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Morphology and Cell Division of the Little Known Freshwater Ciliate *Uroleptus* cf. *magnificus* (Kahl, 1932) Olmo, 2000 (Hypotricha, Uroleptidae), and List of Published Names in *Uroleptus* Ehrenberg, 1831 and *Paruroleptus* Wenzel, 1953

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Summary. In 1988, we found a large (250–400 × 80–150 µm in protargol preparations) *Uroleptus*-like hypotrich in a freshwater pond in Harbin, China. We studied the morphology of non-dividers and the cell division using protargol impregnation. Since we disregarded live observations and due to the lack of a modern revision of the uroleptids, a final identification was not possible. A detailed comparison with the most similar limnetic *Uroleptus*-like hypotrichs and with *Rigidothrix goiseri* revealed that the Chinese population is very likely identical with *Uroleptus magnificus* [basionym *Holosticha (Paruroleptus) magnificus* Kahl, 1932], a very rare species possibly confined to limnetic, stagnant water bodies of the holarctic region. Besides the large size, main features of *U.* cf. *magnificus* are: (i) about 80 adoral membranelles; (ii) three or four inconspicuous transverse cirri; (iii) 5–8 dorsomarginal kineties; (iv) the oral primordium originates *de novo* left of the post-oral midventral cirri; (v) the frontal-ventral-transverse cirri anlagen of the proter and the opisthe originate via primary primordia; (vi) the left frontal cirrus of the proter originates from the middle portion of the disorganizing parental paroral; (vii) the parental endoral becomes the undulating membrane anlage for the proter; and (viii) the frontoterminal cirri originate in the plesiomorphic manner, that is, from the rearmost anlage. A compilation reveals that 59 species, subspecies, etc. have been described in or assigned to *Uroleptus* and *Paruroleptus*, but only about 50% of them seem to be true uroleptids. Many species of this predominantly limnetic group are little known.

Key words: China, Ciliophora, Dorsomarginalia, morphogenesis, ontogenesis, *Rigidothrix*, Stichotrichia.

INTRODUCTION

Uroleptus Ehrenberg, 1831 is a notoriously difficult genus of hypotrichous ciliates to which almost 60 more

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or less distinctly tailed species have been originally assigned or transferred (Berger 2001). Many of these species are described after live observation only so that the exact cirral pattern of the tail-region is not known, that is, it is often uncertain whether or not transverse cirri are present. Consequently, we do not have an ultimate decision about the validity of *Paruroleptus* Wenzel, 1953, a genus originally, but invalidly established by

Kahl (1932) as subgenus of *Holosticha* for *Uroleptus*-like species with transverse cirri.

Until recently, *Uroleptus* and *Paruroleptus* were assigned – separately or as synonyms – to the urostyloids because their members have zigzagging midventral cirri, the main apomorphy of the Urostyloidea (e.g. Bütschli 1889, Borror 1972, Corliss 1979, Jankowski 1979, Borror and Wicklow 1983, Shi *et al.* 1999, Jankowski 2007, Lynn 2008). However, this plausible morphological classification is not supported by 18S rDNA genealogies, where *Uroleptus* and *Paruroleptus* are not in the urostyloid cluster containing *Urostyla grandis* Ehrenberg, 1830, type of the Urostyloidea (e.g. Chen and Song 2001, Snoeyenbos-West *et al.* 2002, Hewitt *et al.* 2003, Foissner *et al.* 2004). In these molecular trees, *Urostyla* branches off at or near the base of the Hypotricha, whereas *Uroleptus/Paruroleptus* is more closely related to the oxytrichids than to the urostyloids (for reviews, see Berger 1999, 2006a). To explain the discrepancy between morphological and molecular classifications, Foissner *et al.* (2004) postulated the CEUU hypothesis (*C*onvergent *E*volution of *U*rostylids and *U*roleptids), which assumes that the zigzagging midventral pattern evolved convergently in *Urostyla*, *Uroleptus*, and some oxytrichids, for example, *Territricha* and *Pattersoniella*. *Uroleptus* was therefore not reviewed in the monograph of the urostyloids by Berger (2006a), where the Dorsomarginalia have been established to summarize all hypotrichs – including *Uroleptus* – with a dorsomarginal kinety.

Foissner and Stoeck (2006) described one of the most curious hypotrichs, *Rigidothrix goiseri*, which has features of rather different groups, for example, a midventral pattern like *Uroleptus*, an oral apparatus like *Stylonychia* and *Laurentiella*, and an 18S rDNA gene sequence which is obviously very similar to that of *Oxytricha granulifera*, type of *Oxytricha* and the oxytrichids. Because of this uncommon combination of features, Foissner and Stoeck (2006) established the Rigidotrichidae, comprising *Rigidothrix*, *Afrophrya*, *Territricha*, and *Uroleptus*. Somewhat later, Foissner and Stoeck (2008) removed *Uroleptus* from the rigidotrichids and introduced the monotypic Uroleptidae for the "very flexible midventral hypotrichs forming a distinct clade within the oxytrichids in molecular trees."

More than 900 publications relate to *Uroleptus* and/or *Paruroleptus*, most of them covering faunistics and ecology (Berger 2006b). By contrast, the morphogenesis, which provides – besides morphology and molecular biology – useful features to estimate the phylogeny of hypotrichs and ciliates in general, is investigated in detail of only three species, namely of *U. musculus* (Müller, 1773) Ehrenberg, 1831 by Martin *et al.* (1981), of *U. lepisma* (Wenzel, 1953) Foissner, 1998 by Olmo (2000), and of *U. caudatus* (Stokes, 1886a) Borror, 1972 by Eigner (2001). In addition, Foissner and Stoeck (2006) described in great detail the cell division of *Rigidothrix goiseri*, a striking species from a flood plain in West Africa.

In 1988, we found a large, *Uroleptus*-like species in a freshwater pond in China. It grew very well in cultures and therefore we could study the cell division in detail. The identification of large, limnetic uroleptids is almost impossible at the present state of knowledge because a detailed revision of this group, solving the many taxonomic and nomenclatural problems, is not yet available (e.g. Foissner *et al.* 1991, Foissner and Stoeck 2008). Unfortunately, we disregarded detailed live observation, that is, we do not know the exact body outline (e.g. slender as *Uroleptus caudatus* or wide as *U. magnificus* and *Rigidothrix goiseri*) and important details of the oral apparatus, for example, the natural shape of the undulating membranes and the buccal field (e.g. stylonychid as in *U. magnificus* and *R. goiseri* or non-stylonychid). Thus, we cannot provide a complete description and, much more serious, it is impossible to assign the population to *Uroleptus/Paruroleptus* or *Rigidothrix* with reasonable certainty. Consequently, we identify our population provisionally as *Uroleptus* cf. *magnificus* (Kahl, 1932). In addition to the morphometric characterization and the morphogenesis of the Chinese population, we provide a list of all species so far described or assigned to *Uroleptus* and/or *Paruroleptus* and the very similar, but perhaps not very closely related genus *Rigidothrix*. This brief review may stimulate the interest in this very fascinating, but rather complicated group.

MATERIALS AND METHODS

Uroleptus cf. *magnificus* was isolated from the eastern shore of Hei-Yu-Pao pond in the west suburb of the city of Harbin (lat 45°44′N, long 126°32′E; 117 m above sea level), Northeast China, in spring 1988. Later this pond dried up and has become a residential area, that is, the population is very likely extinct. Isolated specimens were cultured in Petri dishes containing filtrated water from the sample site. Some rice grains were added to promote the growth of *Chilomonas paramaecium*, the main food of *Uroleptus* cf. *magnificus* in our non-clonal cultures. Subsequently, the freshwater was gradually substituted by Pringsheim solution to get more cells

into division. Cultures were kept at 20°C. Protargol impregnation was used in order to reveal the infraciliature and nuclear apparatus (Shi and Frankel 1990). Counts and measurements on impregnated specimens were performed at a magnification of 1250 ×. Drawings were made with a drawing device.

Nomenclature of higher taxa follows Table 3 in Berger (2008). General terminology is mainly according to Lynn (2008); for explanation of hypotrich-specific terms (e.g. DE-value, 18-cirri hypotrich, midventral complex, pseudorow, mixed row), see Berger (1999, 2006a, 2008, 2011), Foissner and AL-Rasheid (2006), and Foissner and Stoeck (2008). The zigzagging ventral cirri of the urostyloids and uroleptids were termed midventral cirri by Borror (1972). Berger (2004) introduced the more precise and comprehensive term midventral complex for this part of the ventral ciliature. According to the CEUU hypothesis, the zigzagging midventral pattern evolved convergently in various taxa (see introduction). Thus, we suggest preceding the term midventral complex the name of the group concerned, for example, uroleptid midventral complex, neokeronopsid midventral complex, or, as already proposed by Foissner and Stoeck (2008), oxytrichid midventral complex. The same proposal was made by Eigner and Foissner (1994) for the term median cirral row. For the designation of the frontal-ventral-transverse cirri anlagen and cirri in 18-cirri hypotrichs, the numbering system by Wallengren (1900) is used (details see Berger 1999: 16, 2008: 27). Cirri which are unambiguously homologous in 18-cirri hypotrichs and uroleptids have the same designation, for example, cirrus II/3 is identical with the middle frontal cirrus, even when anlage II usually does not form three cirri in uroleptids, as it does in 18-cirri hypotrichs.

Voucher slides are deposited in the Laboratory of Protozoology, Ocean University of China (Qingdao) and in the Upper Austrian Museum in Linz (LI). Since the list of species is a major part of the paper, all authorities of taxonomic names are mentioned in the reference section.

RESULTS

Morphology and infraciliature of the Harbin population of *Uroleptus* cf. *magnificus* (Figs 1A, B, 2A; Table 1)

The following description of interphasic specimens is based exclusively on protargol-impregnated specimens of the Chinese population. Thus, some important taxonomic details (e.g. body shape, flexibility of cell, cortical granulation) are not known.

Body size 312 × 112 µm and length : width ratio 2.8 : 1 on average (Table 1); specimen illustrated with a ratio of 3.2 : 1 (Figs 1A, B). Body with distinct tail occupying about 20% of body length in specimen illustrated (Fig. 1A). Invariably two macronuclear nodules slightly left of midline about in central body portion, arranged relatively close together; anterior and posterior nodule of equal size, on average about 35 × 19 µm;

contain small chromatin bodies. Usually one slightly ellipsoidal micronucleus close to left side of each macronuclear nodule (Figs 1B, 2A). No cortical granules recognizable with the impregnation method used. Contractile vacuole not recognizable in protargol slides.

Adoral zone occupies 35% of body length and composed of 79 membranelles on average, formed like a question mark (Figs 1A, B, 2A; Table 1); distal end extends rather far posteriorly on right body margin, DE-value 28% in specimen illustrated (Fig. 1A). Individual membranelles of usual fine structure, that is, composed of one short, one medium-length, and two long rows of basal bodies; largest membranelles up to 17 µm wide. Buccal field and frontal area large in prepared specimens. Undulating membranes intersect optically right of proximal portion of adoral zone. Paroral slightly to distinctly curved, commences behind left frontal cirrus and about at same level as midventral complex; endoral of about same length and curvature as paroral, commences about in center of buccal cavity and terminates close to rear end of adoral zone. Pharyngeal fibers impregnate with protargol, extend obliquely backwards (Fig. 2A).

Cirral pattern typically uroleptid and of usual variability (Figs 1A, 2A; Table 1). Three distinctly enlarged frontal cirri form curved pseudorow left of distal end of adoral zone. Left frontal cirrus (= cirrus I/1) ahead of distal end of paroral. One slightly enlarged buccal cirrus (II/2) behind middle frontal cirrus (II/3) and somewhat behind anterior end of paroral. Parabuccal cirrus (III/2) about in between right frontal cirrus (III/3) and buccal cirrus, slightly enlarged. First and second midventral pair sometimes slightly displaced from major portion of midventral complex. Midventral complex extends from near distal end of adoral zone into tail region, on average composed of about 33 pairs forming characteristic zigzag pattern; distance between individual pairs distinctly wider in posterior region than in anterior and central portion; complex typically uroleptid, that is, right cirrus of each pair larger (about two times in present case) than left cirrus and differently aligned. Invariably two frontoterminal cirri between distal end of adoral zone and anterior end of midventral complex. Pretransverse ventral cirri likely lacking in interphasic specimens, that is, they obviously become disintegrated during late stages of cell division because in middle and late dividers at least the left pretransverse cirrus is present (Figs 1A, I, K). Three or four inconspicuous transverse cirri arranged in hook-shaped pseudorow in between rearmost portion of marginal rows (Figs 1A, 4H). Right marginal row commenc-

Table 1. Morphometric data on *Uroleptus* cf. *magnificus*[a].

Character	Mean	SD	SE	CV	Min	Max	n
Body, length	311.7	45.5	10.2	14.6	250	400	20
Body, width	112.4	21.5	4.8	19.2	80	150	20
Anterior macronuclear nodule, length	35.1	5.5	1.2	15.7	28	48	20
Anterior macronuclear nodule, width	19.9	3.0	0.7	15.2	16	27	20
Posterior macronuclear nodule, length	34.9	5.9	1.3	17.0	26	48	20
Posterior macronuclear nodule, width	18.9	2.7	0.6	14.4	14	25	20
Macronuclear nodules, number	2.0	0.0	0.0	0.0	2	2	20
Micronucleus, length	8.5	1.1	0.3	13.0	7	11	20
Micronucleus, width	7.0	2.0	0.5	28.6	5	11	16
Micronuclei, number	2.1	0.2	0.1	11.8	2	3	17
Adoral zone of membranelles, length	108.9	14.9	3.3	13.7	88	135	20
Adoral membranelles, number	79.4	4.8	1.1	6.1	70	89	20
Buccal cirri, number	1.0	0.0	0.0	0.0	1	1	20
Frontal cirri, number	3.0	0.0	0.0	0.0	3	3	20
Cirri behind right frontal cirrus, number	1.0	0.0	0.0	0.0	1	1	20
Midventral complex, number of right cirri	33.9	2.6	0.6	7.6	30	40	20
Midventral complex, number of left cirri	32.7	2.2	0.5	6.8	30	38	20
Transverse cirri, number	3.9	0.3	0.1	6.6	3	4	15
Right marginal cirri, number	46.9	3.7	0.8	7.9	39	54	20
Left marginal cirri, number	36.7	3.3	0.7	8.8	32	44	20
Dorsal kineties, number	10.3	0.9	0.2	8.6	8	11	19
Dorsal kinety 1, number of bristles	73.4	6.6	1.5	9.0	63	90	20
Rightmost dorsomarginal kinety, number of bristles	9.0	5.0	1.1	56.0	2	19	21
Caudal cirri, number	3.0	0.0	0.0	0.0	3	3	16

[a] Measurements in µm. Data based on protargol-impregnated and randomly selected specimens. CV – coefficient of variation in %; Max – maximum; Mean – arithmetic mean; Min – minimum; n – number of specimens investigated; SD – standard deviation; SE – standard error of arithmetic mean.

es near frontoterminal cirri, extends – like left row – to end of tail leaving blank a small gap optically occupied by the dorsally inserted caudal cirri; left marginal row begins left of proximal end of adoral zone. Marginal cirri somewhat smaller than right cirri of midventral pairs (Figs 1A, 2A, C).

Dorsal bristles about 5 µm long in protargol preparations, arranged in 8–11 kineties (Figs 1A, B, 2A; Table 1). Kineties 1–3 more or less bipolar, that is, only slightly shortened anteriorly and terminating with each one conspicuous caudal cirrus at rear end of tail. Remaining rows are dorsomarginal kineties and therefore gradually decreasing in length from left to right. Basal body pairs rather narrowly spaced within rows; kinety 1 composed of 73 bristles on average, rightmost kinety of nine bristles (Table 1).

Cell division of *Uroleptus* cf. *magnificus* (Figs 1C–L, 2B–L, 3A–L, 4A–L, 5A–E)

About 100 very well impregnated dividers are available in the protargol slides showing the whole process rather clearly.

Oral apparatus: Ontogenesis commences with the apokinetal formation of small, oblique groups of basal bodies immediately left of the left midventral cirri in the postoral region (Figs 1C, 2B, C). These groups subsequently merge by further proliferation of basal bodies forming a wedge-shaped anarchic field with some short, indistinct streaks extending anteriorly in the area between buccal vertex and midventral complex (Figs 1D, 2D).

The oral primordium becomes larger by further proliferation of basal bodies, and the first membranelles
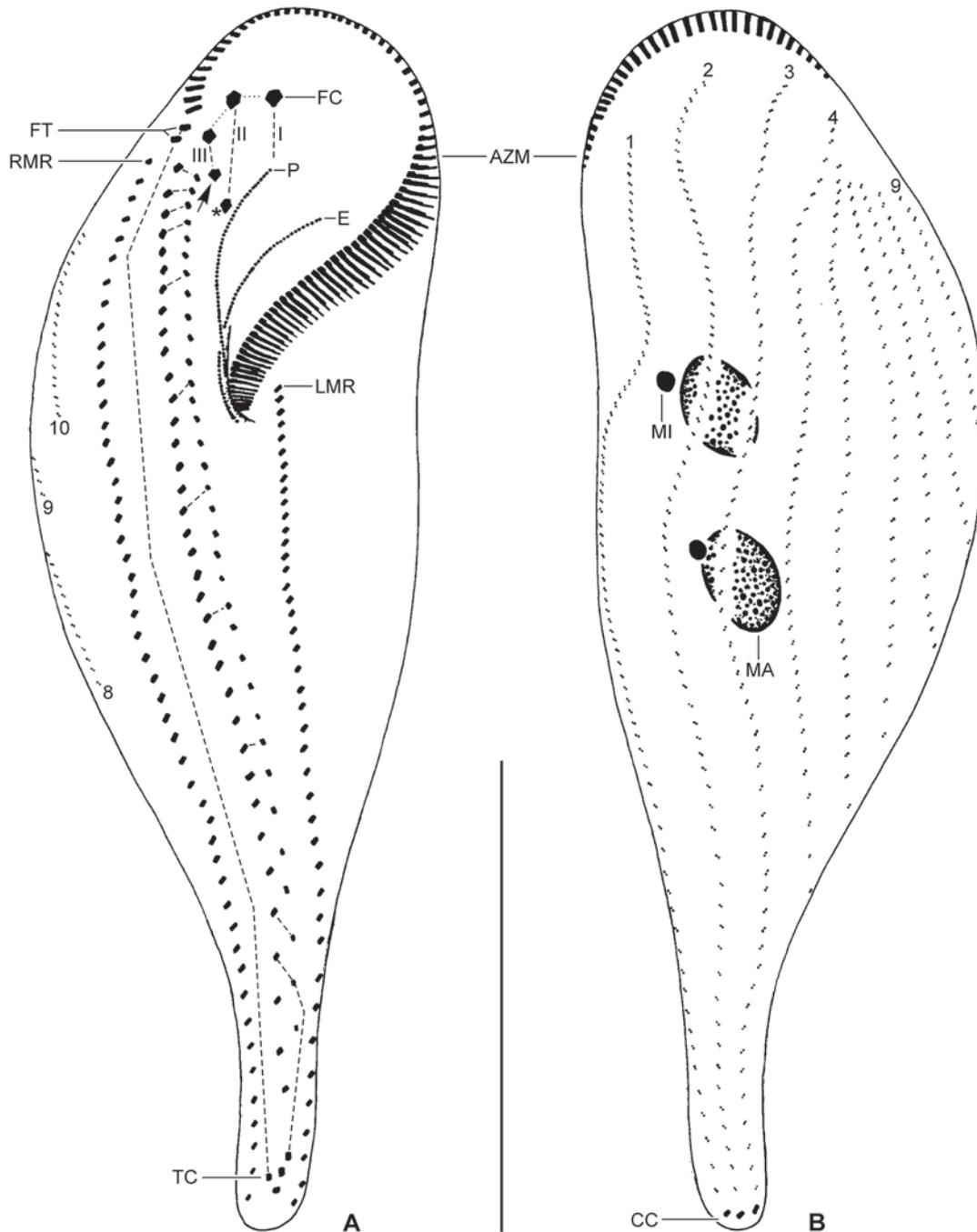
Figs 1A, B. *Uroleptus* cf. *magnificus* after protargol impregnation. Infraciliature of ventral and dorsal side and nuclear apparatus. Arrow marks cirrus behind right frontal cirrus (= cirrus III/2 or parabuccal cirrus), asterisk denotes buccal cirrus. Dotted line connects frontal cirri, broken lines connect cirri originating from same anlage (not shown for all anlagen). AZM – adoral zone of membranelles, CC – caudal cirri at end of dorsal kineties 1–3, E – endoral, FC – frontal cirri, FT – frontoterminal cirri, LMR – anterior end of left marginal row, MA – macronuclear nodule, MI – micronucleus, P – paroral, RMR – anterior end of right marginal row, TC – rightmost transverse cirrus, I–III – frontal-ventral-transverse cirri anlagen I–III, 1–10 – dorsal kineties. Scale bar: 100 µm.
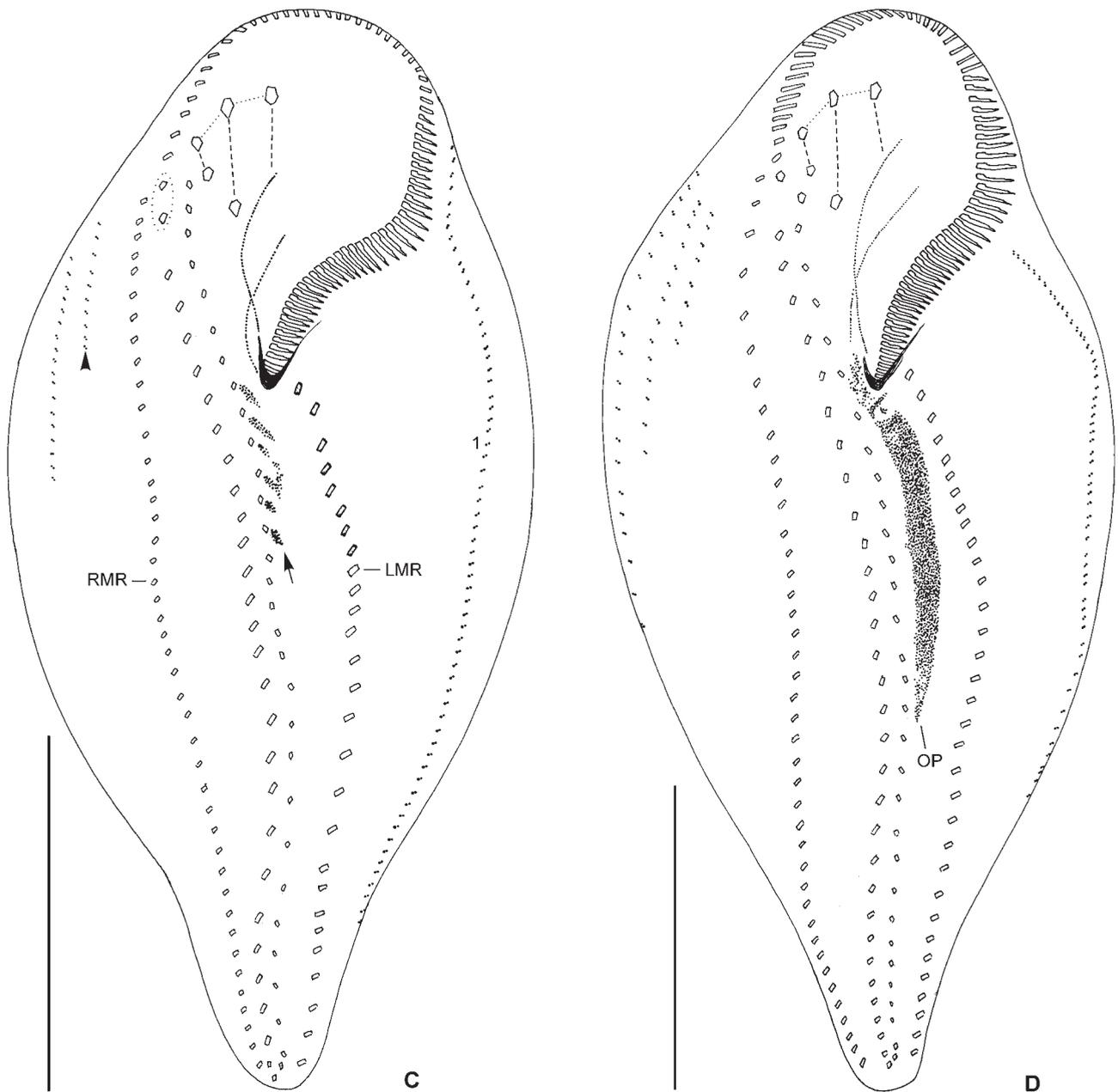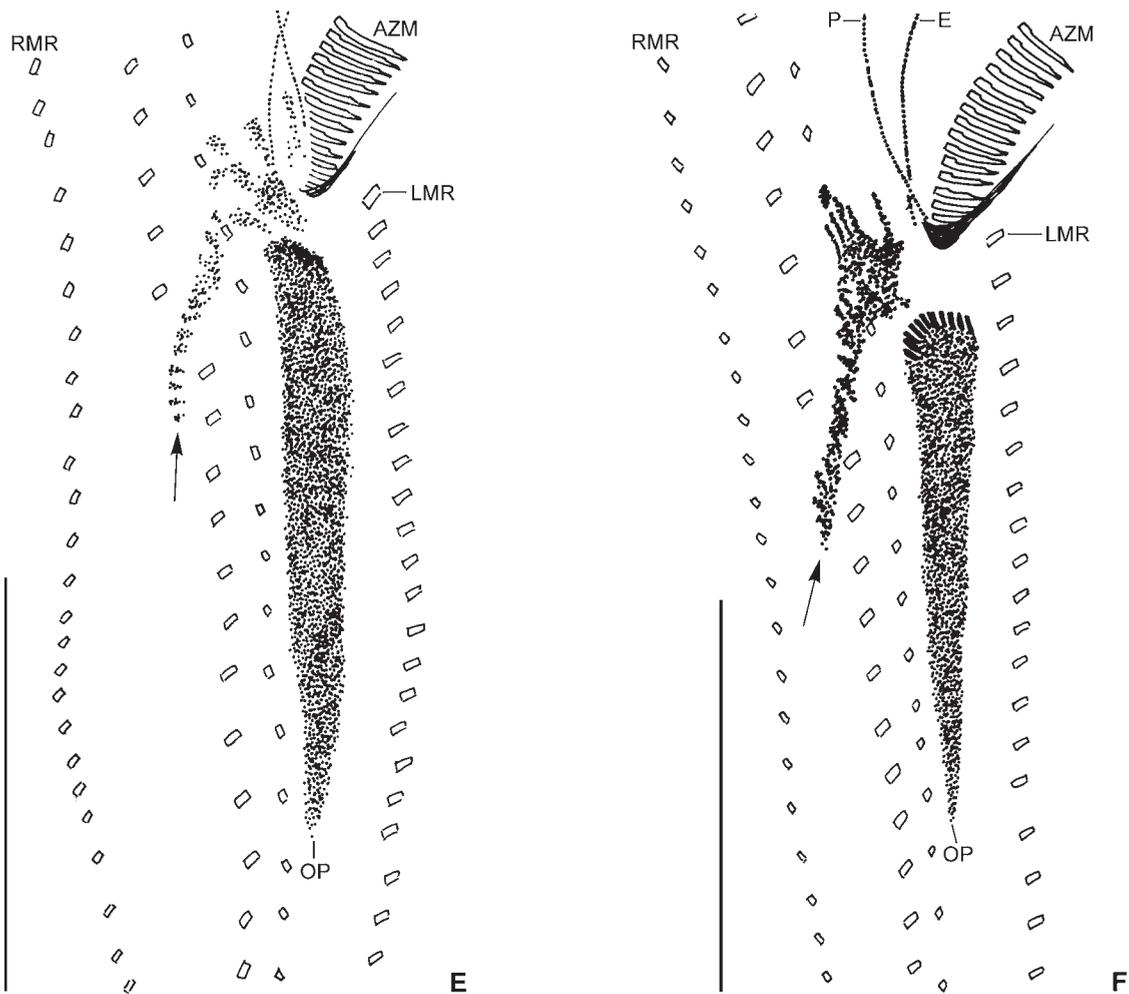
Figs 1C, D. *Uroleptus* cf. *magnificus* after protargol impregnation. Infraciliature of ventral side of very early divider (C) and early divider (D). Arrow marks small basal body patches left of some postoral midventral cirri. Cirri originating from anlagen I–III connected by broken lines; frontal cirri connected and frontoterminal cirri encircled by dotted line. No parental cirri are obviously involved in primordia formation. Arrowhead denotes shortest dorsomarginal kinety. LMR – left marginal row, OP – oral primordium, RMR – right marginal row. Scale bars: 100 μm.

develop at the anterior end (Figs 1E, F, 2G–J). No primordium for a new adoral zone is formed in the proter. To the right of the anterior portion of the oral primordium, some scattered basal body pairs remain (or are newly formed) and become the anlage for the undulating membranes of the opisthe (Fig. 3B). The differen-

tiation of new adoral membranelles proceeds. The parental undulating membranes begin to disintegrate and the buccal cavity flattens (Fig. 3A).

In the next stage, the formation of membranelles is almost complete. The undulating membranes anlage in the opisthe is clearly differentiated and the left frontal

Figs 1E, F. *Uroleptus* cf. *magnificus* after protargol impregnation. Infraciliature of ventral side. **E** – early divider with wedge-shaped oral primordium and an oblique array of basal body patches (arrow) crossing the parental midventral complex in continuation of the proximal portion of the adoral zone; **F** – early to middle divider showing the cuneate oral primordium of the opisthe and the oblique primordium (arrow) for the frontal-ventral-transverse cirri anlagen. Obviously only few, if at all, parental midventral cirri are involved in primordium formation. AZM – parental adoral zone of membranelles, E – endoral, LMR – left marginal row, OP – oral primordium, P – paroral, RMR – right marginal row. Scale bars: 50 µm.

cirrus develops from its anterior end (Figs 3H, L). The parental paroral is disorganized and the middle portion forms the anlage for the first frontal cirrus (Figs 3F, I). Later, the anterior and posterior portions of the parental paroral are reabsorbed (Figs 3I–K). By contrast, the old endoral begins to dedifferentiate into the undulating membranes anlage for the proter (Figs 3K, 4A). Simultaneously, the left frontal cirrus for the proter is clearly recognizable, and the anterior end of the new adoral zone curves rightwards (Figs 1G, 3J–L).

Subsequently, the anterior end of the new adoral zone starts with the final shaping, that is, the distal end bends strongly to the right. The parental paroral is already reabsorbed and the endoral modified into the long undulating membrane anlage of the proter (Figs 1I, K, 4A–E). Finally, the undulating membrane anlage of both the proter and the opisthe split longitudinally and form the new paroral and endoral (Figs 1I, K, 4E, F).

The two most interesting features of this process are: (i) the formation of proter's left frontal cirrus (I/1)
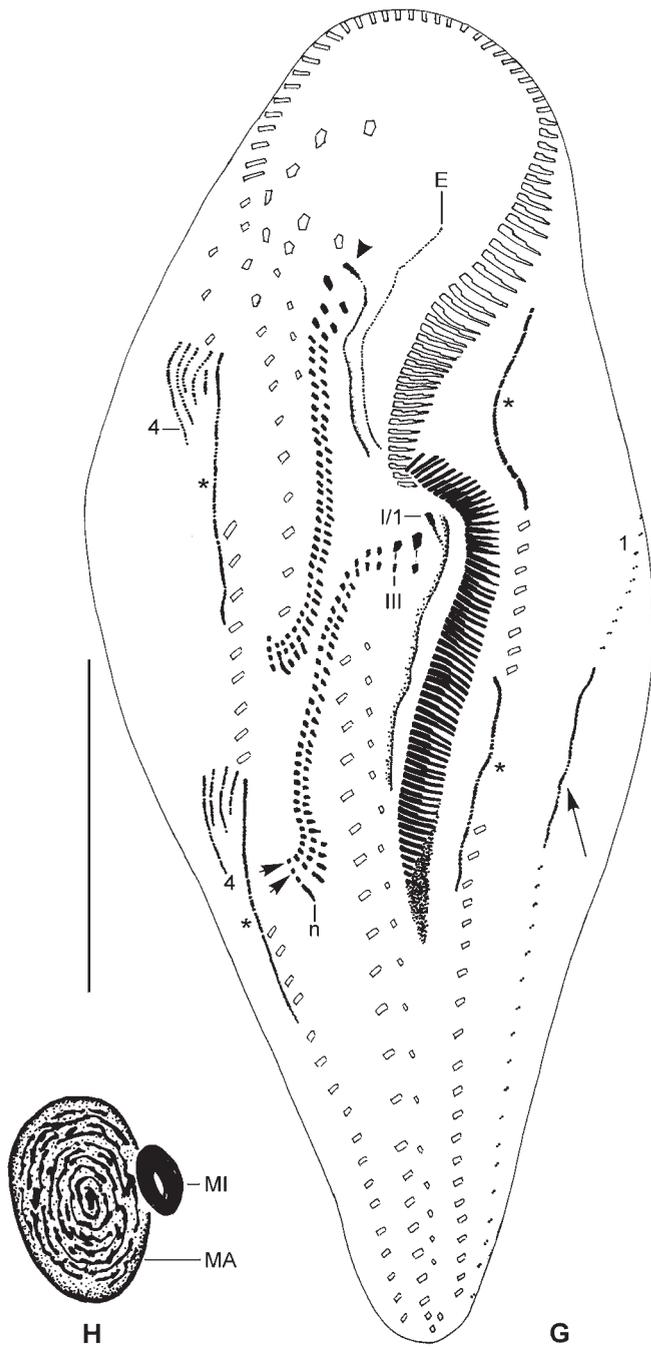
from the central portion of the parental paroral which subsequently is disintegrated, and (ii) the formation of the undulating membrane anlage of the proter from the modified parental endoral.

Frontal-ventral-transverse cirri: When the oral primordium is rather large and wedge-shaped, several small groups of basal bodies form an oblique, irregular field in extension of the proximal portion of the parental adoral zone crossing the midventral complex (Figs 1E, F, 2E–H). Whether these basal body patches originate *de novo* or are formed from the anterior portion of the oral primordium is not known. The space required for the crossing of the midventral complex by the oblique anlagen field is likely not formed by resorption of midventral cirri, but by increasing the distance between the abutting midventral cirri.

Subsequently, the oblique field becomes larger and roughly comb-shaped, that is, the numerous streaks elongate by increasing the number of basal bodies and organize into the individual, obliquely to longitudinally arranged cirri anlagen (Figs 1F, 2I, J). Somewhat later, these individual anlagen, which are basically primary primordia, divide to form the secondary anlagen of the proter (anterior portion) and opisthe (posterior portion) (Figs 2K, 3B).

Simultaneously, the parental buccal cirrus is dedifferentiated into anlage II of the proter and later forms the middle frontal cirrus and the buccal cirrus. Left of anlage II, the disorganizing parental paroral gives rise to the new left frontal cirrus of the proter before it is disintegrated (Fig. 3A; see above). In the opisthe, the left frontal cirrus develops, as is usual, from the anterior end of the undulating membrane anlage (Figs 3H, L).

The frontal-ventral-transverse cirri anlagen of the proter and the opisthe separate further and begin to differentiate (Figs 3A, B, E–I). Each anlage – except for the undulating membrane anlage (= anlage I) which forms only one cirrus (I/1) and the rightmost (= rearmost) 3–5 anlagen which form three or four cirri – develops into two cirri, a so-called midventral pair; these pairs form
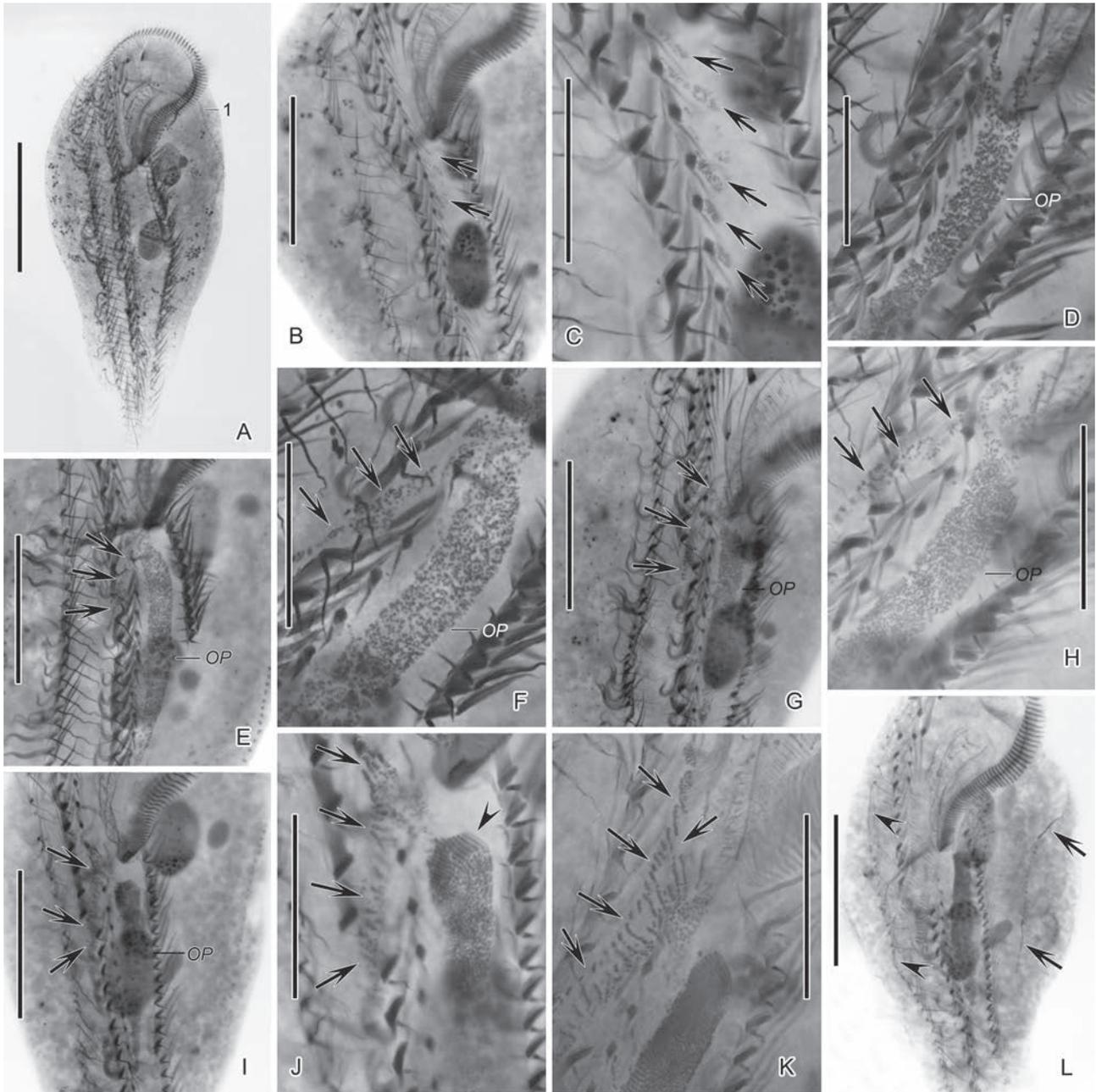
Figs 1G, H. *Uroleptus* cf. *magnificus* after protargol impregnation. Infraciliature of ventral side (G) and nuclear apparatus (H) of a late divider. Short arrows mark frontoterminal cirri of opisthe, long arrow denotes dorsal kinety 1 anlage of opisthe; marginal row anlagen (asterisks) originate with parental marginal rows. The two macronuclear nodules have fused to a single, ellipsoidal mass. Arrowhead denotes new left frontal cirrus of proter originating from middle portion of disintegrating parental paroral. The parental endoral is modified to the undulating membrane anlage of the proter. E – parental endoral, MA – fused macronucleus, MI – micronucleus, n – rightmost frontal-ventral-transverse cirri anlage (anlage XXXV in present case, but actually homologous to anlage VI of 18-cirri hypotrichs), I/1 – left frontal cirrus, III – frontal-ventral transverse cirri anlage III (forms right frontal cirrus and cirrus III/2), 1 – parental dorsal kinety 1 (= leftmost kinety), 4 – new dorsal kinety 4 (= leftmost and longest dorsomarginal kinety). Scale bar: 100 μm.
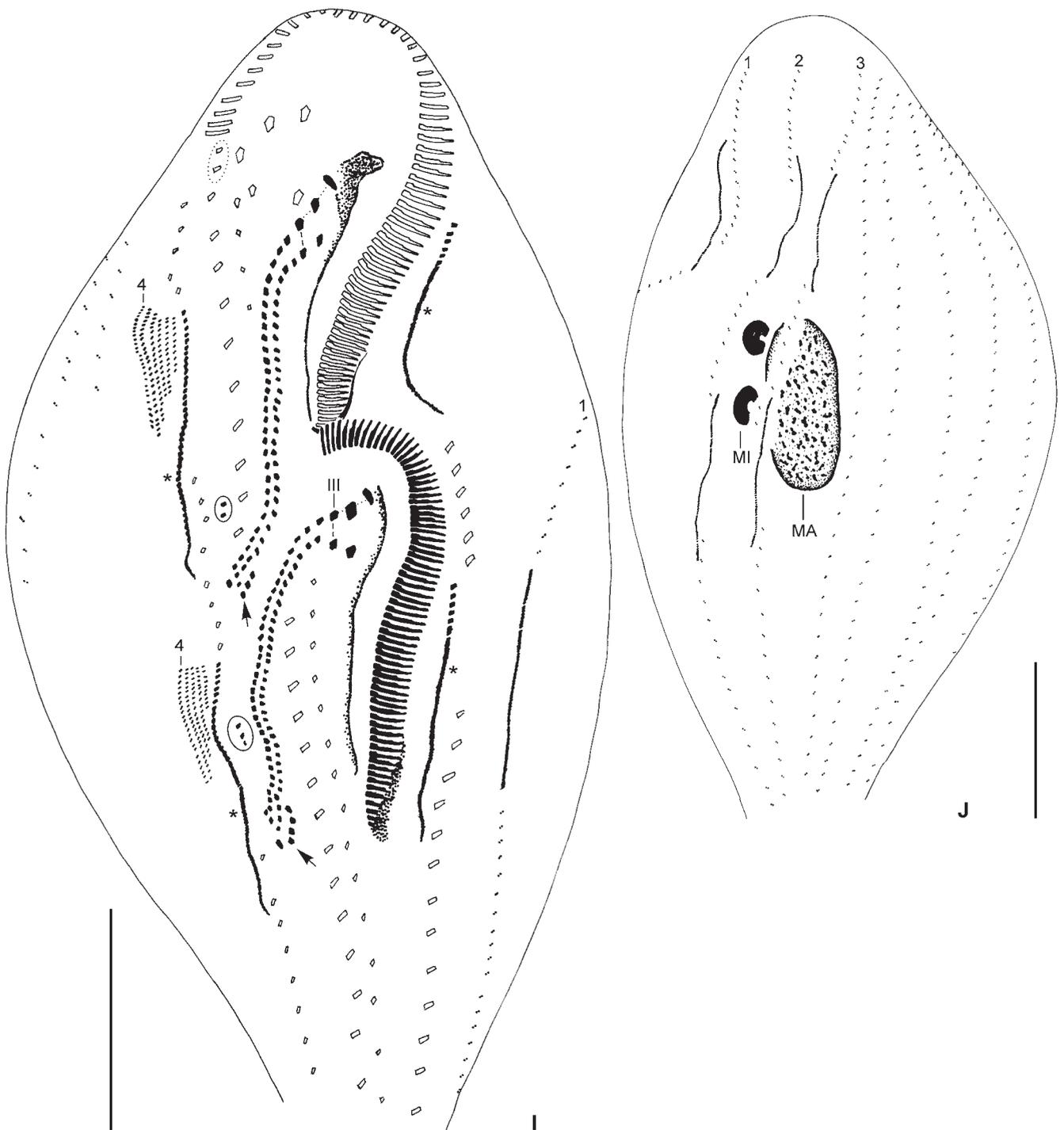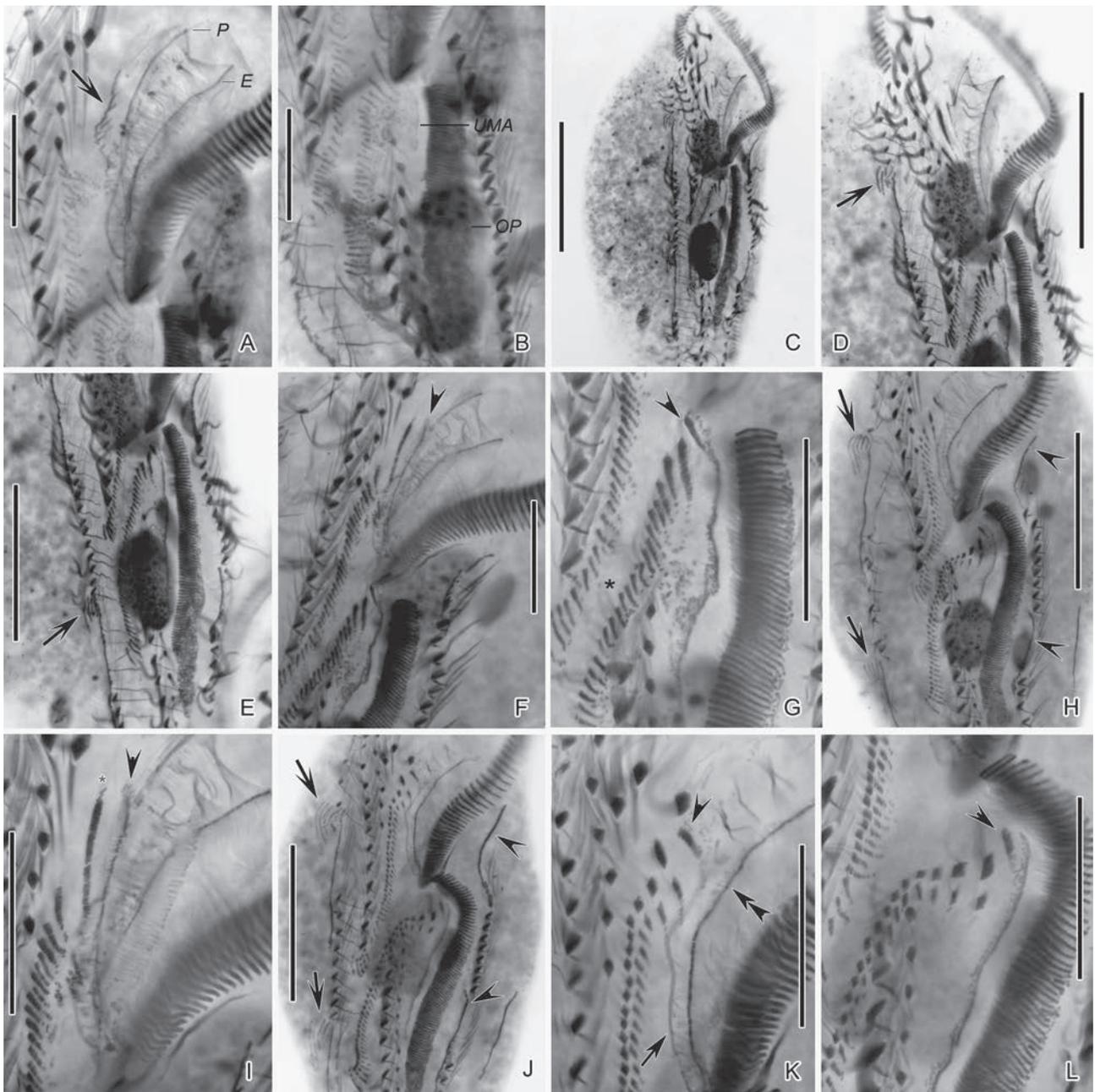
Figs 1I, J. *Uroleptus* cf. *magnificus* after protargol impregnation. Infraciliature of ventral and dorsal side and nuclear apparatus of very late divider. New frontoterminal cirri encircled by solid line in both filial products, parental frontoterminal cirri encircled by dotted line. New frontal cirri connected by dotted line, right frontal cirrus and cirrus III/2 by broken line. Marginal rows anlagen marked with asterisk. Arrows denote penultimate transverse cirrus both in proter and opisthe. Six dorsomarginal kineties are formed in the proter, five in the opisthe. The parental adoral zone is retained for the proter, the parental endoral has been modified to the undulating membrane anlage of the proter. MA –fused macronucleus, MI – micronucleus, III – frontal-ventral cirri anlage III, 1–3 – parental dorsal kineties 1–3, 4 – new dorsal kinety 4 (= leftmost dorsomarginal kinety). Scale bars: 100 µm.
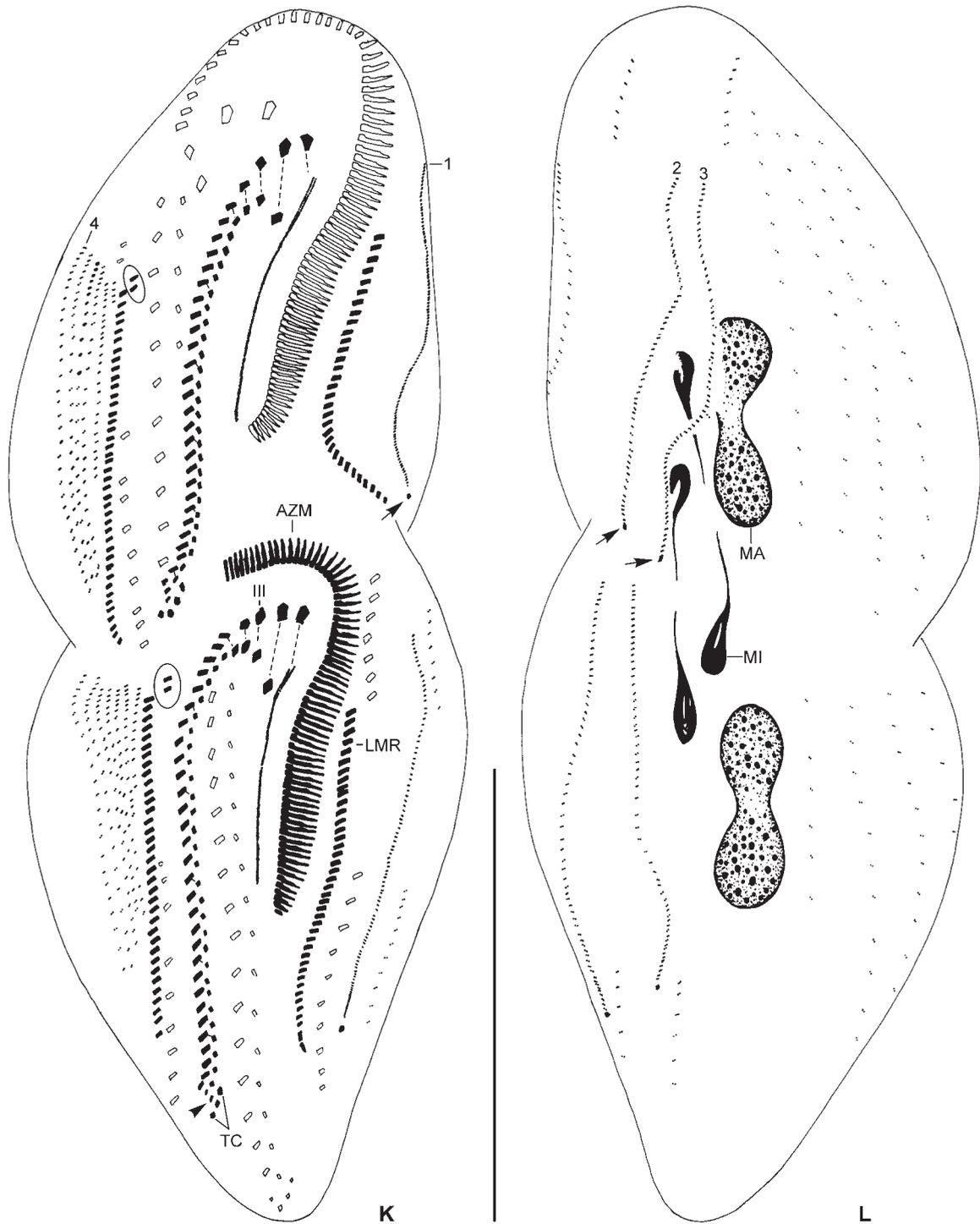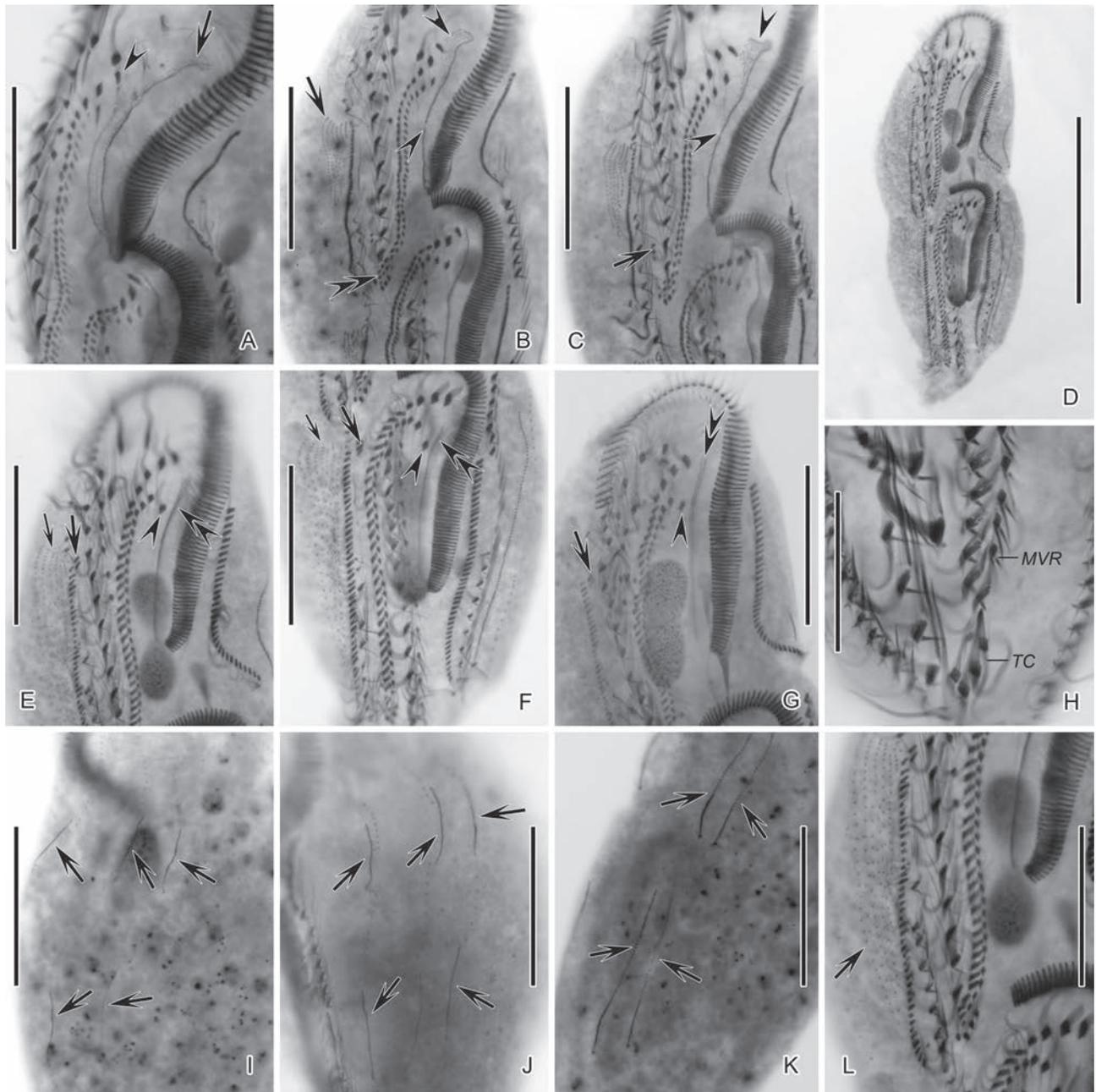
Figs 1K, L. *Uroleptus* cf. *magnificus* after protargol impregnation. Infraciliature of ventral and dorsal side and nuclear apparatus of very late divider already showing the division furrow. Parental infraciliature white, new black. Arrowhead marks the left pretransverse ventral cirrus of the opisthe which will be reabsorbed later; the right pretransverse ventral cirrus is already reabsorbed. Arrows denote new caudal cirri of proter at end of dorsal kineties 1–3. Broken lines connect cirri originating from same anlage (only shown for anlagen I–V and for each further fifth anlage). New frontoterminal cirri encircled. AZM – adoral zone of opisthe, LMR – left marginal row of opisthe, MA – dividing macronuclear nodule of proter, MI – dividing micronucleus, TC – transverse cirri (three in number) of opisthe, 1–3 – new dorsal kineties 1–3 of proter, 4 – new dorsal kinety 4 of proter (= leftmost dorsomarginal kinety). Scale bar: 200 μm.
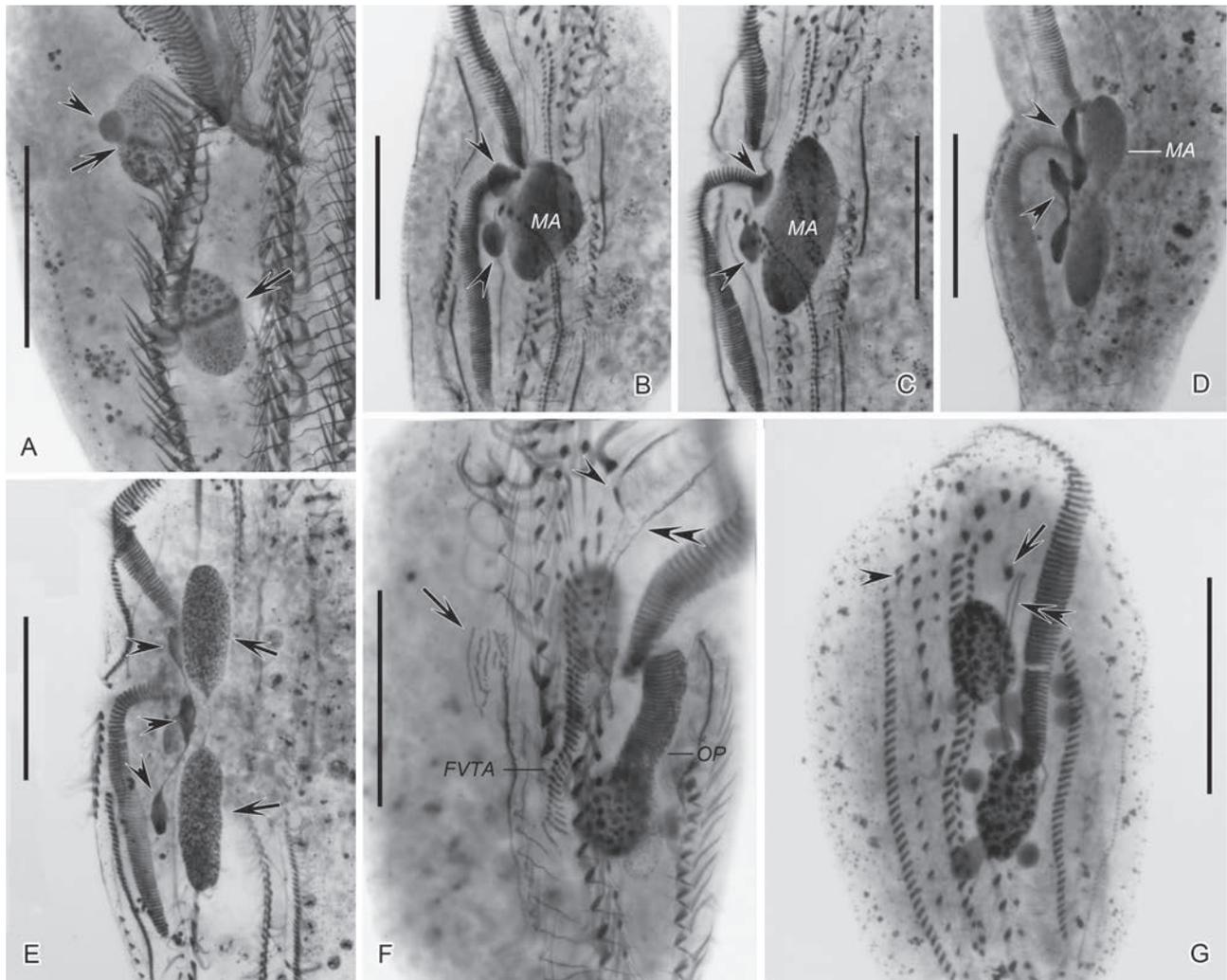
Figs 2A–L. *Uroleptus* cf. *magnificus* after protargol impregnation. **A** – infraciliature of ventral side and nuclear apparatus of interphasic specimen; **B**, **C** – very early divider. The oral primordium originates from small, oblique basal body patches (arrows) occurring in the postoral region left of the midventral complex; **D** – oral primordium of an early divider. The midventral cirri obviously are not incorporated in primordia formation; **E**, **F** – ventral view of an early divider. The primordium for the frontal-ventral-transverse cirri anlagen is an oblique field (arrows) extending from anterior right corner of oral primordium obliquely backwards across the midventral complex. Parental midventral cirri do not contribute to primordia formation; **G**, **H** – ventral view of early to middle divider with frontal-ventral-transverse cirri anlagen field (arrows) crossing the parental midventral complex. The parental buccal cirrus (arrowhead) is obviously not involved in the formation of this anlagen field; **I**, **J** – ventral view of middle divider showing that the oblique field crossing the midventral complex differentiates into many oblique frontal-ventral-transverse cirri streaks (arrows); the anterior portion of the oral primordium is modified to adoral membranelles (arrowhead); **K** – middle divider showing that the primary primordia for the frontal-ventral-transverse cirri begin to divide in an anterior portion for the proter (arrows) and a posterior portion for the opisthe; **L** – middle divider with anlagen for right marginal rows (arrowheads) and for dorsal kinety 1 (arrows). The left cirri of the midventral complex obviously have been involved in the formation of the anterior frontal-ventral cirri anlagen of the proter (details see Figs 3A, B). OP – oral primordium, 1 – leftmost dorsal kinety. Scale bars: 100 μm (A, B, E, G, I, L), 50 μm (C, D, F, H, J, K).

Figs 3A–L. *Uroleptus* cf. *magnificus* after protargol impregnation. Middle stages of morphogenesis. **A**, **B** – details of specimen shown in Fig. 2L. The parental undulating membranes begin to reorganize, the buccal cirrus is modified to anlage II (arrow) of the proter. Some scattered basal bodies, which will become the anlage for opisthe's undulating membranes, remain right of anterior portion of oral primordium (B; UMA); **C–E** – ventral view of same specimen showing formation of dorsomarginal kineties anlagen from/at right anterior end of right marginal row anlagen (arrows). The frontal-ventral-transverse cirri anlagen of proter and opisthe are clearly separated; **F**, **G**, **I** – ventral views of the same divider. The parental paroral is disorganized to the anlage for the left frontal cirrus of the proter (arrowhead in F, I). Asterisk in (I) denotes anlage II which originated from the parental buccal cirrus. In the opisthe the left frontal cirrus (= cirrus I/1) separates from anlage I (arrowhead in G). Asterisk in (G) denotes gap between frontal-ventral-transverse cirri anlagen of proter and opisthe; **H** – ventral view showing, inter alia, dorsomarginal kineties anlagen (arrows) and left marginal row anlagen (arrowheads); **J–L** – ventral views of the same specimen showing dorsomarginal kineties anlagen (arrows in J), left marginal row anlagen (arrowheads in J), and the separation of the left frontal cirrus from the parental paroral (arrowheads in K [proter] and L [opisthe]). Note that the rear portion of the old paroral is reabsorbed just now (arrow in K) and the parental endoral becomes the anlage for the undulating membranes of the proter (double-arrowheads in K). E – parental endoral, OP – oral primordium, P – parental paroral, UMA – undulating membranes anlage of opisthe. Scale bars: 130 μm (A, B, D–G, J), 150 μm (C), 65 μm (I, H, K, L).

Figs 4A–L. *Uroleptus* cf. *magnificus* after protargol impregnation. **A** – ventral view of middle to late divider. The left frontal cirrus (arrowhead) is formed from the dedifferentiated old paroral and the parental endoral becomes the undulating membrane anlage of the proter (arrow); **B** – ventral view of late divider showing modification of parental endoral to undulating membrane anlage in proter (arrowheads). Arrow marks dorsomarginal kineties anlagen of proter. Note that only the last and the penultimate frontal-ventral-transverse cirri anlage form four cirri (double arrowhead); however, the pretransverse ventral cirri are obviously reabsorbed in later stages; **C** – ventral view of proter of late divider showing undulating membrane anlage for proter (arrowheads) and anteriorly migrating frontoterminal cirri (arrow); **D–F** – ventral views of very late divider. The undulating membrane anlage begins to split into endoral and paroral in both filial product (double-arrowheads). Arrowheads mark new buccal cirri originating from anlage II; the frontoterminal cirri (large arrows) migrated far anteriorly and the dorsomarginal kineties (6 in proter, 7 in opisthe; small arrows) are still right of the new right marginal row; **G, H** – ventral views of late divider. The undulating membrane anlage (double-arrowhead) begins to split longitudinally into paroral and endoral; arrowhead marks buccal cirrus and arrow denotes frontoterminal cirri (G). (H) is the rear body portion of the opisthe showing the newly formed transverse and midventral cirri and parental midventral cirri; **I–K** – morphogenesis of dorsal kineties 1–3 (arrows); details, see text; **L** – late divider showing, inter alia, large field of new dorsomarginal kineties (arrow) of proter. This proter gets four new transverse cirri; note the three cirri (rearmost midventral pair and left pretransverse ventral cirrus) ahead of the penultimate transverse cirrus. MVR – newly formed midventral cirri, TC – transverse cirri. Scale bars: 90 μm (A, L), 130 μm (B, C, E–G, I–K), 250 μm (D), 40 μm (H).

Figs 5A–G. *Uroleptus* cf. *magnificus* after protargol impregnation (A–E, cell division; F, G, physiological reorganization). **A–E** – dorsal views showing division of nuclear apparatus. Arrows in (A) mark replication bands; arrowheads in (B–E) denote dividing micronuclei; arrows in (E) mark new (undivided) macronucleus of proter (above) and opisthe (below); **F** – ventral view of middle reorganizer showing, inter alia, the undulating membrane anlage (double-arrowheads), new left frontal cirrus (arrowhead), and dorsomarginal kinety anlagen (arrow); **G** – ventral view of a late reorganizer. Double-arrowhead marks longitudinally splitting undulating membrane anlage, arrow denotes new buccal cirrus, and arrowhead marks new frontoterminal cirri. FVTA – frontal-ventral-transverse cirri anlagen, MA – macronucleus, OP – oral primordium. Scale bars: 90 µm (A), 130 µm (B–G).

the characteristic zigzag pattern of the uroleptid midventral complex (Figs 1G, I, K, 3J–L, 4A–F). The right frontal cirrus and the parabuccal cirrus are formed by anlage III, whereas anlage IV produces the anteriormost midventral pair. The rightmost/rearmost three, four, or five (Fig. 1I, opisthe) anlagen form each a transverse cirrus and a cirral pair. The rightmost and the penultimate anlage form, in addition, each one pretransverse ventral cirrus; however, very likely none of them is retained in postdividers. The anterior two cirri (= frontoterminal

cirri; strictly speaking they form the rightmost midventral pair) of the rightmost anlage migrate anteriorly near to the distal end of the adoral zone. By contrast, the cirral pair of the penultimate anlage forms the rear end of the midventral complex (Figs 1K, 4L).

Some scattered basal body pairs remain at the left side of the streaks and will be gradually reabsorbed (Figs 3K, L, 4A–C). Finally, the divider begins to elongate and the new ciliary structures move further apart as they migrate towards their final positions. The fronto-

terminal cirri reach their final position only in very late dividers and in post-dividers, where they arrange close to the anterior end of the midventral complex and right marginal row so that they are difficult to recognize as frontoterminal cirri in non-dividers (Fig. 1A).

The parental cirri and dorsal bristles become disintegrated in early to late post-dividers (Fig. 4L), that is, no parental structures remain in morphostatic cells, except for the adoral zone of membranelles.

Marginal cirral rows: The new marginal rows originate as is usual, that is, in middle dividers one anlage each develops for the proter and the opisthe within each parental row (Fig. 2L). Anlagen formation commences earlier in the right than in the left marginal row (Figs 3G, J, 4B, C), but simultaneously in proter and opisthe. In the left parental row, the frontmost cirri and those in mid-body develop to an anlage each (Figs 3C–E). The parental marginal cirri not used for anlagen formation are reabsorbed later. For dorsomarginal kinety formation, see next paragraph.

Dorsal ciliature: Anlagen development commences in early dividers (Figs 3D, 4I). The ciliature develops according to type 2 of Foissner and Adam (1983; = *Urosomoida*-type according to Berger and Foissner 1997 and Berger 1999), that is, new kineties 1–3 are produced at two levels within parental rows 1–3 (Figs 1G, I–L, 2L, 4I–L). The remaining 5–8 rows are dorsomarginal kineties which originate, as is usual, close to/from the right anterior end of the right marginal row anlagen (Figs 1G, 3D, J, 4E). The dorsomarginal rows decrease in length towards the right marginal row, and migrate onto the dorsal side in late dividers to form the dorsal kineties 4 to 9–11. One caudal cirrus is formed at the posterior end of kineties 1, 2, and 3 (Figs 1L, 4K).

Nuclear apparatus: The division of the nuclear apparatus proceeds as described for the ground pattern of the Hypotricha (Berger 2008). Briefly, the replication band moves, as is usual, from the distal to the proximal end in each nodule. Later, the two macronuclear nodules fuse to a single mass which subsequently makes successive amitotic divisions to produce the species-specific number of nodules in each filial product (Figs 1H, J, L, 4D, 5A–E). The micronuclei divide mitotically (Figs 1L, 5C–E).

Physiological regeneration of *Uroleptus* cf. *magnificus* (Figs 5F, G)

Only few stages of this part of the life cycle have been found. An oral primordium is formed in the area behind the old adoral zone. About at the same level, the anlagen for the frontal-ventral-transverse cirri and the marginal rows are formed. The dorsomarginal kineties originate, as is usual, right of the anterior end of the right marginal row anlage. The oral primordium forms about 30 membranelles which replace the proximal portion of the old adoral zone. The undulating membranes, the cirri, and the dorsal ciliature originate and develop basically in the same way as during cell division.

Occurrence and ecology

Uroleptus magnificus is probably confined to limnetic, stagnant waters. Kahl (1932) did not mention a type locality; probably he found it somewhere in northern Germany, perhaps in the Hamburg area where Kahl lived and worked. According to Kahl (1932), *U. magnificus* is common, but not regularly among macrophytes (*Utricularia*, *Hottonia*) above sapropelic sediment. By contrast, the remaining faunistic data indicate that *U. magnificus* is a very rare holarctic species because only two further records – both without morphological data – are available: carp pond enriched with wastes from beet sugar factory, Gołysz, Poland (Grabacka 1977); rare in limnetic habitats in southeastern Louisiana, USA (Bamforth 1963). We found it in a pond in Harbin (China), which, however, does not exist anymore (see Materials and Methods). *Uroleptus magnificus* feeds on algae, but can also be cultivated by adding small ciliates as food (Kahl 1932); our population mainly fed on *Chilomonas paramaecium*.

DISCUSSION

Brief remarks on *Uroleptus* Ehrenberg, 1831, *Paruroleptus* Wenzel, 1953, and *Rigidothrix* Foissner and Stoeck, 2006

Systematics of *Uroleptus*, especially of limnetic forms, is a difficult task (e.g. Kahl 1932, Foissner *et al.* 1991, Eigner 2001). One problem is that *Uroleptus* was established by Ehrenberg (1831) with four species (basionyms *U. hospes* Ehrenberg, 1831; *Trichoda musculus* Müller, 1773; *T. piscis* Müller, 1773; *U. lamella* Ehrenberg, 1831), but none was fixed as type. Unfortunately, this problem was not resolved in early revisions, that is, for example neither by Fromentel (1875), who fixed the type for many genera, nor by Kahl (1932) who provided the last detailed revision. Just Borror (1972) subsequently designated *Trichoda musculus* Müller, 1773 as type species. Although this fixation needs some

discussion – *Trichoda musculus* sensu Müller (1773, 1786) is perhaps a rotifer (e.g. Stein 1859; Foissner *et al.* 1990, 1991) – it has to be accepted because no later designation is valid (ICZN 1999, Article 69.1). In addition, *Trichoda musculus* is not mentioned by rotifer specialists (e.g. Koste 1978, Segers 2007), indicating that they accepted Ehrenberg's decision to classify it as hypotrichous ciliate. Thus, the fixation of "*Paruroleptus (Amphisia) piscis*" sensu Kahl (1932) as type by "Berger 1992" in Foissner *et al.* (1991) is of no consequence. In addition, the work (Berger 1992), to which Foissner *et al.* (1991) refer, was never published.

Other serious problems in *Uroleptus* are: (i) many original descriptions and redescriptions are based on live observations only; (ii) the cirral pattern of the tailed body portion – especially the presence/absence of transverse and caudal cirri – is difficult to recognize, even in protargol preparations (e.g. Foissner 1984, Foissner *et al.* 1990); (iii) the dorsal kinety pattern, including the number of dorsomarginal kineties, is not known for most species; (iv) the last more or less detailed revision is almost 80 years old (Kahl 1932); (v) as a result of points (i) and (ii), the status of *Paruroleptus* Wenzel, 1953 (originally established as subgenus of *Holosticha*), with *Holosticha caudata* Stokes, 1886a as type species, is not yet certain (e.g. Kahl 1932 – for details on his subgenus *Paruroleptus* see next paragraph; Borror 1972; Foissner *et al.* 1990, 1991; Eigner 2001); (vi) since most species have been described in the pre-protargol era, holotypes and syntypes are lacking in most cases.

Kahl (1932: 571, 586) established *Paruroleptus* for hypotrichs with a distinct tail. Because transverse cirri are present in the species assigned, he classified *Paruroleptus* as subgenus of *Holosticha* ("with transverse cirri") and not of *Uroleptus* ("without transverse cirri"). Since he fixed no type species, *Holosticha (Paruroleptus)* Kahl, 1932 is invalid (ICZN 1999, Articles 13.3, 67.4.1). Wenzel (1953) re-established it – again as subgenus of *Holosticha* – and fixed *Holosticha caudata* Stokes, 1886a as type, a species with inconspicuous transverse cirri (see below). Borror (1972) synonymized *Paruroleptus* with *Uroleptus* because he supposed that the transverse cirri in *Uroleptus* have been overlooked sometimes. This synonymy was accepted, for example, by Foissner *et al.* (1991) and Eigner (2001), but not supported by Corliss (1979), Foissner *et al.* (1990), Jankowski (2007), and Lynn (2008). Unfortunately, the problem is rather difficult to solve because as long as we do not have a reliable description of a uroleptid without transverse cirri we cannot make a final

decision. The situation in other taxa shows that obviously closely related genera with (e.g. *Pseudokeronopsis*, *Gonostomum*) and without (*Uroleptopsis*, *Paragonostomum*) transverse cirri exist (e.g. Foissner *et al.* 2002; Berger 2004, 2006a). The descriptions available so far indicate that two groups can be distinguished within *Uroleptus/Paruroleptus*, namely, species with few, inconspicuous transverse cirri (e.g. *Uroleptus caudatus*; *U. lepisma*; present population) and species with many, conspicuous transverse cirri (e.g. *Uroleptus piscis* sensu Kowalewski 1882; *U. musculus* sensu Kahl 1932; *U. gallina*).

Rigidothrix goiseri, the sole species of this recently established genus, is one of the most interesting hypotrichs because it has a rather curious combination of features (see introduction; Foissner and Stoeck 2006). Basically it looks like a rigid *Uroleptus* with a *Stylonychia/Laurentiella*-like oral apparatus and obviously it has a SSU rRNA gene sequence which is very similar to that of *Oxytricha granulifera* (type of *Oxytricha* and the oxytrichids), a flexible 18-cirri hypotrich.

The listed problems clearly demonstrate that the situation in the uroleptids is rather tricky. A reliable solution can only be achieved via a thorough revision and neotypification of some key species.

Identification of our population as *Uroleptus* cf. *magnificus*

The aforementioned problems with *Uroleptus*, in combination with the lack of live observations on our population, hamper the final identification of the Chinese material. The cirral pattern of our population is very similar to that of the uroleptids *Holosticha (Paruroleptus) magnificus* Kahl, 1932, *Uroleptus caudatus* (Stokes, 1886a) Borror, 1972, and *Uroleptus piscis* (Müller, 1773) Ehrenberg, 1831 *sensu* Stein (1859), and the rigidothrichid *Rigidothrix goiseri* Foissner and Stoeck, 2006. Since the situation is very complicated, the comparison is rather detailed.

***Uroleptus magnificus* (Kahl, 1932) ?Olmo, 2000** [basionym *Holosticha (Paruroleptus) magnificus* Kahl, 1932]. According to the original description, this species is very large (400–500 μm long) and has a length : width ratio *in vivo* of 3.5–4.0 : 1, that is, body rather wide; no information provided about contractility and consistence (flexible? rigid?) of body; left margin straight, right convex with concave turn to tail; two macronuclear nodules, each with a micronucleus attached; contractile vacuole behind buccal vertex, with canals; tail varyingly long; three frontal cirri; one, rarely two

or three cirri along buccal lip; all parts of oral apparatus well developed, the straight undulating membranes and the broadly rounded anterior body end are reminiscent of *Rigidothrix*; the five transverse cirri protrude by about one third of their length beyond rear body margin; three caudal cirri; dorsal bristles short; common, but not regularly among macrophytes (*Utricularia*, *Hottonia*) and above saprobelic sediment (Kahl 1932: 587). The description matches very well our Chinese population, especially in body size (400–500 µm long *in vivo* vs. 250–400 µm in protargol preparations), body shape (the large cell width in our protargol slides indicates that the specimens are also rather wide *in vivo*), cirral pattern (including transverse cirri), nuclear apparatus, and habitat (stagnant freshwater habitats). There is basically only one noteworthy difference, namely, in the undulating membranes which are straight (stylonychid) in the original live-illustration provided by Kahl (1932), but distinctly curved and optically intersecting in the protargol-impregnated Chinese material. However, the same difference occurs within *Rigidothrix goiseri* (cp. Figs 10, 11, 14 in Foissner and Stoeck 2006), indicating that the undulating membrane pattern shown in Figs 1A, 2A is a preparation artifact. The different number of midventral pairs (about 19 in original illustration of *U. magnificus* vs. about 33 in Chinese material) must not be over-interpreted, because we are rather sure that Kahl did not count them exactly. Since Kahl (1932) could not study the dorsal kinety pattern, this part of the infraciliature drops out for the identification.

Martin *et al.* (1981) studied the cell division of "*Holosticha (Paruroleptus) musculus* Kahl, 1932." This species has, according to the original description (Kahl 1932: 588), 15–20 rather conspicuous transverse cirri extending along the left margin of the tail, a feature confirmed by Foissner (1984; for review see Foissner *et al.* 1991: 248). By contrast, the population studied by Martin *et al.* (1981) has only four very inconspicuous transverse cirri proving a misidentification by the Spanish workers. The low number and inconspicuousness of the transverse cirri are reminiscent of *U. caudatus* (Foissner *et al.* 1991), but also on *U. magnificus*, with which the population studied by Martin *et al.* (1981) was synonymized by Olmo (2000). Unfortunately, Martin *et al.* (1981) did not provide morphometric data (e.g. size *in vivo* or after protargol impregnation [scale bars lacking]) making a re-identification rather difficult. An identity with the Chinese population is very unlikely because of the different number of dorsomarginal kineties (4 vs. 5–8 in Chinese population) and adoral mem-

branelles (around 40 [from Fig. 1 in Martin *et al.* 1981] vs. about 80). Especially, the last feature indicates that the specimens of the Spanish population are not as long as *U. magnificus* (400–500 µm). Thus, we suppose that the synonymy proposed by Olmo (2000) is incorrect.

***Uroleptus caudatus* (Stokes, 1886a) Borror, 1972** (basionym *Holosticha caudata* Stokes, 1886a). This slender, up to 508 µm long species agrees more or less perfectly with *U. piscis sensu* Stein (1859; see below), except that Stokes (1886a) described and illustrated five inconspicuous transverse cirri, a feature almost perfectly matching our observations. Stokes (1886a) neither mentioned nor illustrated the nuclear apparatus and, in addition, he did not compare his new species with previously described taxa, for example *U. piscis sensu* Stein (1859). Kahl (1932: 587) accepted *H. caudata* and transferred it, like Kowalewski's population of *U. piscis* (see chapter *U. piscis*), to *Holosticha (Paruroleptus)* because transverse cirri are present. Kahl (1932, his Fig. 110₇; erroneously designated as "*Paruroleptus piscis*") confirmed Stokes' observations and illustrated two macronuclear nodules. Thus, our Chinese population matches more or less perfectly *U. caudatus* as described by Stokes (1886) and Kahl (1932), apart from the body outline in life, a feature not known in detail for our population.

Uroleptus caudatus has been redescribed more or less detailed several times after protargol impregnation (Grolière 1975, Foissner 1980, Hemberger 1982, Eigner 2001). In the present paragraph these data will be briefly compared with the old descriptions mentioned above and our population. The population studied by Groliére (1975) is 120–350 µm long (*in vivo*?) and has 35–40 adoral membranelles. The upper size matches the previous populations and our material rather well, whereas the number of membranelles is about twice as high in the Chinese population (Table 1). By contrast, the number of marginal cirri is about the same. Unfortunately, Grolière (1975) did not count the dorsal kineties and therefore it is impossible to come to a final decision, but the rather different number of adoral membranelles strongly indicates that the Chinese population is not identical with Grolière's material. *Uroleptus caudatus sensu* Foissner (1980) is 240–350 µm long *in vivo*, which roughly matches the older descriptions and the Chinese population. Foissner (1980) counted 30–40 adoral membranelles (vs. 70–89 in Chinese population), three transverse cirri (vs. usually four in Chinese population), usually four, rarely three caudal cirri (vs. invariably three), and four bipolar and one shortened

dorsal kineties (vs. three bipolar and 5–8 shortened). Especially the significant differences in the number of adoral membranelles and dorsal kineties indicate (actually prove) that these populations are not conspecific. Foissner (1980) mentioned a lorica and could not exclude the presence of symbiotic green algae, features which are reminiscent of *U. willii* Sonntag *et al.*, 2008. *Uroleptus caudatus sensu* Hemberger (1982) is about 200 μm long in protargol preparations, has about 35 adoral membranelles, and invariably three transverse and caudal cirri. The dorsal kinety pattern is not described; the morphometric data (e.g. size, number of adoral membranelles) are reminiscent of the population studied by Grolière (1975). Eigner (2001) described *Uroleptus caudatus* only briefly because he assumed a broad agreement with the original description; actually, Eigner (2001: 74) identified his population as *U. caudatus* mainly because of the body shape and the length of the midventral complex. However, an average size of 97 μm in protargol preparations (range 64–155 μm) is a striking difference to the 508 μm mentioned by Stokes (1886a), even when one takes into consideration a shrinkage of about 20% caused by the protargol impregnation procedure. Our specimens are 250–400 μm long after protargol impregnation and have on average 3.3 times more adoral membranelles (79.4 vs. 24.4) and a distinctly higher number of dorsomarginal kineties (5–8 vs. 2). These differences prove that (i) the identification by Eigner (2001) is incorrect, and (ii) our population is not identical with Eigner's material. From the morphological point of view, Eigner's population is basically inseparable from *U. lepisma sensu* Olmo (2000). However, there are some differences in the cell division (see below) so that a final synonymy seems premature.

***Uroleptus piscis* (Müller, 1773) Ehrenberg, 1831**. It was discovered in a limnetic habitat with *Lemna* and described by Müller (1773) as *Trichoda piscis*, however, without supplying an illustration. The first illustration was provided by Müller (1786), showing an organism with the characteristic *Uroleptus* habitus. Understandably, no details, except of the contractile vacuole and the front adoral membranelles, are recognizable. In addition, no size was given. Ehrenberg (1830) transferred it to *Oxytricha*, together with *Trichoda pellionella* Müller, 1773 (now *Tachysoma pellionellum*) and *Trichoda pullaster* Müller, 1773 (now *Holosticha pullaster*). Just one year later, Ehrenberg (1831) established the genus *Uroleptus* and included four species, *inter alia*, *Trichoda piscis* (further details see above). Ehrenberg (1838) provided a description and an illustration which were not much better than those of Müller (1773, 1786). The body length of Ehrenberg's specimens ranged from about 80 to 180 μm (1/24–1/12 line; Hellwig 1988). The first detailed description of *U. piscis* was provided by Stein (1859), who found it in limnetic habitats in Prague and near Berlin. The specimens were up to about 500 μm long with a length : width ratio of 5–6 : 1 (rarely 7–8 : 1), distinctly tailed, had two macronuclear nodules with each one micronucleus attached, three enlarged frontal cirri, a midventral complex extending to (into?) the narrow tail, and one left and one right marginal row. Stein did not describe transverse cirri, indicating that they were either lacking or indistinct and thus not distinguishable from the marginal cirri. No distinct caudal cirri have been illustrated. Since the description by Müller (1773, 1786) is rather vague, we will never know whether or not Stein's identification was correct. The small size (80–180 μm) mentioned by Ehrenberg (1838) indicates that he did not observe the same species as Stein (1859), who found specimens up to a length of 500 μm. By contrast, the size of our Chinese material matches rather perfectly the size given by Stein (1859). The three or four transverse cirri and the three caudal cirri of our population are very inconspicuous in the protargol preparations, so that one may not wonder when they have been overlooked or misinterpreted as marginal cirri by Stein (1859) who used live observation only. Since the body shape in protargol preparations is sometimes little expressive – especially in uroleptids which are often contractile – our population could be identified with *Uroleptus piscis sensu* Stein (1859; for review, see Kahl 1932: 550).

As discussed before, it might be possible that Stein (1859) has overlooked or misinterpreted the inconspicuous transverse cirri, and therefore synonymy of *U. piscis sensu* Stein (1859), *Holosticha caudata* Stokes, 1886a, and *H. caudata sensu* Kahl (1932: 587) cannot be excluded. Since all these early workers did not have the advantage of protargol impregnation, nothing is known about the dorsal kinety pattern.

Kowalewski (1882) redescribed *Trichoda piscis* and transferred it to *Amphisia*, a junior synonym of *Holosticha* (details see Berger 2006a). This population differs distinctly from that described by Stein (1859), especially in body length (800 μm vs. up to 500 μm) and the ciliature of the tail region (about 17 very long, conspicuous transverse cirri, four long caudal cirri, and left marginal cirri of tail region stiff and long vs. inconspicuous or lacking transverse and caudal cirri and left marginal cirri of tail region also inconspicuous). It is almost

impossible that Stein (1859), who made very detailed live observations, has overlooked the conspicuous tail ciliature described by Kowalewski (1882). Kahl (1932: 587) confirmed the data provided by Kowalewski and therefore separated this type of *U. piscis* from Stein's type (Kahl 1932: 550) in that he transferred it to the subgenus *Holosticha (Paruroleptus)*, however, without establishing a new species.

Rigidothrix goiseri **Foissner and Stoeck, 2006**. The infraciliature and some ontogenetic details (see corresponding chapter) of the Chinese population closely resemble that of *R. goiseri*, a semiterrestrial species from flood plains in West Africa. The populations differ significantly in body size (body length 311 μm vs. 201 μm in protargol preparations) as well as in the number of adoral membranelles (on average 79 vs. 40), dorsomarginal kineties (5–8 vs. 4 or 5), and transverse cirri (3 or 4 vs. 2) so that synonymy can be excluded. The question is rather whether or not the Chinese population belongs to *Rigidothrix*? Unfortunately, we do not know how does the oral apparatus of our population look like in life, that is, *Stylonychia/Laurentiella*-like as in *R. goiseri* or as ordinary as in *Uroleptus/Paruroleptus*. After protargol impregnation the oral apparatus of the Chinese population and *R. goiseri* look rather similar. The second important life feature not known for our population is the consistency of the cell, namely rigid as in *Rigidothrix* or flexible as in *Uroleptus/Paruroleptus*. There are only two features recognizable in the protargol preparations which suggest that *R. goiseri* and the Chinese population are not congeneric, namely, the spindle-shaped fibrillar basket at the base of each dorsal dikinetid and the position of the left frontal cirrus. Our preparations do not show these spindle-shaped baskets around the dorsal bristles. Since we used the same impregnation method which clearly revealed this structure in *Stylonychia* (Shi *et al.* 1990, Shi and Ammermann 2004) and since the fibrils around the cirri are very well impregnated (Figs 2A–F), we suppose that a dorsal kinety basket is really absent in the Chinese population. By contrast, the baskets are very prominent in *R. goiseri* (Foissner and Stoeck 2006). These baskets, the rigid body, and the conspicuous oral apparatus of *Rigidothrix* are reminiscent of the *Stylonychia mytilus*-complex and *Laurentiella* (for review see Berger 1999), whereas gene sequence data and the lack of dorsal kinety fragmentation indicate a very distinct separation of *R. goiseri* from the stylonychines (Foissner and Stoeck 2006, 2008).

In *R. goiseri* the left frontal cirrus is obliquely behind the middle frontal cirrus and both cirri are rather close to the distal end of the adoral zone, perhaps due to spatial constraints by the large, discoidal frontal/buccal area (Foissner and Stoeck 2006). By contrast, in the Chinese population and in *Holosticha musculus sensu* Martin *et al.* (1981), the left and middle frontal cirrus are at the same level, and the left cirrus is ahead of the paroral and distinctly separated from the distal end of the adoral zone, similar as, for example, in *Paruroleptus musculus sensu* Foissner (1984), a true uroleptid. Of course both features (dorsal baskets, frontal cirri) are not very strong, but together with the geographic separation (*R. goiseri* so far only recorded from West Africa; other populations [*U. magnificus*, *H. musculus sensu* Martin *et al.*, 1981, Chinese population] recorded in Eurasia) they indicate that the Eurasian populations do not belong to *Rigidothrix*. Of course, further morphological and molecular data are needed to support or disprove this hypothesis.

The comparison of the Chinese population with the most similar populations and species described so far shows that it is probably identical with the very little known *Holosticha (Paruroleptus) magnificus* Kahl, 1932, only recently – although not formally – combined with *Uroleptus* by Olmo (2000). Since the determination is uncertain for the reasons discussed above, we precede the species-group name the open nomenclature qualifier "cf." (Richter 1948, Bengtson 1988). Further, we preliminary accept Olmo (2000) as combining author because we are uncertain about the final generic assignment.

The discussion demonstrates that identification of uroleptids is difficult when the tail ciliature is inconspicuous and life data are lacking. The populations described so far after protargol impregnation differ obviously mainly in morphometric data, for example, number of adoral membranelles and dorsomarginal kineties. Unfortunately, both features are not available from the old descriptions so that a final decision is often impossible at present. Much more morphological, ontogenetic, and molecular data are needed to solve the problem seriously.

Morphogenetic comparison within *Uroleptus*

The cell division of three *Uroleptus* species and *Rigidothrix goiseri* has been described (Martin *et al.* 1981, Olmo 2000, Eigner 2001, Foissner and Stoeck 2006; note that the species-identifications by Martin *et al.* 1981 and by Eigner 2001 are incorrect, see above). Expectably, the processes largely agree and therefore only the differences and conspicuous agreements will

be discussed. The systematic relevance of these differences has to be ascertained by the investigation of further uroleptids.

(i) The oral primordium is formed *de novo* from some basal body clusters originating immediately left of the middle portion of the midventral complex in the Chinese population (Figs 1C–F, 2B–D), in *Uroleptus musculus* sensu Martin *et al.* (1981), *U. caudatus sensu* Hemberger (1982), and in *U. lepisma* (Olmo 2000). Foissner and Stoeck (2006) also write that anlagen formation in *R. goiseri* begins left of some postoral cirri of the midventral complex. By contrast, in the *Uroleptus* population studied by Eigner (2001), three small fields of basal bodies develop from disaggregating midventral cirri. This difference is somewhat surprising because *U. lepisma sensu* Olmo (2000) and *Uroleptus* sp. *sensu* Eigner (2001) are morphologically very similar.

(ii) The frontal-ventral-transverse cirri anlagen of the proter and the opisthe of the Chinese population are formed via so-called primary primordia, these are common anlagen for proter and opisthe which somewhat later divide in the "secondary" primordia (Foissner 1983). In the other three uroleptids studied so far, no stage of this probably rather short phase of the division was found. *Rigidothrix goiseri* also has primary primordia which split into secondary primordia (Foissner and Stoeck 2006). Because of the sparse data, the systematic and phylogenetic relevance of this feature is not known at present.

(iii) In the Chinese population the new left frontal cirrus of the proter is formed mainly from the middle portion of the disintegrating parental paroral, while the new undulating membranes of the proter are formed via a primordium originating from the parental endoral (Figs 1G, I, 3F, I–K). The micrographs published by Martin *et al.* (1981, their Figs 4–7) show an identical or at least very similar process in their *Uroleptus* population. By contrast, in *U. lepisma* (Olmo 2000) and probably also in *U. caudatus sensu* Eigner (2001), the left frontal cirrus (I/1) originates, as in most other hypotrichs, from the undulating membrane anlage. In *R. goiseri* the left frontal cirrus originates from the disorganizing parental paroral and an anlage for the new undulating membranes of the proter appears left of the new frontal cirrus; Foissner and Stoeck (2006) could not clarify the origin of these basal bodies, but they supposed that they are remnants from the midventral cirri anlagen. A comparison of our data with the corresponding figures published by Foissner and Stoeck (2006, their Figs 18–20, 22, 25, 26) indicates that the process-

es could proceed similar or even identical in both populations. Interestingly, both the Chinese population, the population studied by Martin *et al.* (1981), as well as *R. goiseri* have more than two dorsomarginal kineties. By contrast, the populations studied by Olmo (2000) and Eigner (2001), which produce the left frontal cirri in the ordinary way, have only two dorsomarginal kineties.

(iv) The two frontoterminal cirri of the Chinese population are formed in the plesiomorphic way, that is, the anteriormost two cirri of the rightmost/rearmost frontal-ventral-transverse cirri anlage migrate anteriorly (Figs 1A, G, I, K, 4B–F). The anteriormost two cirri of the penultimate anlage form the rearmost midventral pair and the second cirrus from behind forms the left pretransverse ventral cirrus which is obviously reabsorbed later. These cirri can be easily homologized with the cirri V/3 and V/4 (two of three postoral ventral cirri) and V/2 (left pretransverse ventral cirrus) of an 18-cirri hypotrich. The same pattern is recognizable in *U. lepisma* (Olmo 2000, his Figs 14, 15), in *U. musculus* sensu Martin *et al.* (1981, their Figs 5–7), and also in *R. goiseri* (Foissner and Stoeck 2006, their Figs 20, 22, 26). By contrast, Eigner (2001) described a rather different formation, namely, the anterior frontoterminal cirrus is formed from the penultimate anlage, whereas the posterior one is formed by the rightmost/rearmost anlage. Further *Uroleptus lepisma*-like populations have to be studied to check whether or not this deviating origin of the frontoterminal cirri actually exists or is only a misinterpretation of the process.

The morphogenetic data indicate that the Chinese population is obviously more similar to *U. musculus sensu* Martin *et al.* (1981) and *R. goiseri* than to the relatively small *U. lepisma*-like species described by Olmo (2000) and Eigner (2001).

Comparison of *Uroleptus/Paruroleptus* with other Dorsomarginalia bearing a midventral-complex

Previously almost all hypotrichs with zigzagging frontoventral cirri have been classified in the urostyloids (e.g. Borror 1972, Corliss 1979). Foissner *et al.* (2004) postulated the CEUU-hypothesis which explains that the conspicuous zigzagging pattern has evolved convergently in the urostyloids, *Uroleptus*, and some other hypotrichs. A convergent evolution of this so-called midventral pattern is not only indicated by molecular data, but also by some morphological/morphogenetic features. For example, the urostyloids lack dorsomarginal kineties, whereas these part of the dorsal ciliature is characteristic for the Dorsomargina-

lia, a group which contains some, obviously not closely related genera also bearing a more or less distinct midventral pattern, namely, *Uroleptus, Neokeronopsis, Pattersoniella, Rigidothrix, Territricha, Afrophrya* (e.g. Berger 1999, 2006a; Warren *et al.* 2002; Foissner and Stoeck 2006, 2008; Wang *et al.* 2007; Foissner *et al.* 2010). The dorsal kinety pattern indicates that these genera can be separated into two groups, namely those which lack kinety fragmentation (*Uroleptus/Paruroleptus, Rigidothrix*) and those with kinety fragmentation (*Neokeronopsis, Territricha, Pattersoniella*); for *Afrophrya* the dorsal kinety pattern is not known. This difference is, at least partially, supported by gene sequence data (Foissner and Stoeck 2006, 2008; Sonntag *et al.* 2008; Paiva *et al.* 2009).

Annotated list of published names in *Uroleptus* Ehrenberg, 1831, *Paruroleptus* Wenzel, 1953, and *Rigidothrix* Foissner and Stoeck, 2006

Fifty-nine species, subspecies, and varieties have been originally assigned or were transferred to *Uroleptus, Paruroleptus*, and *Rigidothrix*. However, only about 50% of them certainly or very likely belong to the Uroleptidae. The remaining species are divided into three groups in the following list, namely, (i) non-uroleptid hypotrichs; (ii) non-hypotrichous ciliates; and (iii) species indeterminata or nomina nuda. Within all groups the species are arranged alphabetically using the combination with *Uroleptus* or *Paruroleptus*, which does not always correspond the basionym. *Rigidothrix goiseri* is, at the present state of knowledge, the sole species of the Rigidotrichidae and mentioned after the "true" uroleptids.

More than in other hypotrich taxa, many older descriptions are improper and/or lack suitable illustrations. Thus, the validity of a considerable number of species remains ambiguous and needs confirmation. In addition, many nomenclatural problems exist, which cannot be corrected within this brief compilation. For example, Stiller (1974) transferred, although not formally, several species from *Holosticha (Paruroleptus)* Kahl to *Paruroleptus* Kahl, a subgenus and genus which is actually invalid. The type locality and – if available – key references (e.g. Kahl 1932, Borror 1972, Foissner *et al.* 1991) are given for each species.

Borror and Wicklow (1983) made short shrift with the complicated taxonomy of *Uroleptus* in that they merged all species in only two species, namely (i) *U. lamella* Ehrenberg, 1831 with *U. rattulus* Stein, 1859 as synonym and (ii) *U. musculus* (Müller, 1773) Eh-

renberg, 1831 with all other species as synonyms. Of course, this approach was exaggerated.

Species certainly or very likely belonging to the Uroleptidae: The following species have the characteristic body shape and cirral pattern so that the classification in the uroleptids is beyond reasonable doubt. Perhaps few species, for example, *Holosticha magnificus*, belong to the rigidotrichids.

***Paruroleptus gibbosus* Vuxanovici, 1963**: 209. Remarks: A junior synonym of *U. caudatus* (Stokes, 1886a) according to Borror (1972: 12). Type locality: lake (Lacul Tei) in the northern area of the city of Bucharest, Romania.

***Paruroleptus magnificus* (Kahl, 1932) Stiller, 1974 or *Uroleptus magnificus* (Kahl, 1932) ?Olmo, 2000**. Basionym: *Holosticha (Paruroleptus) magnificus* Kahl, 1932: 587. Remarks: A junior synonym of *U. violaceus* Stein, 1859 according to Borror (1972: 12). Hemberger (1982) and we do not agree with this synonymy. Stiller (1974) transferred the species to *Paruroleptus* Kahl and not to *Paruroleptus* Wenzel; thus, the combination is invalid. Type locality: not fixed, likely northern Germany; limnetic.

***Paruroleptus musculus* var. *minor* in Kahl (1932: 585, legend to Fig. 110_{13}). Remarks: Likely an unintended name for *Holosticha (Paruroleptus) musculus simplex* Kahl, 1932 (see *Paruroleptus musculus simplex*).

***Paruroleptus musculus simplex* (Kahl, 1932) Stiller, 1974**. Basionym: *Holosticha (Paruroleptus) musculus simplex* Kahl, 1932: 588. Remarks: Established as variety and therefore of subspecific rank according to ICZN (1999, Article 45.6.4). Borror (1972: 12) raised it to species rank ["*Holosticha (Paruroleptus) simplex* Kahl, 1932"] and simultaneously classified it as junior synonym of *U. musculus*. *Paruroleptus musculus minor* in the legend to the figure (Kahl 1932: 584, Fig. 110_{13}) is very likely an unintended name for the present taxon. Type locality: not fixed; limnetic.

***Paruroleptus ophryoglena* (Gelei, 1954) Stiller, 1974**. Remarks: Gelei (1954: 330), who followed Kahl's (1932) classification, described this species as "*Paruroleptus ophryoglena*," but within the genus *Holosticha* (Gelei 1954: 327); thus, the correct basionym is *Holosticha (Paruroleptus) ophryoglena* Gelei, 1954. Borror (1972: 12) and Berger (2001: 70) incorrectly assumed that *Paruroleptus ophryoglena* is the correct basionym. Borror (1972) classified it as junior synonym of *U. caudatus* (Stokes, 1886). Type locality: a temporary pond (Tümpel I) on a woody mountain pasture

("Csapásbérc") at the upper margin of the village of Diósjenő, Börzsöny Mountains, Hungary.

***Paruroleptus pectinatus* Vuxanovici, 1963**: 209. Remarks: A junior synonym of *U. violaceus* Stein, 1859 according to Borror (1972: 12). Type locality: lake (Lacul Floreasca) in Bucharest, Romania.

***Paruroleptus viridis* Vuxanovici, 1963**: 208. Remarks: A junior synonym of *U. piscis* (Müller, 1773) according to Borror (1972: 12). Type locality: lake (Lacul Herăstrău) in Bucharest, Romania.

***Uroleptus caudatus* (Stokes, 1886a) Borror, 1972**. Basionym: *Holosticha caudata* Stokes, 1886a: 25. Remarks: Type species of *Holosticha (Paruroleptus)* Wenzel, 1953. Current systematic status uncertain, that is, *Uroleptus caudatus* (Stokes, 1886a) Borror, 1972 when *Paruroleptus* is considered as junior synonym of *Uroleptus* or *Paruroleptus caudatus* (Stokes, 1886a) ?Grolière, 1975 when *Paruroleptus* is accepted. Note that Wenzel (1953) cannot be the author for the latter combination because he established *Paruroleptus* as subgenus of *Holosticha*. Borror (1972: 12) incorrectly assumed that Kahl (1932) is the author for the combination in *Uroleptus*. However, Kahl (1932: 587) assigned this species to his invalid (no type species fixed) subgenus *Holosticha (Paruroleptus)*; thus the correct name in Kahl (1932) is *Holosticha (Paruroleptus) caudatus* Stokes, 1886a. Consequently, Borror (1972) was the first authority which used the binomen *U. caudatus* (Stokes, 1886a) and he is therefore proposed as author for this combination. Further combinations, see Berger (2001: 34). Morphogenesis studied by Eigner (2001), however, identification uncertain (see above). Perhaps synonymous with *U. piscis sensu* Stein (1859; see above). Detailed redescription and neotypification urgently needed. Type locality: marsh water with *Sphagnum* from/near Trenton, New Jersey, USA.

***Uroleptus (Oxytricha) caudatus* (Clap. u. L., 1858)** in Kahl (1932: 548). Remarks: Kahl introduced this nomenclaturally invalid (non-existing) name for "*Oxytricha caudata* Ehr." in Claparède and Lachmann (1858: 146). Obviously this population has zigzagging midventral cirri and one right, but two left marginal rows, indicating that it is not identical with other *Uroleptus* species. Found in limnetic habitats in the surroundings of Berlin, Germany. For *O. caudata* Ehrenberg, 1833, see Berger (1999: 398).

***Uroleptus dispar* Stokes, 1886a**: 26. Remarks: About 40 times recorded, but detailed redescription not yet available. For review, see Kahl (1932: 549). A junior synonym of *U. violaceus* Stein, 1859 according to Borror (1972: 12). Type locality: marsh water with *Sphagnum* near Trenton, New Jersey, USA.

***Uroleptus dubius* Vuxanovici, 1963**: 210. Remarks: No further records available. A junior synonym of *U. violaceus* Stein, 1859 according to Borror (1972: 12). Type locality: lake (Lacul Herăstrău) in Bucharest, Romania.

***Uroleptus gallina* (Müller, 1786) Foissner, Blatterer, Berger and Kohmann, 1991**. Basionym: *Trichoda gallina* Müller, 1786: 209. Remarks: According to Foissner *et al*. (1990; 1991: 244), *Uroleptus musculus sensu* Ehrenberg (1838) and Stein (1859) belong to this species. Type locality: running water in Denmark.

***Uroleptus lacteus* (Kahl, 1932) Borror, 1972**. Basionym: *Holosticha (Paruroleptus) lacteus* Kahl, 1932: 587. Remarks: A valid species according to Borror (1972: 12). Type locality: pond of the Botanical Gardens of Hamburg, Germany.

***Uroleptus lamella* Ehrenberg, 1831**: 117. Remarks: The senior synonym of *U. rattulus* Stein, 1859 according to Borror (1972: 12). Foissner *et al*. (1991) doubt this proposal because the sizes are rather different (up to 116 μm vs. up to 416 μm). A little known species which needs detailed redescription. Further combination, see Berger (2001). Type locality: limnetic habitat in Berlin, Germany.

***Uroleptus lemani* Jankowski, 1979**: 84. Remarks: Established for *U. rattulus* Stein, 1859 *sensu* Dragesco (1960). Type locality: sandy sediment of Lake Geneva near the village of Excenevex, France.

***Uroleptus lepisma* (Wenzel, 1953) Foissner, 1998**. Basionym: *Holosticha (Paruroleptus) lepisma* Wenzel, 1953: 109. Remarks: Detailed redescription by Berger and Foissner (1989), cell division studied by Olmo (2000). Type locality: not fixed in detail; dry mosses, *Sphagnum* from Bavaria, Germany.

***Uroleptus limnetis* Stokes, 1885**: 187. Remarks: For review, see Kahl (1932: 549). A junior synonym of *U. piscis* according to Borror (1972: 12). Type locality: pond water with *Lemna* and marsh water with *Sphagnum*, likely in/near Trenton (New Jersey, USA) where Stokes lived and worked.

***Uroleptus longicaudatus* Stokes, 1886a**: 27. Remarks: For review, see Kahl (1932: 549). A junior synonym of *U. piscis* according to Mermod (1914: 97) and Borror (1972: 12). Type locality: marsh water with *Sphagnum* in/near Trenton (New Jersey, USA) where Stokes lived and worked.

***Uroleptus musculus* (Müller, 1773) Ehrenberg, 1831**. Basionym: *Trichoda musculus* Müller, 1773: 74.

Remarks: Type species of *Uroleptus* by subsequent designation by Borror (1972: 12; details see above). For review, see Kahl (1932: 550). Type locality: not fixed; old infusions.

***Uroleptus musculus* (Kahl, 1932) Foissner, Blatterer, Berger and Kohmann, 1991**. Basionym: *Holosticha (Paruroleptus) musculus* Kahl, 1932: 588. Remarks: Kahl (1932: 588) established the variety *Holosticha (Paruroleptus) musculus simplex*. Thus, he automatically activated the nominotypical variety *Holosticha (Paruroleptus) musculus musculus* Kahl, 1932. For review, see Foissner *et al.* (1991: 248). In the present combination, it is the junior secondary homonym of the previous entry (needs detailed analysis). Type locality: not fixed; limnetic, perhaps in/near the city of Hamburg, Germany.

***Uroleptus novitas* (Horváth, 1933) Borror, 1972**. Basionym: *Holosticha* (*Paruroleptus) novitas* Horváth, 1933: 286 (actually established as "*Paruroleptus novitas*," but Horváth made no comment that he has raised the subgenus *Paruroleptus* to genus rank). Remarks: A valid species according to Borror (1972: 12). Type locality: sodium bicarbonate ponds in the so-called "Sziliszék" area, north of the city of Szeged, Hungary.

***Uroleptus opisthobolus* (Stokes, 1886a) Kahl, 1932**. Basionym: *Platytrichotus opisthobolus* Stokes, 1886a: 29. Remarks: Type species of *Platytrichotus* Stokes, 1886a. A junior synonym of *U. musculus* (Müller, 1773) according to Mermod (1914: 97) and Borror (1972: 12). For review, see Kahl (1932: 550). Type locality: marsh water with *Sphagnum* in/near Trenton, New Jersey, USA.

***Uroleptus piscis* (Müller, 1773) Ehrenberg, 1831**. Basionym: *Trichoda piscis* Müller, 1773: 73. Remarks: A valid species according to Borror (1972: 12). For review, see Kahl (1932: 550) and Foissner *et al.* (1991: 252). Mereschkowsky (1877) established the variety *U. piscis brevicauda*. Thus, he automatically activated the nominotypical variety *U. piscis piscis* (Müller, 1773) Ehrenberg, 1831. Type locality: limnetic habitat with *Lemna*, Denmark?

***Uroleptus piscis brevicauda* Mereschkowsky, 1877**: 236. Remarks: This variety is only briefly mentioned in the original description, but not listed by Mereschkowsky (1879), Kahl (1932), and Borror (1972). Type locality: Northern Russia?

***Uroleptus piscis minor* Mermod, 1914**: 90. Remarks: Mermod (1914) established this variety because it is smaller than the populations described by previous authors. No illustration given. Not mentioned by Kahl

(1932) and Borror (1972). Type locality: bog in/near Saint-Croix (Jura vaudois), Switzerland.

***Uroleptus poianae* Lepsi, 1957**: 236. Remarks: A junior synonym of *U. piscis* according to Borror (1972: 12). Type locality: ombrogenic bog in the commune Poiana Stampei, East Carpathians, Romania.

***Uroleptus rattulus* Stein, 1859**: 180. Remarks: For reviews, see Kahl (1932: 549) and Foissner *et al.* (1991: 255). A junior synonym of *U. lamella* according to Borror (1972: 12). Type locality: peat-ditch near the city of Niemegk, Germany.

***Uroleptus setiformis* Bary, 1950**: 12. Remarks: A junior synonym of *U. musculus* according to Borror (1972: 12). Type locality: Wellington, New Zealand, where Bary (1950) found it in an ephemeral pond at Maori Bank, Upper Hutt, and a tarn on Bull Mound (about 1200 m) in the Tararua Range.

***Uroleptus sphagni* Stokes, 1886b**: 111. Remarks: A junior synonym of *U. violaceus* Stein, 1859 according to Mermod (1914: 97) and Borror (1972: 12). For review, see Kahl (1932: 549). Type locality: standing water with *Sphagnum*, likely in/near Trenton (New Jersey, USA) where Stokes lived and worked.

***Uroleptus violaceus* Stein, 1859**: 180. Remarks: For review, see Kahl (1932: 550). A valid species according to Borror (1972: 12). Type locality: peat-ditch near the city of Niemegk, Germany.

***Uroleptus willii* Sonntag, Strüder-Kypke and Summerer, 2008**: 281. Remarks: A pelagic species with symbiotic green algae. Type locality: pelagial of a lake (Piburgersee) in Tyrol, Austria.

Species belonging to the Rigidotrichidae: Foissner and Stoeck (2006) assigned *Rigidothrix* (name-bearing type genus), *Afrophrya*, *Uroleptus*, and *Territricha* to this family. Somewhat later, they removed *Uroleptus* and placed it in the uroleptids (Foissner and Stoeck 2008). *Territricha* has dorsomarginal kineties and a multiple fragmentation of dorsal kinety 3, indicating that it belongs to the oxytrichids (Berger 1999). *Afrophrya* is based on little known species and therefore of uncertain phylogenetic position. Thus, we list only the *Uroleptus*-like *R. goiseri*.

***Rigidothrix goiseri* Foissner and Stoeck, 2006**: 251. Remarks: Type species of *Rigidothrix* Foissner and Stoeck, 2006. Sole species of the genus and characterized by a *Uroleptus*-like cirral pattern (inconspicuous transverse cirri present), a *Stylonychia/Laurentiella*-like oral apparatus, a rigid body, and dorsomarginal kineties. According to the molecular data, however, neither closely related to *Uroleptus* nor to the stylonychines

(Foissner and Stoeck 2006, 2008; Paiva *et al.* 2009). Type locality: floodplain soil from the Niger River near the town of Timbuktu, Republic of Mali, West Africa.

Non-uroleptid hypotrichs: The following species are hypotrichs, but obviously do not belong to the uroleptids.

***Paruroleptus dubium* (Gelei, 1954) Stiller, 1974**. Basionym: *Holosticha (Parurosoma) dubium* Gelei, 1954: 332. Current systematic status: *Parurosoma dubium* (Gelei, 1954) Berger, 1999. Remarks: Type species of *Holosticha (Parurosoma)* Gelei, 1954 and *Parurosoma* Gelei, 1954. For review, see Berger (1999: 492). Type locality: ephemeral, hypertrophic pond on a meadow in the Börzsöny Mountains, Hungary.

***Paruroleptus (?) interrupta* Foissner** in Foissner (1981: 19). Current systematic status: *Hemisincirra interrupta* (Foissner, 1982) Foissner in Berger, 2001. Remarks: "*Paruroleptus (?) interrupta* Foissner" in Foissner (1981) is a nomen nudum because published without description; somewhat later validly described as *Perisincirra interrupta* Foissner, 1982. For review of *H. interrupta*, see Berger (2008: 432). Type locality: soil from near the Hotel Wallackhaus, Großglockner-area, Salzburg, Austria.

***Paruroleptus strenuus* Dingfelder, 1962**: 617. Current systematic status: *Laurentiella strenua* (Dingfelder, 1962) Berger and Foissner, 1989. Remarks: For review, see Berger (1999: 753). Type locality: puddles with hay south of the city of Forchheim, Bavaria, Germany.

***Uroleptus agilis* Engelmann, 1862**: 386. Current systematic status: *Urosomoida agilis* (Engelmann, 1862) Hemberger in Foissner, 1982. Remarks: Type species of *Urosomoida* Hemberger in Foissner, 1982. For review, see Berger (1999: 347). Type locality: saline lake near Eisleben, Germany.

***Uroleptus contortus* Gelei, 1954**: 318. Current systematic status: *Strongylidium contortus* (Gelei, 1954) Borror, 1972. Remarks: Transfer to *Strongylidium* Sterki, 1878 by Borror (1972) accepted in the recent review by Paiva and Silva-Neto (2007). Detailed redescription urgently needed. Type locality: a temporary pond (Tümpel III) on a woody mountain pasture ("Csapásbérc") at the upper margin of the village of Diósjenő, Börzsöny Mountains, Hungary.

***Uroleptus elliptica* Wang and Nie, 1933**: 58. Remarks: Very likely not a uroleptid because body very broadly rounded posteriorly and ventral cirral rows widely separated, strongly indicating that this species lacks a midventral complex. Borror (1972) synonymized it with *Paraurostyla hymenophora* (Stokes,

1886) Borror, 1972 (now *Apoamphisiella hymenophora*; for review, see Berger 1999: 786). However, Borror's synonymy is likely incorrect because *U. elliptica* obviously lacks transverse cirri whereas these cirri are very prominent in *A. hymenophora*. According to Wang and Nie (1933), a classification in *Paraholosticha* is not possible because of distinct differences in the frontal ciliature. Detailed redescription needed. *Uroleptus* is masculine (Aescht 2001), thus the species-group name has to be adapted: *U. ellipticus* Wang and Nie, 1933 nom. corr. Type locality: small pool near the Campus of the Biological Laboratory of the Science Society in China, Nanjing.

***Uroleptus elongatus* Fernandez-Leborans, 1981**: 5. Current systematic status: Supposed synonym of *Deviata abbrevescens* Eigner, 1995 according to Berger (2011: 574). Remarks: Certainly not a uroleptid because zigzagging midventral cirri lacking. Type locality: freshwater from the Parque del Oeste, Madrid, Spain.

***Uroleptus gibbus* (Claparède and Lachmann, 1858) Kent, 1882**. Basionym: *Oxytricha gibba* Claparède and Lachmann, 1858: 144. Current systematic status: *Australothrix gibba* (Claparède and Lachmann, 1858) Blatterer and Foissner, 1988. Remarks: For reviews, see Kahl (1932: 547) and Berger (2006a: 724). Must not be confused with the marine *Holosticha gibba* (Müller, 1786) Wrzesniowski, 1877 (basionym *Trichoda gibba*; for review see Berger 2006a: 99). Type locality: limnetic habitats in the surroundings of Berlin, Germany.

***Uroleptus halseyi* Calkins, 1929**: 61. Current systematic status: Junior synonym of *Engelmanniella mobilis* (Engelmann, 1862) Foissner, 1982. Remarks: Further details, see *U. mobilis* below. Type locality: pond with *Sphagnum*, *Myriophyllum*, and other plants in Westchester County, New York, USA.

***Uroleptus hospes* Ehrenberg, 1831**: 116. Current systematic status: *Mucotrichidium hospes* (Ehrenberg, 1831) Foissner, Oleksiv and Müller, 1990. Remarks: Type species of *Mucotrichidium* Foissner, Oleksiv and Müller, 1990. For review, see Berger (2008: 441). Type locality (neotype): pond at Salzburg University, Austria.

***Uroleptus humicola* Gellért, 1956**: 345. Current systematic status: *Bistichella humicola* (Gellért, 1956) Berger, 2008. Remarks: For review, see Berger (2008: 556). Type locality: humus under moss collected in the south-western region of the hill Magoska north-east of the village of Boldogkóváralja, Hungary.

***Uroleptus kahli* Buitkamp, 1977**: 121. Current systematic status: *Hemisincirra buitkampi* (Jankowski,

1979) Berger, 2008. Remarks: Type species of *Hemisincirra* Hemberger, 1985. For explanation of complicated nomenclature and review, see Berger (2008: 393). Type locality: upper soil layer from Venusberg, Melbtal near city of Bonn, Germany.

Uroleptus kahli **Grolière, 1975**: 482. Current systematic status: *Perisincirra kahli* (Grolière, 1975) Jankowski, 1978. Remarks: Type species of *Perisincirra* Jankowski, 1978. For review, see Berger (2011: 471). Type locality: forest pond (Creux de Pisseport) near the Station Biologique Besse-en-Chandesse, France.

Uroleptus mobilis **Engelmann, 1862**: 386. Current systematic status: *Engelmanniella mobilis* (Engelmann, 1862) Foissner, 1982. Remarks: Type species of *Engelmanniella* Foissner, 1982. For detailed redescription, see Foissner (1982) and Wirnsberger-Aescht *et al.* (1989, 1990); for review, see Berger (2011: 502). Kahl (1932) established the variety *U. mobilis americanus* (see next entry). Thus, he automatically activated the nominotypical variety *U. mobilis mobilis* Engelmann, 1862. Type locality: brook (Boticzbach) near the city of Prague, Czech Republic.

Uroleptus mobilis americanus **Kahl, 1932**: 548. Current systematic status: Junior synonym of *Engelmanniella mobilis* (Engelmann, 1862) Foissner, 1982. Remarks: Established by Kahl (1932) for the so-called "*Uroleptus mobilis* New York variety" described by Calkins (1919, 1929). According to ICZN (1999, Article 45.6.4) now of subspecific rank because established as variety by Kahl (1932). Type locality uncertain because original sample site not given: Calkins (1919) found it in an old hay infusion (composition – hay plus pond water or hay plus tap/distilled water – not described) standing for several months in the Zoological Laboratory of Columbia University, New York, USA.

Uroleptus muscorum **Kahl, 1932**: 548. Current systematic status: *Birojimia muscorum* (Kahl, 1932) Berger and Foissner, 1989. Remarks: For review, see Berger (2006a: 683). Type locality: not fixed in original description and neotypification not yet made; terrestrial.

Uroleptus natronophilus **Dietz, 1965**: 25. Current systematic status: *Apourosomoida natronophila* (Dietz, 1965) Berger, 2008. Remarks: For review, see Berger (2008: 530). Type locality: Lake Elmenteita, Kenya.

Uroleptus notabilis **(Foissner, 1982) Foissner, 1998**. Basionym: *Paruroleptus notabilis* Foissner, 1982: 64. Current systematic status: *Caudiholosticha notabilis* (Foissner, 1982) Berger, 2006a. Remarks: For review, see Berger (2006a: 260). Type locality: soil of a highly eutrophic alpine pasture of the Hochmais-Alm near the Großglockner-Hochalpenstraße, Salzburg, Austria.

Uroleptus packii **Calkins in Pack, 1919**: 277. Current systematic status: *Strongylidium packii* (Calkins in Pack, 1919) Borror, 1972. Remarks: The senior synonym of *Cladotricha koltzowii* Gaievskaia, 1925 according to Borror (1972). For reviews, see Paiva and Silva-Neto (2007) and Berger (2011: 276). Type locality: Great Salt Lake in the vicinity of Salt Air Pavilion, USA.

Uroleptus paranotabilis **Foissner, Agatha and Berger, 2002**: 566. Current systematic status: *Caudiholosticha paranotabilis* (Foissner, Agatha and Berger, 2002) Berger, 2006a. Remarks: For review, see Berger (2006a: 254). Type locality: dung balls formed by a large *Scarabaeus* at the Bambatsi Guest Farm, Mopane forest, Namibia.

Uroleptus retractilis **(Claparède and Lachmann, 1858) Song and Warren, 1996**. Basionym: *Oxytricha retractilis* Claparède and Lachmann, 1858: 148. Current systematic status: *Psammomitra retractilis* (Claparède and Lachmann, 1858) Borror, 1972. Remarks: For review, see Berger (2006a: 222). Type locality: fjord of Bergen, North Sea, Norway.

Uroleptus roscovianus **Maupas, 1883**: 566. Current systematic status: *Uroleptopsis roscoviana* (Maupas, 1883) Kahl, 1932. Remarks: For review, see Berger (2006a: 1006). Type locality: likely the French Atlantic Coast near Roscoff because Maupas (1883) found it for the first time in the Marine Biological Laboratory of Roscoff.

Uroleptus zignis **Entz, 1884**: 373. Current systematic status: *Australothrix zignis* (Entz, 1884) Blatterer and Foissner, 1988. Remarks: For review, see Berger (2006a: 721). Type locality: littoral of Gulf of Naples, Italy.

Non-hypotrichous ciliates: The following two species – originally, respectively, subsequently classified in *Uroleptus* – belong to the heterotrichs, a basal branching group of ciliates (e.g. Lynn 2008).

Uroleptus filum **Ehrenberg, 1833**: 277. Remarks: A junior synonym of the heterotrich *Spirostomum caudatum* (Müller, 1786) Delphy, 1939 (e.g. Foissner *et al.* 1992: 324).

Uroleptus patens **(Müller, 1786) Ehrenberg, 1833**. Basionym: *Trichoda patens* Müller, 1786: 181. Current systematic status: *Condylostoma patens* (Müller, 1786) Bory de Saint-Vincet in Lamouroux *et al.*, 1824. Remarks: Type of *Condylostoma* Bory, 1824 (Aescht 2001). For review, see Kahl (1932: 453). Type locality: marine; sea near Denmark?

Species indeterminate or *nomina nuda*: The following species are very likely either species indeterminata, that is, species that cannot be identified from the original description or *nomina nuda*, that is, names published without description or a hint to such a description.

Uroleptus bacillifer **Lackey, 1961**: 277. Remarks: Only a provisional name, that is, a *nomen nudum* because it is neither accompanied by a description or definition, nor by a bibliographic reference to a published statement (ICZN 1999, Article 13.1; Berger 2001). Not listed by Borror (1972).

Uroleptus matthesi **Wenzel, 1953**: 105. Remarks: Classified as species of questionable position by Borror (1972), but very likely a species indeterminata. Type locality not fixed in detail: Bavaria, Germany.

Uroleptus subtilis **Lepsi, 1960**: 1099. Remarks: Not mentioned by Borror (1972); likely a species indeterminata. Type locality: saprobic pond in a wood (Pădurea Băneasa) in the north of Bucharest, Romania.

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