – ordinary somatic kineties. Scale bars 20 µm.

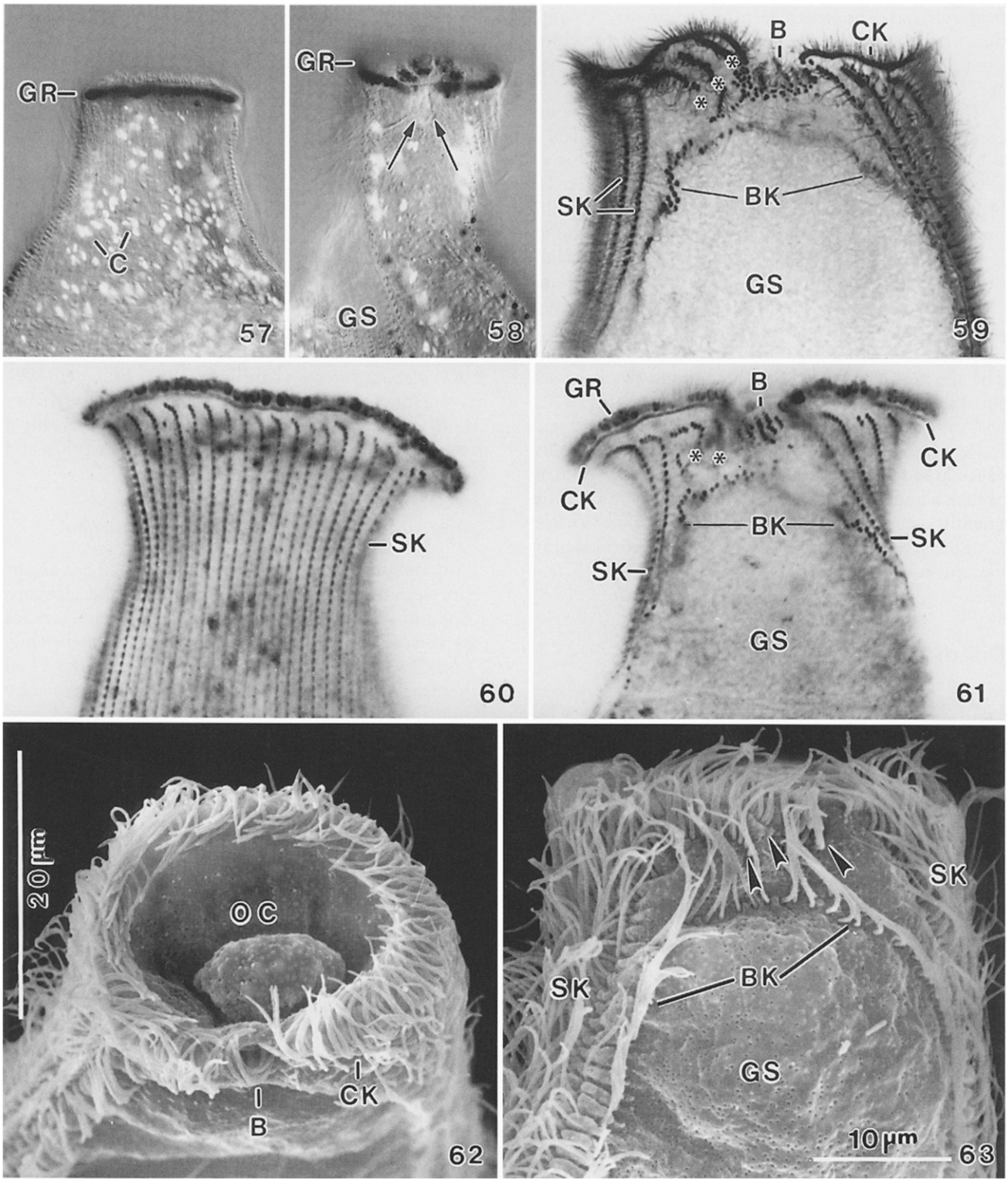

Fig. 57–63. *Sultanophrys arabica*, oral apparatus from life (57, 58), after silver impregnation (59–61), and in the SEM (62, 63). The oral apparatus consists of the circumoral kinety (CK), the brosse cleft (arrows in 58), the brosse (B, arrowheads in 63), and the oral cavity (OC). The oral bulge is interrupted at the brosse site and contains a conspicuous ring of brilliant brown, large cortical granules (GR). Asterisks mark kinety fragments right of brosse. Figures 60, 61 are from a conjugating specimen, in which the head becomes trumpet-shaped. B – brosse, BK – bristle kinety, C – highly refractive cytoplasmic crystals, CK – circumoral kinety, GR – granule ring, GS – glabrous stripe, OC – oral cavity, SK – somatic kineties.

posterior basal bodies. The nematodesmata of neighbouring dikinetids unite to small bundles, forming a slightly cone-shaped oral basket (Fig. 52); rarely, there are 1–2 dikinetids wide gaps within the kinety.

The brosse is in a flat cavity and interrupts the circumoral kinety (Fig. 53, 55, 56, 58–63). It consists of 1–5, usually 3 short, oblique dikinetidal ciliary rows, which have ciliated only the posterior basal bodies. The brosse kineties are associated with conspicuous fibre bundles extending posteriorly. Around the brosse are few to many scattered dikinetids and, at right, usually three short kinetofragments, very likely of oral origin.

Distribution and ecology: As yet found only at type location, but possibly occurring also in saline ponds at the coast of Benin, West Africa ([8], see discussion). The site we found *S. arabica* has a highly varying seasonal salinity (about 10–40‰) and temperature (20° C – 35° C). This indicates that *S. arabica* can tolerate a wide range of abiotic factors. Considering this and the unspecialised food requirements, it should occur in many brackish and marine habitats. Possibly, it has been frequently confused with other species, especially *Tracheloraphis margaritata*, which has a similar cortical granulation (see discussion).

Discussion

Comparison with related species

Sultanophrys arabica is a conspicuous species, mainly due to the cortical granules, which form dense stripes and make cells dark at low magnification (Fig. 1, 8, 9, 18, 19, 24, 25, 44–46). This particular granulation evolved convergently in several genera and species, namely, in *Tracheloraphis margaritata, T. grassei, T. poljanskyi, Trachelocerca binucleata*, and *Kovalevaia sulcata*.

Tracheloraphis margaritata (Kahl, 1930) Dragesco, 1963 is a difficult species. According to the original description [19], it is only 350 µm long when extended, has a narrow glabrous stripe, and possesses only 5 macronuclear nodules forming a short strand. Later authors [6, 9, 22, 23], however, identified large (up to 2000 µm) trachelocercids with a rather broad glabrous stripe and many (9–101) macronuclear nodules forming a long strand with Kahl's species. Certainly, *S. arabica* is distinctly different from the original description of *T. margaritata*, even if the considerable variability trachelocercids generally have is taken into account. The redescriptions mentioned above are more difficult to rate. We checked the protargol slides Dragesco and Dragesco-Kernéis [8] used for the redescription of *T. margaritata*. Unfortunately, they are of poor quality, hardly showing details of the infraciliature. However, the cortical granule stripes recognisable indicate that the anterior secant system is at the right side, not at the left, as illustrated by Dragesco and Dragesco-Kernéis [8]. Thus, the species investigated by these authors could have been *S. arabica*.

Tracheloraphis grassei (Dragesco, 1960) Foissner and Dragesco, 1996b has large brown granules only on the left side. Furthermore, it has a distinct tail and only about 14 ciliary rows (31–40 in *S. arabica*).

Tracheloraphis poljanskyi (Raikov, 1963) Foissner, 1997 has only about 12 ciliary rows (31–40 in *S. arabica*) and a long, narrow neck.

Trachelocerca binucleata Dragesco, 1960 has only 2 macronuclear nodules and is flask-shaped and only 200 µm long.

Kovalevaia sulcata (Kovaleva, 1966) Foissner, 1997 has a distinct, obconical head, less than 25 ciliary rows (31–40 in *S. arabica*) and only 1 brosse kinety (usually 3 in *S. arabica*). See [14] for a detailed redescription and literature review.

Sultanophrys as a new genus and family

Sultanophrys has two unique features, namely, an anterior secant system at the right side of the glabrous stripe and a lateral kinety at the left. Both characters are easy to recognise in well-impregnated specimens (Fig. 29–42). Nevertheless, we checked the type slides of all other trachelocercid genera described or redescribed by Foissner and Dragesco [7,13, 14, 16, 17]. This showed the accuracy of the data, that is, all other genera lack a lateral kinety and have the anterior secant system at the left side of the glabrous stripe. Thus, *S. arabica* is distinctly different from other trachelocercids, requiring separation at genus and family level.

As concerns the anterior secant system, *S. arabica* looks like a mirror image of an ordinary trachelocercid (Fig. 29, 30). This specialisation is not caused by an inversion of the cell itself, as shown by the somatic fibrillar systems, which extend the right way, for instance, the postciliodesmata are right of the kineties (Fig. 34). Likely, the particular location of the secant system of *S. arabica* is in some way associated with the lateral kinety, which extends along the whole body length parallel to the left branch of the bristle kinety. Thus, the ciliary rows cannot abut to the bristle kinety along this side. Generally, the trachelocercid secant system arises by reduction of the body width in the anterior and posterior portion, where the ciliary rows are successively shortened and abut to the bristle kinety [16, 17]. Thus, the narrower the body ends, the more distinct the secant systems. In *Sultanophrys*, which has almost the same width over the whole length, the secant systems are weakly developed and confined to the right side of the glabrous stripe (Fig. 29, 30, 32, 33, 38, 39).

The lateral kinety: a trace for evolution of trachelocercids from loxodids

The data available strongly argue for a sister group relationship of loxodid and trachelocercid karyorelictids [15, 17]: both have the same somatic body plan, that is, a glabrous stripe bordered by a complex bristle kinety. The oral structures, in contrast, are rather different, and the plesiomorphic (ancestral) and apomorphic (derived) state of many characters is unknown or controversial [2, 15, 17]. The geleiids, which also have non-dividing macronuclei, are very differently organised, that is, lack a glabrous stripe and a bristle kinety [15].

We suggest that the lateral kinety of *Sultanophrys* provides a possibility to root evolution in karyorelictids, that is, to obtain an idea about the organisation of the common ancestor of loxodids and trachelocercids. The lateral kinety has two main features: (1) it is located between the bristle kinety and the first ordinary somatic kinety; and (2) the basal bodies have associated conspicuous fibres, especially in the posterior third of the kinety, which extend into the cytoplasm (Fig. 30–32, 35, 39–42). The same specialisations occur in the dorsolateral kinety of all loxodids investigated in detail [11, 12, 18, 20]. Indeed, it is possible to create a *Sultanophrys*-like trachelocercid from a loxodid simply by shifting the ventral oral apparatus of, for instance, *Loxodes* or *Remanella* to the anterior end of the cell. There is thus a spatial and structural homology between the sultanophryid lateral kinety and the loxodid dorsolateral kinety, indicating that the common ancestor possessed a similar kinety, which was maintained in loxodids and reduced in most trachelocercids. Accordingly, the common ancestor was possibly more similar to present-day loxodids than to present-day trachelocercids or, in other words, trachelocercids derived from loxodids. *Sultanophrys*, which still has a lateral kinety, but is otherwise similar to ordinary trachelocercids, might serve as an example how the process passed; very likely it is an ancient trachelocercid close to the node where the common ancestor split into loxodids and trachelocercids.

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