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# *Uroleptopsis* Kahl, 1932 (Ciliophora: Hypotricha): Morphology and Cell Division of Type Species, Redefinition, and Phylogenetic Relationships

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**Summary.** The morphology and the morphogenesis of the marine hypotrich *Uroleptopsis citrina* Kahl, type of *Uroleptopsis* Kahl, were investigated using live observation and protargol impregnation. The results are used for a redefinition of *Uroleptopsis* and a phylogenetic analysis of the Pseudokeronopsidae. Each of the many macronuclear nodules of *U. citrina* divides individually as in *Pseudokeronopsis* spp., that is, the nodules do not fuse to a single mass. Consequently, *Uroleptopsis*, *Pseudokeronopsis*, and *Thigmokeronopsis* - which shows an intermediate type of macronuclear division - are united to the Pseudokeronopsidae. *Uroleptopsis* has three autapomorphies, namely the lack of transverse cirri, the formation of two cirri from the undulating membrane anlage, and a gap in the adoral zone. *Uroleptopsis ignea* has midventral rows which are the autapomorphy for the new subgenus *Uroleptopsis* (*Plesiouroleptopsis*). *Uroleptopsis* (*Uroleptopsis*), which contains the four other *Uroleptopsis* species, lacks a buccal cirrus in the ordinary position right of the paroral; in non-dividers this cirrus is part of the posterior bow of the bicorona. In *U. citrina* some cirral anlagen of the middle portion of the midventral complex do not form an ordinary cirral pair, but only a single midventral cirrus. *Keronopsis tannaensis* Shigematsu is transferred to *Uroleptopsis* because it lacks transverse cirri and has likely a bicorona. *Keronopsis multiplex* Ozaki and Yagiu is synonymized with *U. roscoviana* (Maupas). A key to the five *Uroleptopsis* species is provided and the terminology for urostylids is actualized. The *Uroleptopsis citrina* population from the Adriatic Sea is designated as neotype because (i) no preparations are available of the original type population, and (ii) synonymy with *Pseudokeronopsis rubra* and some other species was proposed by Borror (1979) and Borror and Wicklow (1983).

**Key words:** Adriatic Sea, key to species, neotypification, phylogeny, Protozoa, Pseudokeronopsidae, revision, terminology, *Uroleptopsis* (*Plesiouroleptopsis*) subgen. n., *Uroleptopsis tannaensis* comb. n., Urostylidae.

## INTRODUCTION

Kahl (1932) established *Uroleptopsis* because the lack of transverse cirri in some holostichid species prevailed their classification in *Holosticha* (*Keronopsis*). *Uroleptopsis* was accepted until 1979, when Borror has put it - together with *Trichototaxis* - into the synonymy of *Keronopsis sensu lato*. Later, he synonymized it with *Pseudokeronopsis* (Borror and Wicklow 1983). In 1990, Mihailowitsch and Wilbert described *P. ignea* which lacks transverse cirri. Thus, Foissner (1995) transferred it to *Uroleptopsis*. However, the resurrection of Kahl's genus by Foissner was not accepted by Eigner (2001).

Recently I found the type species *U. citrina* in the Adriatic Sea and could study its morphology and morphogenesis. The data indicate that *Uroleptopsis* is as well defined as many other genera of hypotrichs. Thus, it should not be synonymized with *Pseudokeronopsis*

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which is very likely the sister group of *Uroleptopsis* according to Hennigian argumentation.

## MATERIALS AND METHODS

**Sampling and culture.** *Uroleptopsis citrina* was found in a sample which I collected on the sandy littoral of the northern Adriatic Sea ahead the campground Pra' delle Torri (45°34'N 12°49'E) near the Italian village of Duna Verde on 25.05.2002. The sample contained mainly sand and seagrass run ashore. It was transported to Salzburg in a 1-litre bottle. In the laboratory raw cultures were established using Petri dishes 15 cm across filled with sea water from the sample site. Some squashed wheat grains were added to support microbial growth. The species grew also well in artificial sea water (30‰; Biosal, Aqualine Buschke, Berg, Germany).

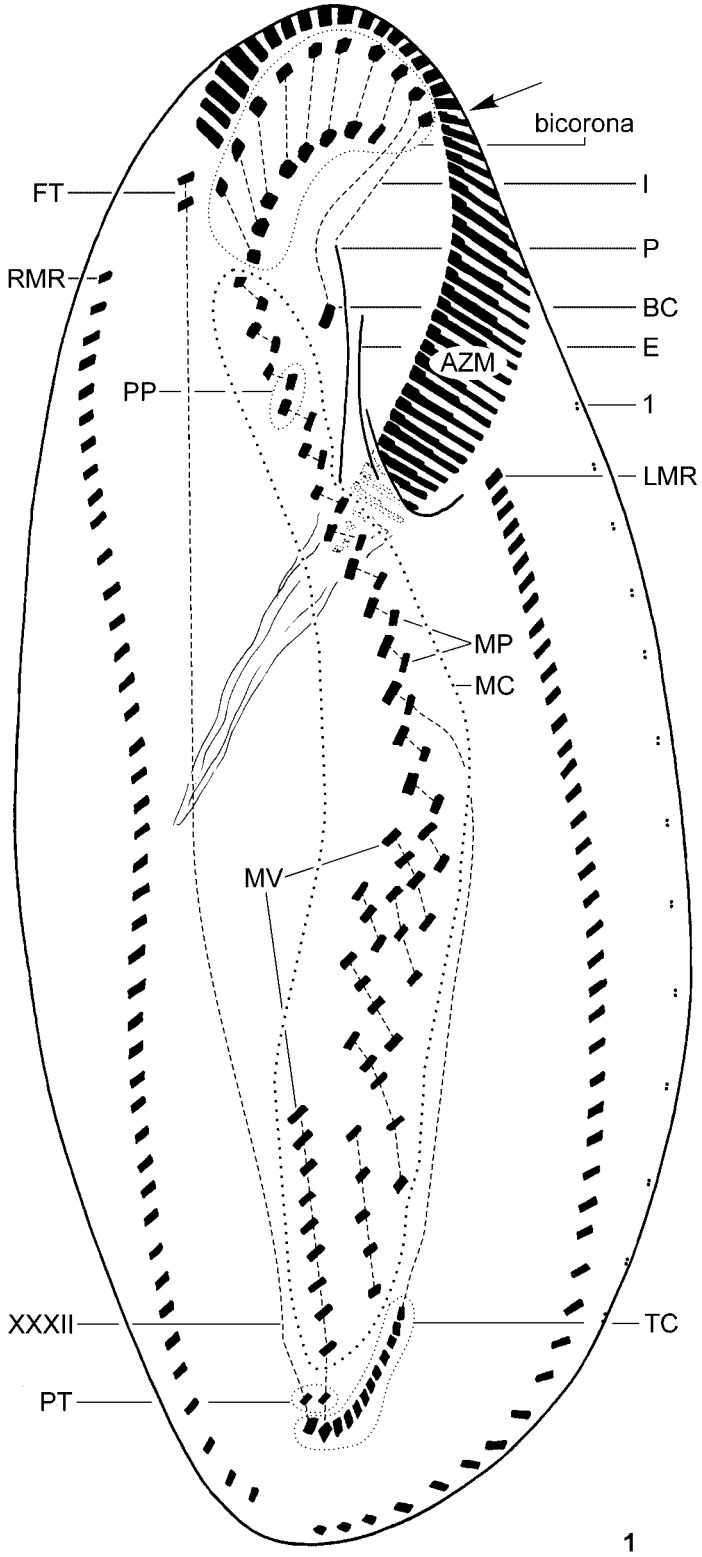
**Morphological methods.** Cells were studied in life using, inter alia, a high-power oil immersion objective and differential interference contrast optics. Live measurements were made at magnifications of 125-1250×. Although live values are more or less rough estimates, it is worth giving such data as specimens usually contract during fixation or shrink in preparations. The infraciliature was revealed with the protargol method according to protocol A in Foissner *et al.* (1999). Counts and measurements on prepared specimens were performed at a magnification of 1250×. Illustrations of live specimens are based on micrographs and freehand sketches, while those of prepared cells were made with a camera lucida. Five neotype slides (accession nos. 2004/301-305) of protargol preparations are deposited in the Oberösterreichische Landesmuseum in Linz (LI), Austria. Since the slides contain a high number of individuals only specimens illustrated have been marked by a ring. Further specimens from the neotype population are in the 5 neotype slides of *Amphisiella annulata* which are deposited in the same museum (accession nos. 2003/146-150).

The morphometric data shown in Table 1 are repeated only as needed for clarity. All observations are from specimens of raw cultures, that is, not from cloned individuals. Consequently it cannot be excluded that similar species are mixed, although this is very unlikely because specimens which deviate in at least one important character are excluded. Certainly, this can generate some bias in the data if applied to uncritically. However, I usually excluded only such individuals which have, for example, a distinctly deviating cirral pattern (very likely often injured, regenerating, or malformed specimens) or an unusually small size (very likely often degenerating or just divided specimens). The inclusion of such specimens would artificially increase variability.

Specimens of the neotype population have been sent to Prof. Martin Schlegel (Leipzig University, Germany) for molecular biology analysis. Results will be published elsewhere.

**Terminology and nomenclature.** The terminology for the supposed autapomorphy of the urostylids, the midventral cirri, is rather confusing since the term has not been used uniformly. The expression midventral cirri was introduced by Borror (1972) as follows: "Between the right and left marginal cirri in members of the Holostichidae is a double row of cirri that often is arranged in a zigzag position. The midventral cirri arise from a longitudinal series of transverse streaks in *Urostyla cristata*, ...". However, this term was not used in all subsequent papers on urostylids. For example, Buitkamp (1977) designated the two rows formed by the zigzagging cirri as ventral rows. Hemberger (1982) and Foissner (1982) basically accepted Borror's expression and designated the two rows as right and left midventral row (note, that each of these two midventral rows originates from many anlagen whereas, for example, a marginal row originates from a single anlage!). In several urostylid genera (e.g., *Bakuella*, *Keronella*) not only cirral pairs but also more or less long rows are formed by the midventral anlagen. Wiackowski (1985) summarized both the cirral pairs and the cirral rows under the term midventral cirri. By contrast, Song *et al.* (1992) confined the expression midventral row to the zigzagging arranged cirral pairs and designated the cirral rows in the posterior body portion as ventral rows. In 1994, Eigner introduced two terms for these cirral rows in the posterior body portion of some taxa, namely (i) short midventral row composed of 3-4 cirri, and (ii) long midventral row composed of more than four cirri. According to Eigner's terminology, for example, a *Bakuella* species has (i) a "midventral row" (composed of zigzagging cirral pairs), (ii) one or more "short midventral rows", and (iii) one or more "long midventral rows". Since the midventral row mentioned under (i) can also be either short or long, the terms introduced by Eigner are somewhat misleading. In addition, the left cirrus of several cirral pairs is lacking in nondividers of *Uroleptopsis citrina* further complicating the terminology (see below). To overcome these terminological problems, the various structures are designated as shown in Figs 1-4. The new generic term is "midventral complex" which can be composed of various structures. For example, in *Holosticha* species the complex consists of midventral pairs only, whereas in *Bakuella* it is composed of midventral pairs and midventral rows. In species with three enlarged frontal cirri,

**Figs 1-4.** Terminology of urostylid ciliates. **1** - infraciliature of ventral side of a species with a bicorona. Arrow marks approximate border between distal and proximal portion of adoral zone of membranelles where in some taxa, for example, *Uroleptopsis citrina*, a more or less distinct break (gap) occurs. Frontal-midventral-transverse cirri which originate from the same anlage are connected by a broken line (for the sake of clarity only the leftmost transverse cirrus and the two rightmost transverse cirri are connected with the corresponding midventral pair, respectively, midventral rows); **2** - infraciliature of ventral side of a species with three frontal cirri. Arrow marks proximal end, arrow head distal end of adoral zone of membranelles. Asterisks mark anlagen which eventually produce only a single midventral cirrus; **3** - schematic cross section showing dorsoventral flattening. **4** - infraciliature of dorsal side, nuclear apparatus, and contractile vacuole. Arrow marks proximal end of adoral zone of membranelles. AZM - adoral zone of membranelles; BC - buccal cirrus; CC - caudal cirri; CV - contractile vacuole; E - endoral; FC - frontal cirri; FT - frontoterminal cirri (= migratory cirri); LMR - left marginal row; MA - macronuclear nodule with nucleoli; MC - midventral complex; MI - micronucleus; MP - midventral pairs; MV - midventral rows; P - paroral; PP - pseudo-pair (composed of rear [= left] cirrus of an anlage and front [= right] cirrus of next anlage, that is, the cirri of a pseudo-pair do not originate from the same anlage); PT - pretransverse ventral cirri; RMR - right marginal row; TC - transverse cirri; I - first (= leftmost) frontal-midventral-transverse cirral anlage; III/2 - cirrus behind right frontal cirrus (according to Wallengren's 1900 terminology); IV - this anlage produces the first midventral pair in species with three frontal cirri; XIII - thirteenth anlage; XXXII - last (= rightmost) frontal-midventral-transverse cirral anlage (number varies among species and often within species); 1, 2, 3, ... - dorsal kineties (kinety 1 is the leftmost one).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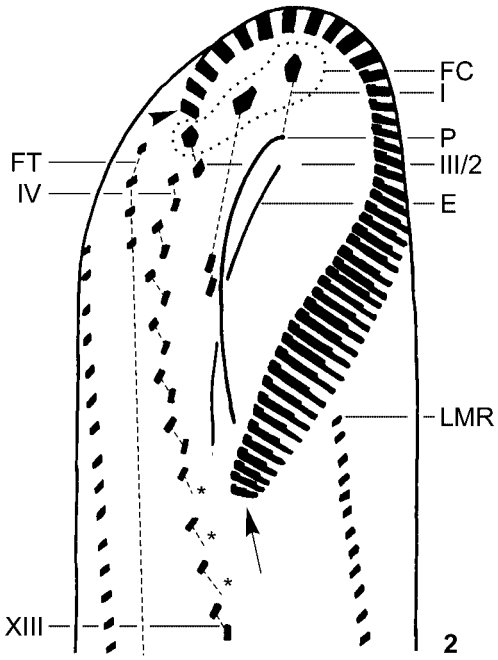
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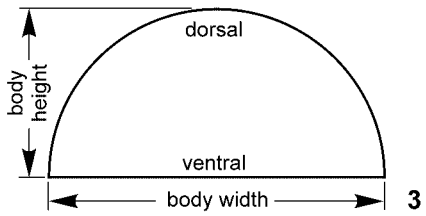
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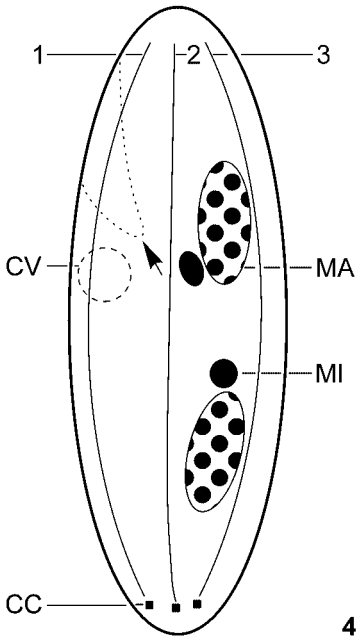
1
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the distinction between the frontal cirri and the midventral complex is straightforward (Fig. 2). In taxa with a bicorona - for example, *Keronella* and *Uroleptopsis* - it is sometimes difficult to define the beginning of the midventral complex (Fig. 1). However, usually the cirri of the anterior corona and even those of the posterior are slightly to distinctly larger than the midventral cirri and often at least slightly set off from them. The dorsoventral flattening of a hypotrich is expressed as the ratio of body width to body height (Fig. 3).

For authorship and date of scientific names, see Berger (2001). Usually, the taxa Pseudokeronopsinae and Pseudokeronopsidae discussed in the chapter on phylogenetic relationships are categorized as subfamily and family, as indicated by the defined endings -inae and -idae (for example, Borror and Wicklow 1983, Lynn and Small 2002). I do not use categories above the obligatory genus because they are useless in phylogenetic analysis (for details on this matter and the resulting conflicts with nomenclature, see Ax 1995, 1999 and Wägele 2001). However, to avoid inflation, I retain these names.

## RESULTS AND DISCUSSION

### Morphology and morphogenesis of type species

### *Uroleptopsis citrina* Kahl, 1932 (Figs 5-28, 35-42; Table 1)

1932 ***Uroleptopsis citrina*** sp. n. - Kahl, *Tierwelt Dtl.*, **25:** 543, Fig. 87 (Fig. 13; original description; no type material available).

1933 ***Uroleptopsis citrina*** Kahl 1932 - Kahl, *Tierwelt N.- u. Ostsee*, **23:** 107, Fig. 16.12 (guide to marine ciliates).

1950 ***Uroleptopsis citrina*** K. - Kudo, Protozoology, p. 672 (textbook).

1972 ***Uroleptopsis citrina*** Kahl, 1932 - Borror, *J. Protozool.*, **19:** 11 (revision).

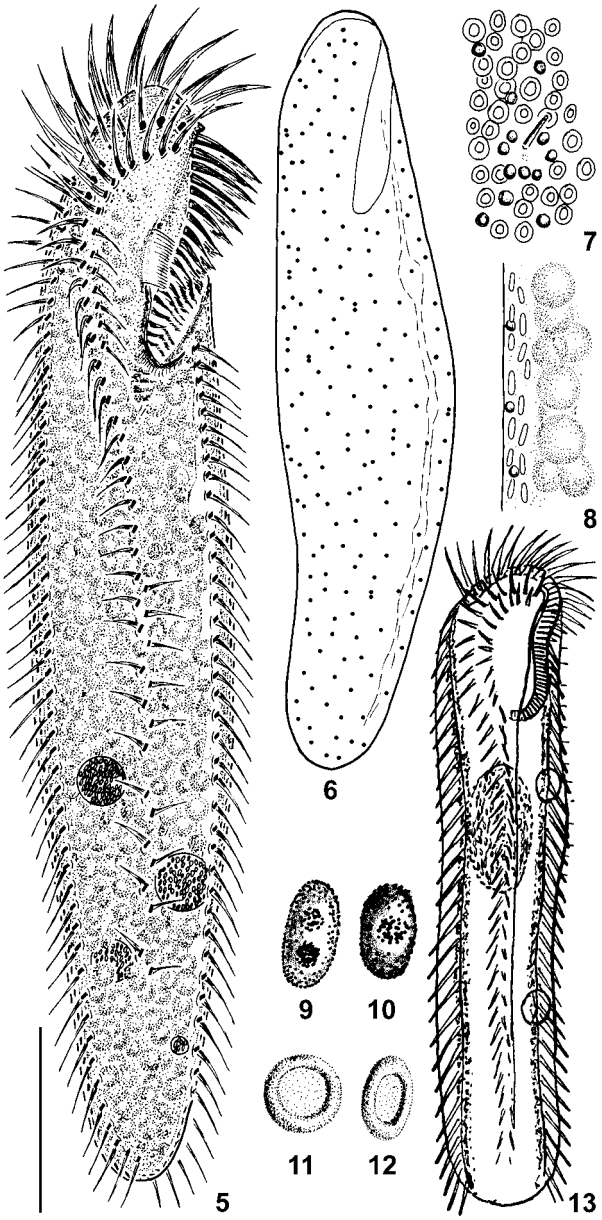
**Nomenclature:** No derivation of the name is given in the original description. The species-group name *citrina* (Latin adjective; lemon-yellow) obviously refers to the yellow colour of this species.

**Improved diagnosis** (based on original data only): Size around 200 × 40 µm in life. Body outline elongate. Cortical granules yellow, ring-shaped arranged around dorsal bristles and scattered. Underneath cell surface a 2-3 µm wide seam formed by ring-shaped structures. On average 39 adoral membranelles (29 proximal, 10 distal); each 7 cirri in anterior and posterior corona; anterior and posterior portion of midventral complex each composed of about 7 cirral pairs, middle portion composed of about 10 right cirri only; 39 left and 48 right marginal cirri. Usually 2 frontoterminal cirri and invariably 3 dorsal kineties. Marine.

**Morphology** (Figs 5-12, 14-19, 35-42; Table 1): At first data from the Adriatic population are provided. For a brief characterization of Kahl's population, see last paragraph of the morphology chapter.

Size of Adriatic population usually 160-220 × 30-50 µm, body length : width ratio about 5 : 1 in life, 3.8 : 1 on average in protargol preparations (Table 1). Body outline elongate-elliptical to almost band-shaped; at left anterior corner a minute process likely causing break in adoral zone (Figs 5, 35). Body about 1.5-2.0 : 1 flattened dorso-ventrally, very flexible, rather resistant against cover-glass pressure, not distinctly contractile. Pellicle slightly to distinctly crenulated along cirral rows. Nuclear apparatus masked by cytoplasmic inclusions, therefore very difficult to recognize in life without staining (Figs 5, 35, 38). Macronuclear nodules scattered throughout cytoplasm, usually ellipsoidal (length : width ratio about 2 : 1 on average in protargol preparations; Table 1), sometimes globular or dumbbell-shaped, with one or few nucleoli (Figs 9, 10); specimen shown in Figs 14-16 with about 100 macronuclear nodules. Micronuclei globular, difficult to distinguish from globular macronuclear nodules in protargol preparations and therefore difficult to count; number likely around five. Contractile vacuole difficult to recognize in freely motile specimens; slightly squeezed cells show distinct lacunar system with several dilatations near left body margin (Figs 5, 6). Cortical granules difficult to recognize, although of ordinary size (0.8-1.2 µm across) and yellow colour; variable number of granules ring-shaped arranged around dorsal bristles, but also scattered over whole cell (Figs 6-8, 36, 37). Yellow colour of specimens basically not caused by cortical granules but due to diffuse colour of cytoplasm. Anterior and posterior body end often more distinctly yellow than remaining body portions. Underneath cell surface a distinct, about 2-3 µm wide seam formed by numerous ring-shaped structures of unknown function; individual structures colourless, 1.5-2.0 µm across (Figs 7, 8, 11, 12, 36-38). Cytoplasm usually packed with fatty-shining globules 2-4 µm across (Figs 5, 8, 35, 38). Food vacuoles 3-10 µm across, contain bacteria. Movement without peculiarities, that is, moderately fast gliding showing great flexibility.

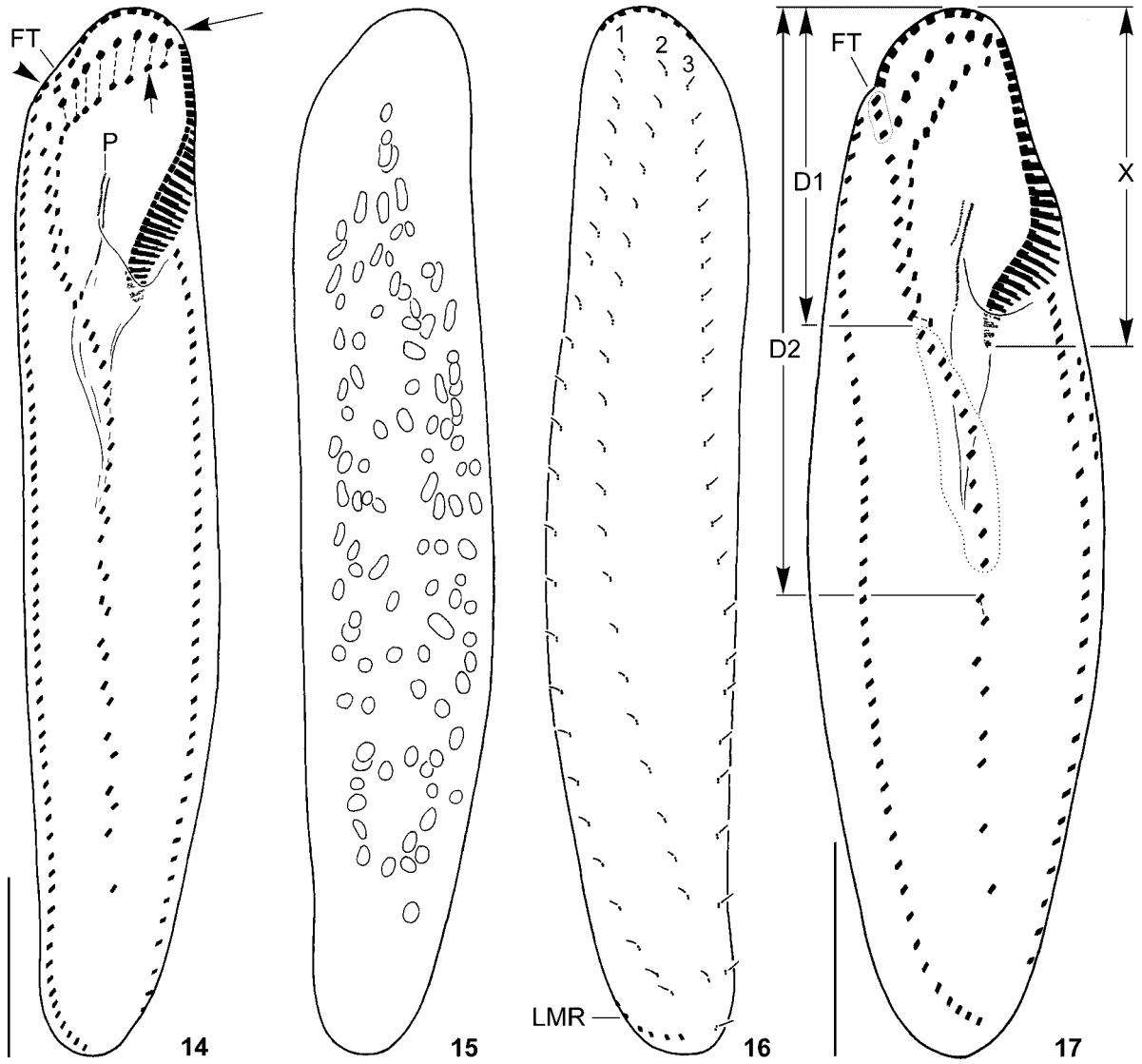
Adoral zone of membranelles occupies 30% of body length on average (Table 1), bipartite by inconspicuous break (gap) about there where zone turns from ventral body surface to dorsal side of frontal scutum (Figs 5, 14, 17-19, 39, 41). Gap usually distinct in protargol preparations, on average 3 µm wide, separates zone into about 10 distal and about 30 proximal membranelles. Proximal portion of adoral zone in most specimens roughly in




**Figs 5-13.** *Uroleptopsis citrina*. Neotype population (5-12) and Kahl's population (13) from life (5-8, 11-13) and after protargol impregnation (9, 10). **5** - ventral view of a representative specimen; **6** - ventral view of a slightly squeezed specimen showing contractile vacuole system and arrangement of cortical granules; **7** - top-view showing ring-shaped structures (1.5-2.0 µm across) and cortical granules (0.8-1.0 µm across) which form more or less distinct circles around base of dorsal bristles; **8** - 2-3 µm wide seam formed by the ring-shaped structures; **9, 10** - macronuclear nodules have few or one nucleoli; **11, 12** - the ring-shaped structures are reminiscent of the erythrocytes of mammals; **13** - ventral view (from Kahl 1932), individual size not indicated. Scale bar 30 µm.

*Gonostomum* pattern, that is, extends along left body margin, performs more or less abrupt right bend and slight clockwise rotation to plunge into the buccal cavity; four-rowed portion of middle membranelles often slightly set off which is sometimes even recognizable in life in that this right portion (or only some cilia) forms a separate ciliary bundle (Fig. 14); width of membranelles increases rapidly up to 10 µm from proximal end to level where left marginal row commences. Distal portion of adoral zone extends onto right body margin to 7% of body length on average (Table 1). In several specimens proximal portion of adoral zone sigmoidally curved (Fig. 19), almost as illustrated by Kahl (1932; Fig. 13). Buccal area very narrow in life, of ordinary size in protargol preparations possibly due to inflation of buccal cavity (Figs 5, 14, 35). Buccal lip distinctly curved and thickened at vertex (Figs 5, 41). Paroral and endoral begin about at same level, that is, at about 14% of body length (Figs 14, 41; Table 1). Paroral short (9 µm on average in protargol preparations; Table 1), straight, composed of 6-8 µm long, likely zigzagging arranged cilia, on anterior portion of buccal lip, optically not intersecting with endoral which is also more or less straight, but about twice as long as paroral. Pharyngeal fibres inconspicuous in life, clearly recognizable after protargol impregnation, of ordinary length and structure, extend obliquely backwards, with long, fine structures (cilia of endoral?) beating inside.

Cirral pattern and number of cirri of usual variability, except for number of cirral pairs in anterior and posterior portion and number of single midventral cirri in middle portion of midventral complex which vary rather strong (Figs 14, 17-19; Table 1). Cirri of bicorona 12-15 µm long, remaining cirri about 12 µm. Frontal ciliature conspicuous because of the bicorona type; anterior and posterior corona composed of each seven cirri on average due to two peculiarities, namely (i) the formation of two cirri from anlage I, and (ii) the buccal cirrus (= cirrus II/2) is formed, but does not migrate posteriorly into the ordinary position (for details, see morphogenesis). Only one out of at least 31 specimens with eight cirri in anterior and only seven cirri in posterior corona. Cirri of anterior corona slightly larger than those of posterior, base of most (all?) coronal cirri of polygonal outline. Bicorona not very distinctly set off from anteriormost cirral pair of midventral complex. No cirrus immediately right of paroral, that is, "buccal cirrus" lacking. Usually two, rarely three frontoterminal cirri in ordinary position, namely near distal end of adoral zone (Figs 14, 17-19). Midventral complex composed of 39 cirri on average; due to a morphogenetic peculiarity separated in three more or less clearly recognizable portions (Figs 14, 17-19): (i) anterior portion composed of seven midventral




**Figs 14-17.** *Uroleptopsis citrina.* Neotype population after protargol impregnation. **14-16** - infraciliature of ventral and dorsal side and nuclear apparatus of neotype specimen. Long arrow marks gap in adoral zone, short arrow marks cirrus II/2 (= "buccal cirrus") which is not right of the paroral in non-dividers. Arrowhead denotes anterior end of right marginal row. Broken lines connect cirral pairs of bicorona. **17** - infraciliature of ventral side of a specimen with 3 frontoterminal cirri. The short cirral row left of the left marginal row is likely a remnant of the parental left marginal row. Middle portion of midventral complex, which is composed of single midventral cirri, is encircled. D1 - distance between anterior body end and last midventral cirral pair of anterior portion of midventral complex; D2 - distance between anterior body end and first midventral pair of posterior portion of midventral complex; FT - frontoterminal cirri; LMR - left marginal row; P - paroral; X - length of adoral zone of membranelles; 1-3 - dorsal kineties. Scale bars 30 µm.

pairs on average; (ii) middle portion made of about 10 single cirri forming a more or less continuous (not zigzagging) row; and (iii) posterior portion composed of around seven cirral pairs whose cirri are usually wider separated than those of the anterior portion; length of these three portions highly variable. Midventral complex terminates at 84% of body length on average; rearmost cirri must not be misinterpreted as transverse cirri which are lacking (checked in many hundred specimens). Right cirri of midventral pairs usually composed of 2 × 4 basal bodies, left cirri often made of 2 × 3 basal bodies. Right marginal row commences close to frontoterminal cirri, curves leftwards to about cell midline at posterior end, and usually terminates about 4 µm ahead rear cell end. Left marginal row begins in ordinary position, that is, slightly ahead proximal end of adoral zone, extends onto

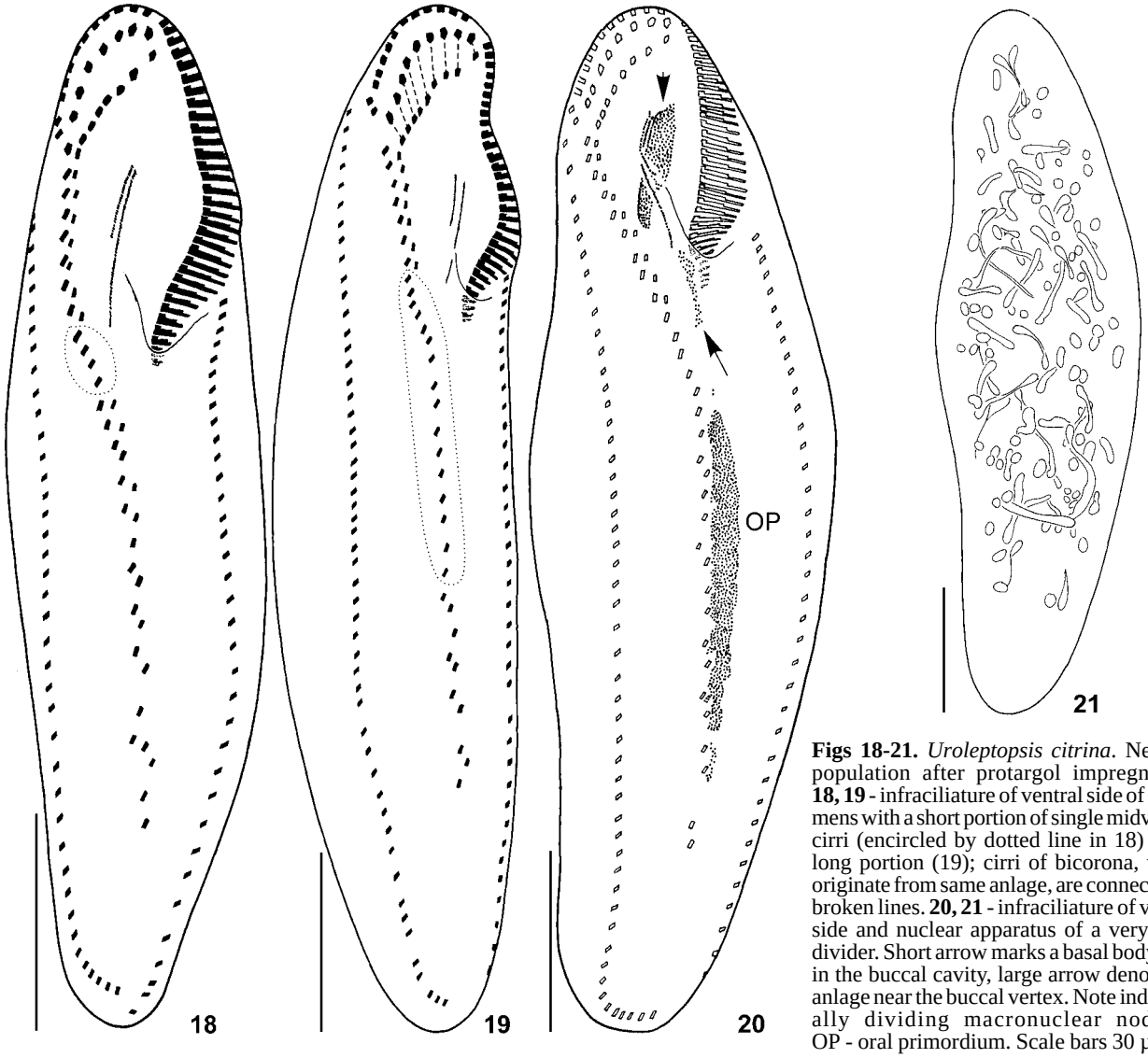
**Table 1.** Morphometric data on *Uroleptopsis citrina*[a]

| Characteristics | $\bar{x}$ | M | SD | SE | CV | Min | Max | n |
|---|---|---|---|---|---|---|---|---|
| Body, length | 155.0 | 154.0 | 19.9 | 3.6 | 12.9 | 99.0 | 188.0 | 31 |
| Body, width | 41.0 | 42.0 | 7.2 | 1.3 | 17.5 | 26.0 | 57.0 | 31 |
| Body length : width, ratio | 3.8 | 3.8 | 0.6 | 0.1 | 14.6 | 3.0 | 5.2 | 31 |
| Adoral zone of membranelles, length[b] | 46.2 | 46.0 | 5.0 | 0.9 | 10.9 | 32.0 | 54.0 | 31 |
| Adoral zone, relative length (%) | 29.9 | 29.3 | 1.9 | 0.3 | 6.5 | 27.0 | 35.0 | 31 |
| Anterior body end to distal end of adoral zone, distance | 11.3 | 11.0 | 2.6 | 0.5 | 22.8 | 5.0 | 18.0 | 31 |
| Anterior body end to rear end of gap in adoral zone, distance | 4.0 | 4.0 | 1.9 | 0.3 | 47.3 | 1.0 | 9.0 | 31 |
| Gap in adoral zone, length | 3.1 | 3.0 | 1.1 | 0.2 | 34.1 | 0.8 | 6.0 | 31 |
| Anterior body end to paroral, distance | 22.3 | 22.0 | 3.3 | 0.6 | 14.8 | 15.0 | 29.0 | 31 |
| Paroral, length | 8.9 | 9.0 | 1.6 | 0.3 | 17.7 | 6.0 | 12.0 | 31 |
| Anterior body end to first midventral cirral pair, distance | 18.4 | 18.5 | 3.3 | 0.6 | 17.9 | 11.0 | 24.0 | 30 |
| Distance 1[c] | 41.5 | 40.0 | 7.6 | 1.4 | 18.4 | 24.0 | 68.0 | 31 |
| Distance 2[c] | 72.8 | 72.0 | 17.2 | 3.1 | 23.6 | 46.0 | 112.0 | 31 |
| End of midventral complex to rear body end, distance | 25.6 | 24.0 | 6.3 | 1.1 | 24.6 | 14.0 | 38.0 | 31 |
| Anterior body end to right marginal row, distance | 14.7 | 15.0 | 3.5 | 0.6 | 23.6 | 8.0 | 21.0 | 29 |
| End of right marginal row to rear body end, distance | 4.0 | 4.0 | 1.6 | 0.3 | 40.4 | 1.0 | 6.0 | 31 |
| Anteriormost macronuclear nodule, length | 4.7 | 4.0 | 1.3 | 0.2 | 27.3 | 3.0 | 8.0 | 31 |
| Anteriormost macronuclear nodule, width | 2.4 | 2.5 | 0.5 | 0.1 | 21.7 | 1.5 | 3.0 | 31 |
| Anteriormost micronucleus, diameter | 2.5 | 2.5 | 0.3 | 0.1 | 13.1 | 1.5 | 3.0 | 28 |
| Adoral membranelles, total number | 39.4 | 39.0 | 4.0 | 0.7 | 10.2 | 29.0 | 47.0 | 31 |
| Proximal adoral membranelles, number | 29.5 | 29.0 | 2.8 | 0.5 | 9.5 | 22.0 | 35.0 | 31 |
| Distal adoral membranelles, number | 9.9 | 10.0 | 1.4 | 0.2 | 13.8 | 7.0 | 12.0 | 31 |
| Anterior corona, number of cirri | 7.5 | 7.0 | 1.2 | 0.2 | 15.2 | 6.0 | 10.0 | 31 |
| Posterior corona, number of cirri | 7.5 | 7.0 | 1.2 | 0.2 | 15.3 | 6.0 | 10.0 | 31 |
| Frontoterminal cirri, number | 2.3 | 2.0 | 0.5 | 0.1 | 20.5 | 2.0 | 3.0 | 31 |
| Midventral pairs in anterior portion of midventral complex, number | 7.1 | 7.0 | 2.0 | 0.4 | 27.6 | 4.0 | 15.0 | 31 |
| Single midventral cirri, number | 10.3 | 11.0 | 4.5 | 0.8 | 43.5 | 4.0 | 18.0 | 31 |
| Midventral pairs in posterior portion of midventral complex, number | 6.8 | 5.5 | 3.3 | 0.6 | 48.2 | 2.5 | 14.0 | 31 |
| Midventral cirri, total number | 39.2 | 38.0 | 6.4 | 1.2 | 16.4 | 26.0 | 53.0 | 31 |
| Left marginal cirri, number | 38.9 | 38.0 | 6.1 | 1.1 | 15.7 | 28.0 | 49.0 | 31 |
| Right marginal cirri, number | 47.7 | 48.0 | 6.3 | 1.1 | 13.3 | 34.0 | 63.0 | 31 |
| Dorsal kineties, number | 3.0 | 3.0 | 0.0 | 0.0 | 0.0 | 3.0 | 3.0 | 31 |
| Dorsal kinety 1, number of bristles | 25.2 | 25.0 | 4.3 | 0.8 | 16.9 | 14.0 | 32.0 | 30 |

[a] Measurements in µm. Data based on mounted, protargol-impregnated, and randomly selected specimens. CV - coefficient of variation in %, M - median, Max - maximum, Min - minimum, n - number of specimens investigated, SD - standard deviation, SE - standard error of arithmetic mean, $\bar{x}$ - arithmetic mean. [b] See Fig. 17. [c] Distance 1 and 2, see Fig. 17.

dorsolateral surface posteriorly where it ends about in midline; marginal rows thus optically more or less confluent (Figs 14, 16). Dorsal cilia 2-3 µm long in life, arranged in three bipolar kineties (Figs 16, 40; Table 1). Caudal cirri lacking.

Brief description of Kahl's population (Fig. 13): body 150-250 µm long; body length : width ratio 5-6 : 1; anteriorly flattened, very flexible, more or less acontractile. Many macronuclear nodules. Invariably a single large globular to ellipsoidal mass in cell centre, stains with methyl green; according to Kahl (1932) this is a kind of mycetom, that is, cytoplasm packed with bacteria; Kahl stated that the constancy of this feature has to be checked. Contractile vacuole near left margin at about 33% of body length, rarely visible; at about 66% obviously a second vacuole, which, however, is not contractile. Cortex packed with pale yellow oval ring-shaped protrichocysts about 1.5 µm across; smaller, solid, lemon-yellow protrichocysts (= cortical granules) near the cirral and bristle rows, form difficult-to-recognize rings around dorsal bristles; these lemon-yellow granules cause the colour of the cell. Oral apparatus occupies 16-20% of body length; adoral zone curiously shaped, narrow, turns rightwards proximally and ends in a short cytopharynx. Distinct buccal lip as well as buccal field and undulating membrane (paroral) lacking; however, sometimes the

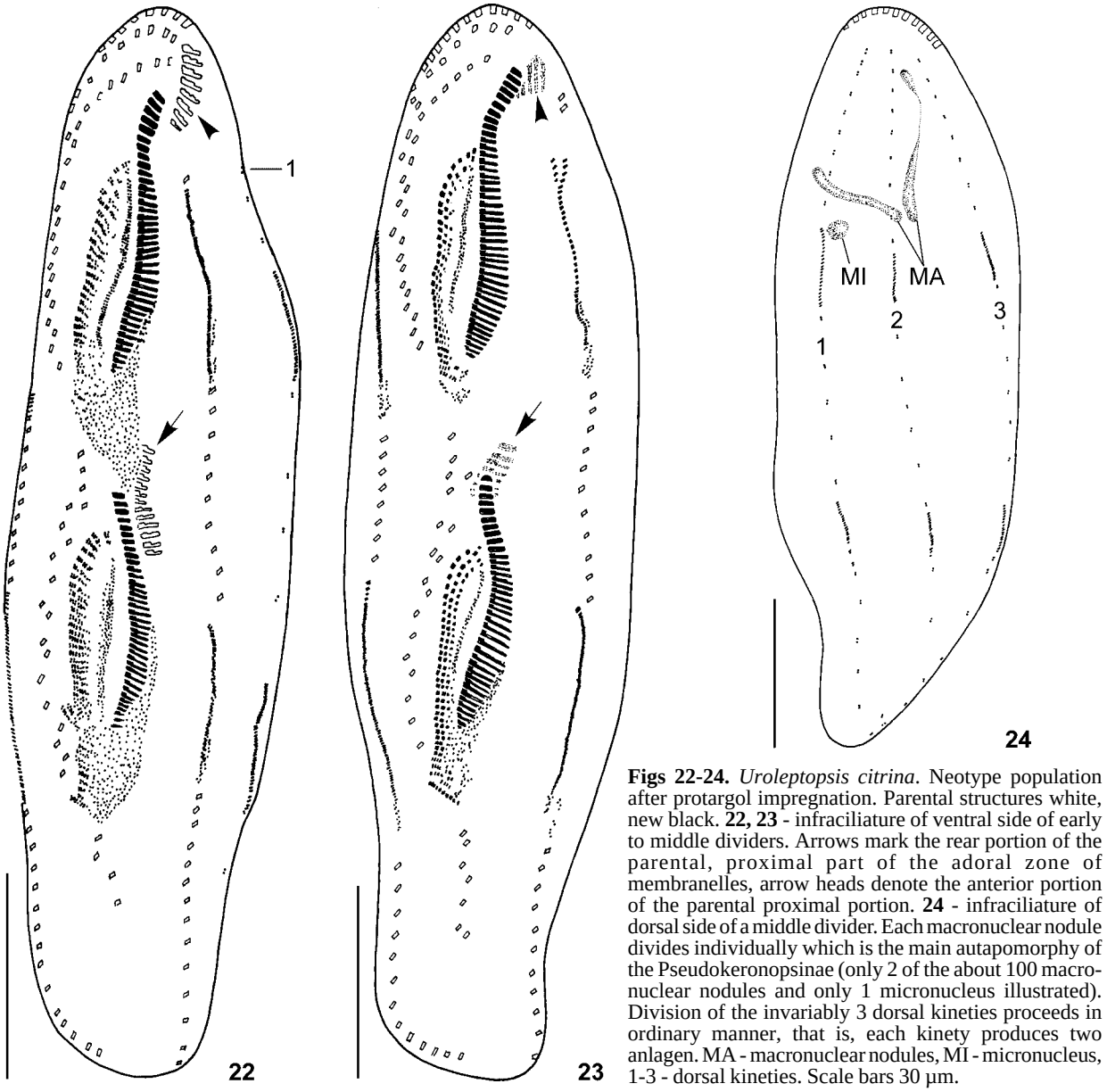



**Figs 18-21.** *Uroleptopsis citrina*. Neotype population after protargol impregnation. **18, 19** - infraciliature of ventral side of specimens with a short portion of single midventral cirri (encircled by dotted line in 18) and a long portion (19); cirri of bicorona, which originate from same anlage, are connected by broken lines. **20, 21** - infraciliature of ventral side and nuclear apparatus of a very early divider. Short arrow marks a basal body field in the buccal cavity, large arrow denotes an anlage near the buccal vertex. Note individually dividing macronuclear nodules. OP - oral primordium. Scale bars 30 µm.

oral seam extends slightly rightwards. Marginal rows separated posteriorly; left row commences near middle portion of proximal part of adoral zone. Cirri of ventral rows (= midventral complex) finer than those of bicorona, making the impression of a single row.

**Cell division** (Figs 20-28, 42): This part of the life cycle proceeds basically as in *Pseudokeronopsis* (Wirnsberger 1987) and in some details also as in *Thigmokeronopsis* (Petz 1995). Consequently I mention only relevant deviations from *Pseudokeronopsis* which is very likely the sister group of *Uroleptopsis*. A very early stage and one or two stages between those shown in Figs 20, 22 are lacking in the sequence presented (Figs 20-28).

**Stomatogenesis:** As in *Thigmokeronopsis* and *Pseudokeronopsis*, the anlage for the new adoral zone of the proter is formed left of the endoral, likely on the "roof" of the buccal cavity (Fig. 20). Distinctly later, the newly formed adoral zone with many differentiated membranelles, the undulating membranes anlage, and the many oblique frontal-midventral cirral anlagen are recognizable (Fig. 22). In this and some later stages the new adoral zone is more or less longitudinally arranged about in cell midline (Figs 22, 23). Meanwhile, the parental adoral zone is successively resorbed. In the stages shown in Figs 22, 23 the disintegrating proximal portion of the parental adoral zone is divided with one part near the anterior cell end and the second about in

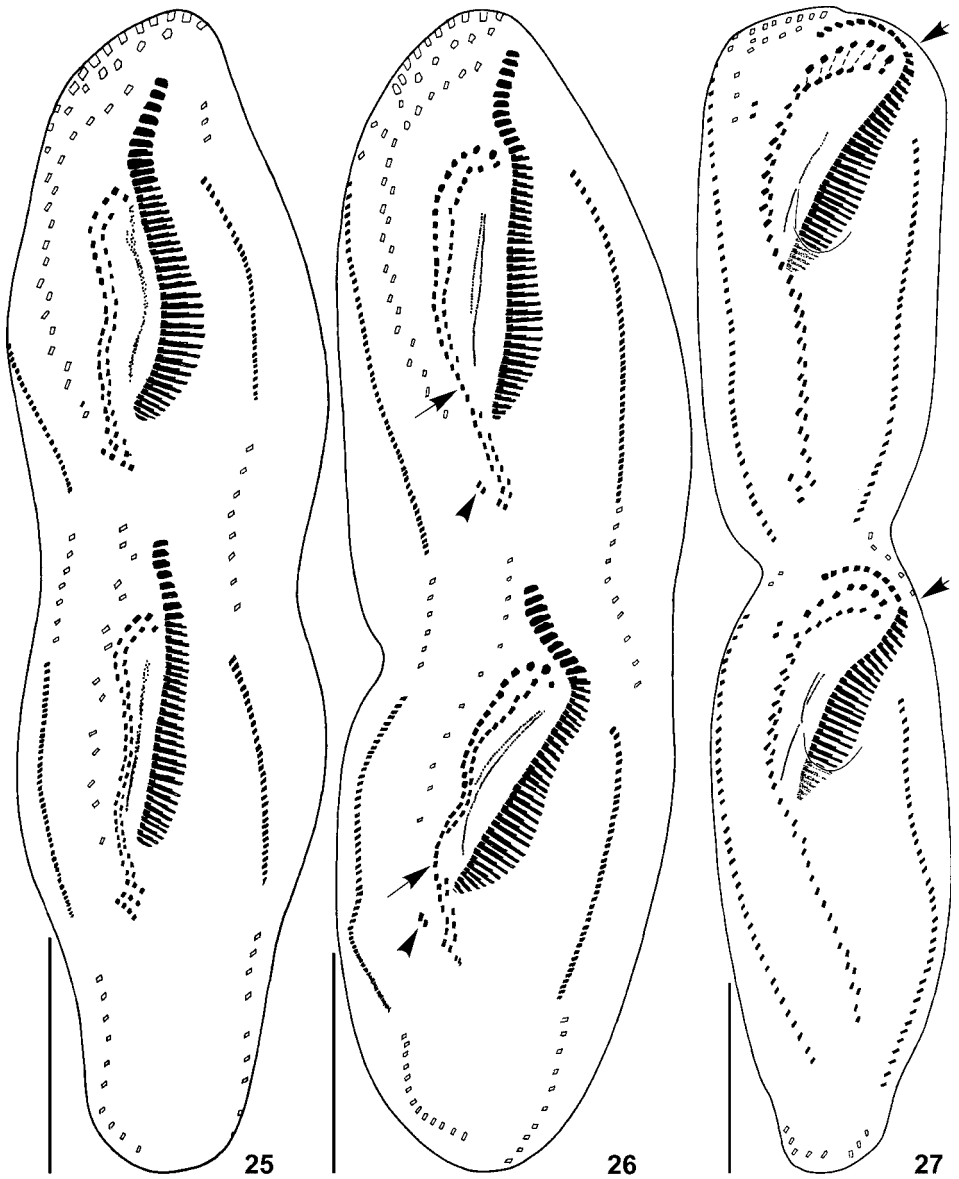



**Figs 22-24.** *Uroleptopsis citrina*. Neotype population after protargol impregnation. Parental structures white, new black. **22, 23** - infraciliature of ventral side of early to middle dividers. Arrows mark the rear portion of the parental, proximal part of the adoral zone of membranelles, arrow heads denote the anterior portion of the parental proximal portion. **24** - infraciliature of dorsal side of a middle divider. Each macronuclear nodule divides individually which is the main autapomorphy of the Pseudokeronopsinae (only 2 of the about 100 macronuclear nodules and only 1 micronucleus illustrated). Division of the invariably 3 dorsal kineties proceeds in ordinary manner, that is, each kinety produces two anlagen. MA - macronuclear nodules, MI - micronucleus, 1-3 - dorsal kineties. Scale bars 30 µm.

mid-body. The break in the new adoral zone occurs obviously rather late, that is, shortly before or after the separation of the proter and the opisthe (Fig. 27).

The oral primordium of the opisthe originates immediately left of the midventral complex about in the middle body region (Fig. 20). Obviously no parental midventral cirrus is incorporated in the formation of the primordium, which agrees with the data on *Pseudokeronopsis* and *Thigmokeronopsis*. Later, the adoral membranelles organize in a posteriad direction and the primordium for the undulating membranes splits into the endoral and paroral (Figs 22, 23, 25-27).

**Development of frontal, midventral, and frontoterminal cirri:** Since some early stages are lacking, the origin of the frontal-midventral cirral anlagen of both the proter and the opisthe remains unknown. In the stage shown in Fig. 22, almost the complete number of anlagen is clearly recognizable in both filial products. In early to middle dividers the differentiation of cirri begins (Figs 22, 23). From anlage I, which forms the undulating membranes, two cirri originate (Figs 25-27). This is an important difference to *Pseudokeronopsis* and *Thigmokeronopsis* where, as usual, only one cirrus is formed. In the stage shown in Fig. 25, the full set of




**Figs 25-27.** *Uroleptopsis citrina*, neotype population. Infraciliature of ventral side after protargol impregnation. Parental structures white, new black. **25** - middle divider. Note that all frontal-midventral cirral anlagen have produced at least two cirri, including anlagen I and II; **26** - middle to late divider. Note that in some midventral cirral anlagen the left cirrus of the pairs is resorbed (arrows). Arrowheads denote new frontoterminal cirri which start to migrate anteriorly; **27** - very late divider (dorsal side, see Fig. 28). Arrows mark site where the gap in the adoral zone is formed. Note that the number of single midventral cirri is rather different in proter (5) and opisthe (about 13). Cirri of bicorona, which originate from same anlage, are connected by broken line. Scale bars 30 µm.

frontal cirri, which form the bicorona, and midventral cirri, which form the midventral complex, is recognizable. However, a somewhat later stage shows that about in the third quarter of the midventral complex the left cirrus of each pair disappears (Fig. 26). This loss explains the curious pattern of the midventral complex of interphasic specimens (Figs 14, 17-19). More or less simultaneously the anterior two cirri of the rightmost (= posteriormost) anlage begin with the migration to near the distal end of the adoral zone where they form the frontoterminal cirri (Figs 26, 27).

**Development of marginal rows and dorsal kineties:** The new marginal rows and dorsal kineties originate in ordinary manner, that is, two primordia each develop within the parental rows and kineties (Figs 22-28). No caudal cirri are formed (Figs 16, 28).

**Nuclear apparatus:** The nuclear apparatus divides as in *Pseudokeronopsis* (for example, Wirnsberger 1987), that is, the many macronuclear nodules divide individually (Figs 21, 24). The micronuclei behave like those of other hypotrichs (Fig. 28).

**Occurrence and ecology:** *Uroleptopsis citrina* is a benthic, marine species. Kahl (1932) found it in the German city of Kiel "not rare" in an aquarium where it was sluggishly borrowing in the mesosaprobic debris. Kahl (1932) did not state from where the material in the aquarium was. However, in his guide to marine ciliates (Kahl 1933) he wrote "in alten Kieler Kulturen und Aquarien nicht selten" (= not rare in old cultures from Kiel and in aquaria) so that we can conclude that he found it (inter alia? exclusively?) in the Baltic Sea at the coast of which the city of Kiel is located.

I found *U. citrina* in the littoral of the northern Adriatic Sea at a water temperature of about 20°C (further details, see materials and methods). Due to the neotypification (see below), this sample site becomes the new type locality. It occurred, inter alia, together with *Amphisiella annulata* (see Berger 2004), *Pseudoamphisiella* sp., and some euplotids. There exist some records from the Bulgarian coast of the Black Sea which are, however, not substantiated by illustrations or morphological data (for review, see Detcheva 1992).

**Systematics:** Kahl (1932) described *U. citrina*, type of *Uroleptopsis*, rather detailed from life (Fig. 13). Subsequently it was listed in several reviews, but no additional data have been provided. Borror and Wicklow (1983) classified it as one of several junior synonyms of *Pseudokeronopsis rubra* which is hardly comprehensible because *U. citrina* is yellow, has no buccal cirrus right of the paroral, lacks transverse cirri, and has invariably three dorsal kineties; in contrast, *Pseudokeronopsis rubra* is red, has an ordinary buccal cirrus and distinct transverse cirri, and usually six dorsal kineties (Wirnsberger *et al.* 1987).

The population from the northern Adriatic Sea very closely resembles the type population from the Baltic. They agree in the following features: (i) marine habitat; (ii) size; (iii) nuclear apparatus; (iv) contractile vacuoles; (v) yellow cortical granules and ring-shaped structures underneath cell surface; (vi) narrow buccal field; (vii) bicorona and long midventral complex basically composed of cirral pairs (the lack of some left cirri in the middle region of the midventral complex is very difficult to recognize without silver impregnation and was therefore possibly overlooked by Kahl although he even wrote that the two ventral rows nearly make the impression of a single row); (viii) lack of a buccal cirrus in ordinary position; (ix) lack of transverse cirri; (x) three dorsal kineties.

Differences concern (i) the oral apparatus; (ii) a so-called "Mycetom" (a plasma-region containing many bacteria) described by Kahl (1932); (iii) the distance between the rear end of the marginal rows; (iv) the body shape; and (v) the colour. The gap in the adoral zone of the Adriatic population is clearly recognisable only in protargol preparations; thus, it is unknown whether or not this feature was present in Kahl's population who did not have the advantage of silver impregnation. Further, Kahl did not see a buccal field and a paroral. The buccal field is obviously very narrow in Kahl's population and therefore one can also say that it is lacking. The lack of the paroral in his specimens is much more difficult to explain because he described this structure in many other hypotrichs; possibly he overlooked it because it is indeed rather inconspicuous. The mycetom was obviously present in all specimens studied by Kahl; however, he wrote that the constancy of this feature has to be checked. Possibly it was a kind of parasitism. In the specimens of Kahl's population the marginal rows are distinctly separated posteriorly (Fig. 13). In contrast, they optically almost overlap in the specimens from the Adriatic Sea (Figs 14, 16, 18). Since this feature is difficult to recognize in life it must not be over-interpreted. Kahl's specimen is more or less band-shaped whereas the specimens from the Adriatic Sea are usually elongate elliptical in outline. Possibly, Kahl's specimens did not have their natural outline due to the mycetom (see above) whose effect on the cell is not known. According to Kahl, the yellow colour of *U. citrina* is due to the yellow cortical granules. However, in my population the number of these granules is usually too low to cause such a distinct colour. In contrast, the yellow colour of the Adriatic population is mainly caused by a diffuse colour of the cytoplasm which is often very distinct in the marginal areas.

**Neotypification:** No type or voucher slides are available from any *U. citrina* population. As mentioned above, Borror and Wicklow (1983) have synonymized it with *Pseudokeronopsis rubra*, a proposal which is certainly incorrect (see also chapter History of *Uroleptopsis*). To avoid such a misclassification in future it seems wise to define *U. citrina* objectively by the designation of a neotype (ICZN 1999, Foissner 2002). The neotypification of *P. rubra* was already done

by Wirnsberger *et al.* (1987). According to Article 75.3 of the ICZN (1999), the designation of a neotype is only valid when seven particulars are published: (i) as mentioned above, the systematic status of *U. citrina* is somewhat unclear because it was synonymized with the rather common *Pseudokeronopsis rubra* in the last revision on urostylids (Borror and Wicklow 1983). (ii) for a differentiation of *U. citrina* from related taxa, see next chapter. (iii) the neotype specimen (Figs 14-16), respectively, neotype population from the Adriatic Sea is described in detail (see above); thus, recognition of the neotype designated is ensured. (iv) it is generally known that no type material is available from species described by Kahl. Further, there is no indication that Detcheva, who recorded it from the Black Sea, made permanent preparations, let alone designated a neotype. (v) there is strong evidence that the neotype is consistent with *U. citrina* as originally described by Kahl (1932). For a detailed comparison, see previous chapter. The differences discussed must not be over-interpreted and are possibly due to some minor misobservations by Kahl (1932). Further, it cannot be excluded that Kahl's specimen were slightly influenced by the so-called mycetom, which was possibly a kind of parasitism. (vi) unfortunately, the neotype does not come from very near the original type locality (northern Adriatic Sea against Baltic Sea near the German city of Kiel; distance about 1000 km). However, both sites are marine habitats from the Holarctic region. As generally known, many ciliates - especially marine ones which live in a comparatively homogenous medium - are cosmopolitans (Patterson *et al.* 1989) so that this point should not be over-interpreted. For a more detailed discussion of this problem, see Foissner *et al.* (2002, p. 44) and Foissner (2002). A detailed description of the new type locality, that is, the sample site of the neotype population, is given in the chapter materials and methods. (vii) the slide containing the neotype specimen and nine slides containing some further specimens, including those depicted in the present paper, of the neotype population are deposited in the Biologiezentrum des Oberösterreichischen Landesmuseums in Linz (LI), Austria.

**Comparison with similar species:** For a separation of *U. citrina* from the other *Uroleptopsis* species, see the key below. According to Kahl (1932) and my experience, *Uroleptopsis citrina* is very easily confused with *Pseudokeronopsis flava* which is also yellow. However, this species has usually two transverse cirri, four dorsal kineties, one buccal cirrus in ordinary position, and lacks a break in the adoral zone (Wirnsberger *et al.* 1987). Protargol impregnation is therefore recommended to check these features.

## Redefinition of *Uroleptopsis* Kahl, 1932

1932 ***Uroleptopsis*** gen. n. - Kahl, *Tierwelt Dtl*., **25:** 543 (original description). Type species (by original designation on p. 543): *Uroleptopsis citrina* Kahl, 1932.

1933 ***Uroleptopsis*** Kahl 1932 - Kahl, *Tierwelt N.- u. Ostsee*, **23:** 107 (guide to marine ciliates).

1950 ***Uroleptopsis*** Kahl - Kudo, Protozoology, p. 672 (textbook).

1972 ***Uroleptopsis*** Kahl, 1932 - Borror, *J. Protozool*., **19:** 11 (revision).

1974b ***Uroleptopsis*** Kahl - Stiller, *Fauna Hung.*, **115:** 62 (revision).

1982 ***Uroleptopsis*** Kahl, 1932 - Hemberger, Dissertation, p. 120 (revision).

1992 ***Uroleptopsis*** Kahl, 1930-5 - Carey, Marine interstitial ciliates, p. 187 (guide).

**Redefinition:** Basing on the new data on the type species and the data on *U. ignea* (Mihailowitsch and Wilbert 1990; see below), *Uroleptopsis* can be redefined by the combination of the following three autapomorphies (A) and several more or less young plesiomorphies: gap in adoral zone (A). Transverse cirri absent (A). Frontal-midventral cirral anlage I forms two cirri (A). Two arched rows (= bicorona) of frontal cirri. Buccal cirrus in ordinary position, that is, right of paroral. 2 or more frontoterminal cirri. Midventral complex basically composed of midventral pairs. 1 left and 1 right marginal row. Caudal cirri absent. Many macronuclear nodules which divide individually. Parental adoral zone completely replaced during morphogenesis, that is, proter gets totally new adoral zone. Living in saline waters.

For a discussion of the autapomorphies, see chapter phylogenetic relationships. Possibly this ground plan has to be changed when new data on the other *Uroleptopsis* species became available.

**Nomenclature:** No derivation of the genus-group name is given in the original description. *Uroleptopsis* is likely a composite of the name of the hypotrich genus *Uroleptus* and the Greek suffix *-opsis* (looking like). Probably, the name should indicate the resemblance of *Uroleptus* and *Uroleptopsis* species. Feminine gender because ending with *-opsis* (ICZN 1999, Article 30.1.2). *Uroleptosis* in Borror and Wicklow (1983, p. 123) is an incorrect subsequent spelling.

**History of *Uroleptopsis*:** Kahl (1932) established *Uroleptopsis* because the lack of transverse cirri in some species prevailed their classification in *Holosticha* (*Keronopsis*) (nowadays most species of this subgenus are classified in *Pseudokeronopsis*). Kahl described

one new species, the type *U. citrina*, and transferred two species to *Uroleptopsis*, namely *Oxytricha viridis* and *Uroleptus roscovianus*. *Uroleptopsis* was accepted - beside the workers listed in the synonymy - for example, by Corliss (1977, 1979), Tuffrau (1979, 1987), and Tuffrau and Fleury (1994). By contrast, Borror (1979) has put it - together with *Trichototaxis* - into the synonymy of *Keronopsis* (*sensu lato*). Later, he synonymized it with *Pseudokeronopsis* because he classified the type species *U. citrina* as junior synonym of *P. rubra*, the type species of *Pseudokeronopsis* (Borror and Wicklow 1983). Borror argued - however, without convincing evidence - that some *P. rubra* populations also lack transverse cirri so that the presence or absence of these cirri cannot be used to define groups. I suggest that he mixed, certainly erroneously, species with and without transverse cirri. In addition, Borror and Wicklow (1983) obviously overlooked that due to this synonymy *Pseudokeronopsis* Borror and Wicklow, 1983 would become invalid, or better its establishment would have been superfluous because it would be the junior synonym of *Uroleptopsis* Kahl, 1932.

In 1990, Mihailowitsch and Wilbert described *Pseudokeronopsis ignea* which lacks transverse cirri. Thus, Foissner (1995) transferred this species to *Uroleptopsis*. However, this resurrection of Kahl's genus by Foissner was not accepted by Eigner (2001) who distinguished two patterns of transverse cirri formation. According to Eigner, *Pseudokeronopsis ignea* has transverse cirri (Figs 29, 30). However, his interpretation of the morphogenetic data of *P. ignea* is not comprehensible for me. I agree with Mihailowitsch and Wilbert (1990) and Foissner (1995) that this species does not have transverse cirri as defined usually. Thus I accept the decision of Foissner to exclude Mihailowitsch and Wilbert's species from *Pseudokeronopsis* and to put it into *Uroleptopsis*.

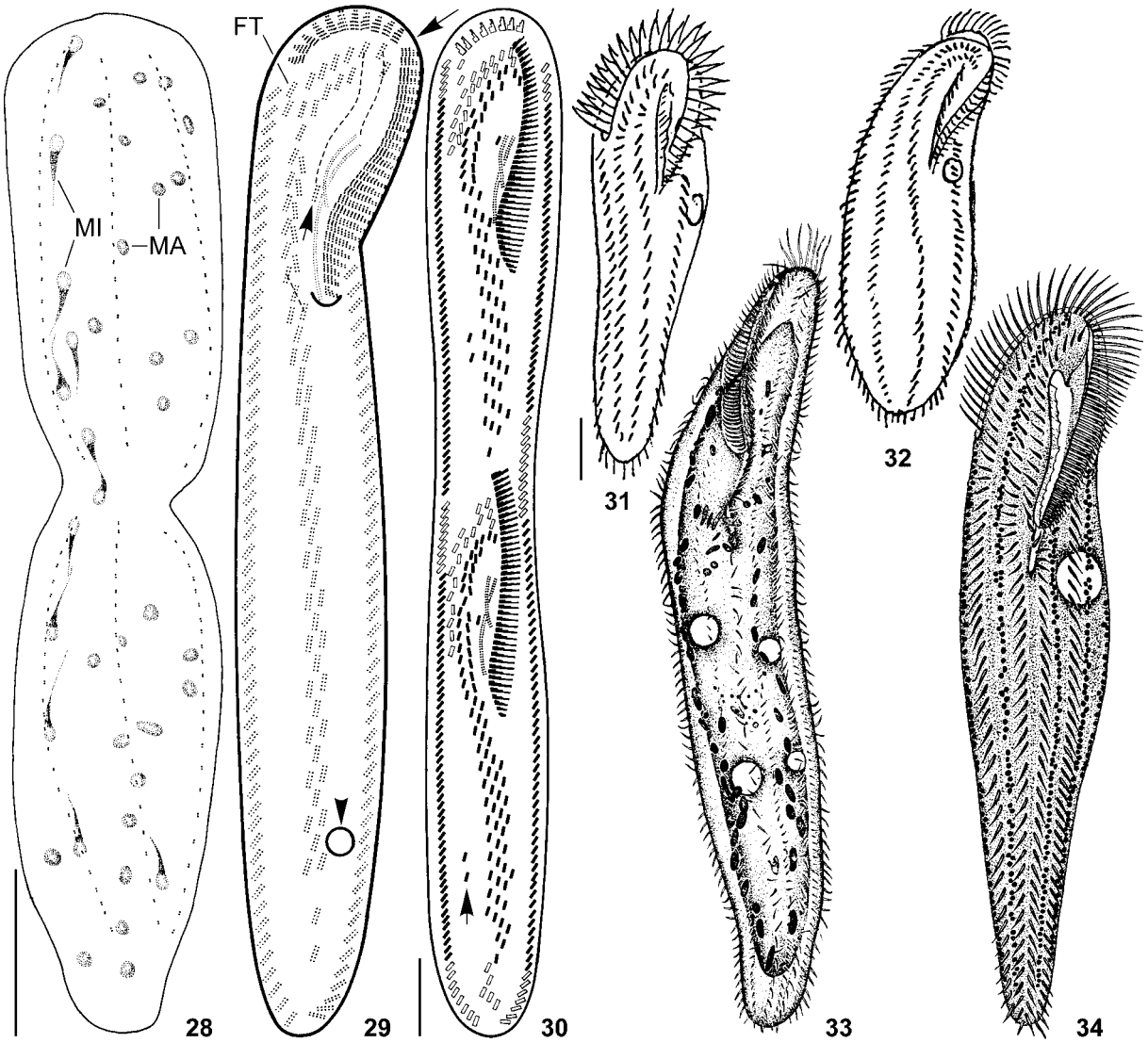
The presence or absence of distinct cirral groups is widely used to establish genera or subgenera. Examples are *Tachysoma* (caudal cirri absent against present in many 18-cirri oxytrichids; for review, see Berger 1999) and *Australothrix* (transverse cirri lacking against present in many urostylids; Blatterer and Foissner 1988). Consequently it seems logically to accept *Uroleptopsis*, inasmuch as it shows - beside the lack of transverse cirri - two further apomorphies, namely (i) two frontal cirri originating from the frontal-midventral anlage I against single cirrus in almost all other hypotrichs, and (ii) a gap in the adoral zone of membranelles. *Uroleptopsis* is therefore as well defined as many other genera of hypotrichs and should not be synonymized with *Pseudokeronopsis*.

**Species included in *Uroleptopsis*:** (i) *Uroleptopsis citrina* Kahl, 1932 (Figs 5-28, 35-42); (ii) *U. roscoviana* (Maupas, 1883) Kahl, 1932 (Fig. 31); (iii) *U. viridis* (Pereyaslawzewa, 1886) Kahl, 1932 (Fig. 32); (iv) *U. tannaensis* (Shigematsu, 1953) comb. nov. (Fig. 33); (v) *U. ignea* (Mihailowitsch and Wilbert, 1990) Foissner, 1995 (Figs 29, 30).

As already mentioned in the history section, Kahl (1932) transferred *Oxytricha viridis* and *Uroleptus roscovianus* to *Uroleptopsis*. Both species, which need detailed redescription, have a more or less distinct bicorona and lack transverse cirri and a buccal cirrus which is in the ordinary position. Thus Kahl's combinations can be accepted. *Holosticha* (*Keronopsis*) *multiplex* Ozaki and Yagiu, 1943 is very similar to *Uroleptopsis roscoviana* in shape, colour, and cirral pattern (Figs 31, 34). Although *H. multiplex* is smaller (body length 70-160 µm against 190-220 µm) I suppose that they are synonymous. Ozaki and Yagiu described their species in the subgenus *Keronopsis* without mentioning the corresponding genus. I suspect that they used Kahl's (1932) system where *Keronopsis* is classified as subgenus of *Holosticha*.

*Keronopsis tannaensis* is described after Haidenhain's haematoxylin preparations (Fig. 33). Shigematsu (1953) stated that this species lacks transverse cirri. A bicorona is neither mentioned nor clearly illustrated. However, the original classification in *Keronopsis* implies that the frontal cirral pattern must be more or less of the bicorona type. Jankowski (1979) transferred it to *Holosticha*. However, this genus has, inter alia, three enlarged frontal cirri and distinct transverse cirri. Borror and Wicklow (1983) synonymized *K. tannaensis* with *Pseudokeronopsis decolor* which has - like its congeners - transverse cirri. All combinations proposed so far would make these taxa (*Keronopsis*, *Holosticha*, *Pseudokeronopsis*) in-homogenous. I transfer it to *Uroleptopsis* because this results in the lowest number of contradictions: *Uroleptopsis tannaensis* (Shigematsu, 1953) comb. nov. (basionym: *Keronopsis tannaensis* Shigematsu, 1953). Detailed redescription needed.

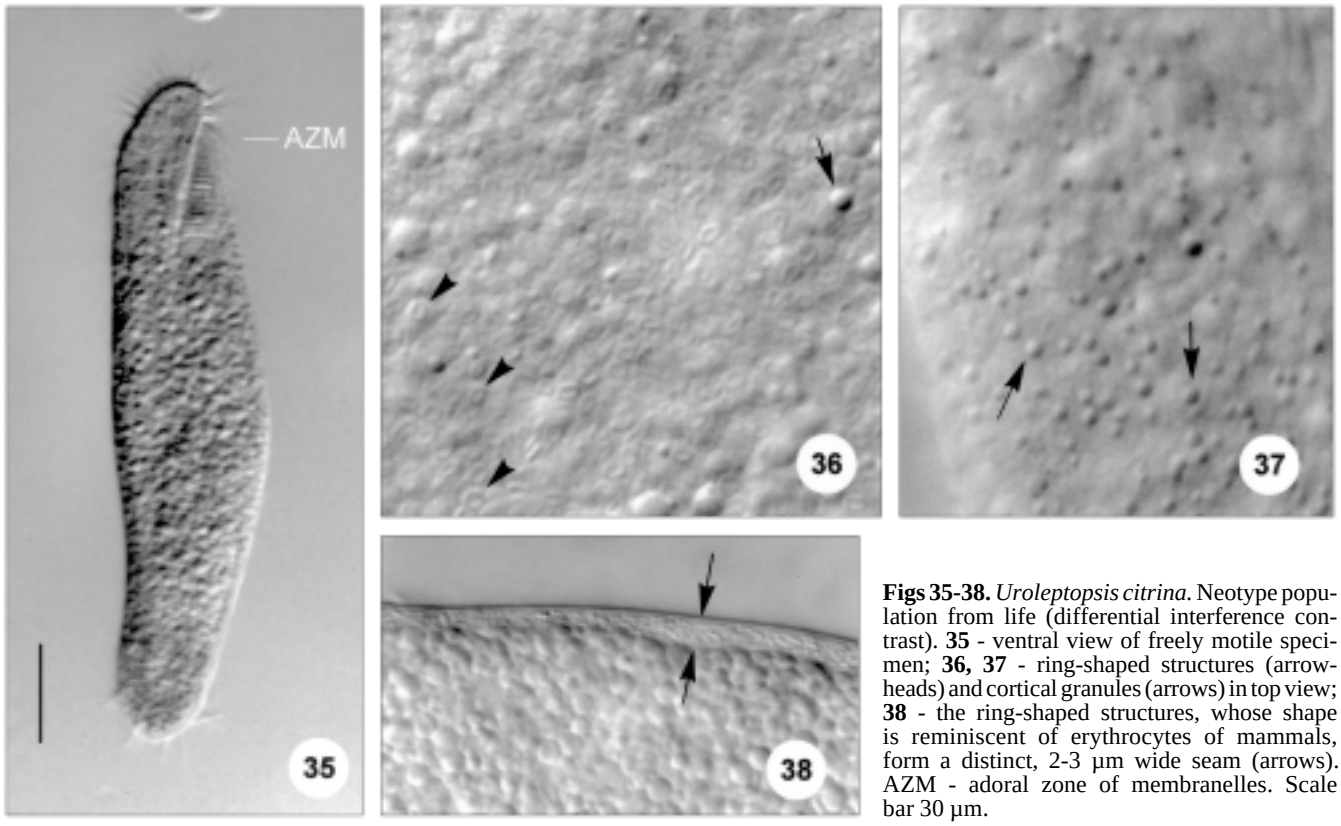
Mihailowitsch and Wilbert (1990) recognised the main features of *Pseudokeronopsis ignea* which separate it from other *Pseudokeronopsis* species, namely the presence of midventral rows and the lack of transverse cirri. They argued that these characters could be used to establish a genus. However, they refrained from this act




**Figs 28-34.** *Uroleptopsis citrina* (28, neotype population) and other *Uroleptopsis* species (29-34) after protargol impregnation (28-30), from life (31, 32, 34), and Haidenhain's haematoxylin preparation (33). **28** - infraciliature of dorsal side and nuclear apparatus of a late divider (ventral side of same specimen, see Fig. 27); **29, 30** - *Uroleptopsis ignea* (from Mihailowitsch and Wilbert 1990), infraciliature of ventral side of a morphostatic specimen (body length 405 µm according to scale bar; 262-353 µm according to their Tabele 6) and a late divider (parental structures white, new black). Long arrow in (29) marks gap in adoral zone, short arrow marks buccal cirrus; arrowhead denotes contractile vacuole. Broken lines connect cirri of anlagen I, which also forms 2 cirri, and II. Arrow in (30) marks new frontoterminal cirri of opisthe. Note that the major portion of the midventral complex is composed of midventral rows each made of usually 3 cirri (anteriormost row marked by broken line). **31** - *Uroleptopsis roscoviana* (after Maupas 1883 from Kahl 1932), ventral view; **32** - *Uroleptopsis viridis* (after Pereyaslawzewa 1886 from Kahl 1932), ventral view, size not indicated. **33** - *Uroleptopsis tannaensis* (from Shigematsu 1953), dorsal view showing nuclear apparatus, contractile vacuoles, cirral pattern and dorsal kineties, and adoral zone of membranelles (individual size not indicated). Shigematsu wrote "ventral view" explaining that he did not distinguish between the infraciliature of the ventral and dorsal side; **34** - *Keronopsis multiplex* (from Ozaki and Yagiu 1943), ventral view, 70-160 µm. I suppose that this is a synonym of *U. roscoviana*. FT - frontoterminal cirri; MA - macronuclear nodules; MI - dividing micronuclei. Scale bars 30 µm.

because Borror and Wicklow (1983) stated a high variability of the feature transverse cirri in many urostylid genera. Foissner (1995) discussed Borror and Wicklow's (1983) decision to reject *Uroleptopsis*. He resurrected Kahl's genus and simultaneously transferred *P. ignea* to *Uroleptopsis*. As already mentioned, Eigner (2001) did not accept the resurrection.

**Species misplaced in *Uroleptopsis*:** Three further species have been assigned to *Uroleptopsis*. However, as discussed below, they do not fit into the ground plan




**Figs 35-38.** *Uroleptopsis citrina.* Neotype population from life (differential interference contrast). **35** - ventral view of freely motile specimen; **36, 37** - ring-shaped structures (arrowheads) and cortical granules (arrows) in top view; **38** - the ring-shaped structures, whose shape is reminiscent of erythrocytes of mammals, form a distinct, 2-3 µm wide seam (arrows). AZM - adoral zone of membranelles. Scale bar 30 µm.

of *Uroleptopsis* and therefore belong elsewhere. *Uroleptopsis multiseta* Dragesco, 1970 has around seven cirral rows. They are longitudinally arranged and widely spaced and therefore do not form a midventral pattern. Dragesco (1970) himself suggested that this species possibly belongs to a new genus, *Plesiotricha*; however, he did not formally transfer it to his own genus. Later, he classified it in *Kahliella* (Dragesco and Dragesco-Kernéis 1986). Due to this act it became a secondary homonym of *Kahliella multiseta* Dragesco, 1970 and therefore the species-group name of *U. multiseta* had to be replaced: *Kahliella microstoma* Dragesco and Dragesco-Kernéis, 1986. For a more detailed discussion of this nomenclatural problem, see Foissner (1987a).

Borror (1972) transferred *Paraholosticha ovata* to *Uroleptopsis*. Stiller (1974a) obviously overlooked this act because she transferred it to *Uroleptopsis* too. This species has, inter alia, only two macronuclear nodules, lacks a distinct midventral complex, and lives in freshwater. All these features strongly indicate that it does not belong to *Uroleptopsis*. Probably it is a junior synonym of *Paraholosticha muscicola* (Berger 2001).

A further species transferred to *Uroleptopsis* is *Uroleptus kahli* Grolière, 1975 because Jankowski (1979) mentioned "*Uroleptopsis kahli*, ibidem" under the heading *Perisincirra* Yankowskij, 1978 for which Grolière's species is the type. I do not understand the word *ibidem* ("the same reference" or "in the same place") in this context because neither Grolière (1975) nor Yankowskij (1978) mentioned a combination of *Uroleptus kahli* with *Uroleptopsis*. I therefore assume that Jankowski (1979) made the combination with *Uroleptopsis*, possibly par lapsus. Anyhow, the classification of Grolière's species in *Uroleptopsis* is incorrect because recently we found that *Perisincirra* is a valid group (Foissner *et al.* 2002).

**Comparison of *Uroleptopsis citrina* and *U. ignea*:** *Uroleptopsis citrina* and *U. ignea* are the sole *Uroleptopsis* species whose morphology and morphogenesis are described by modern methods. Thus they can be compared thoroughly. They share the following synapomorphies: lack of transverse cirri, two frontal cirri originate from anlage I, gap in adoral zone. The following two conspicuous differences exist: (i) the type species lacks a buccal cirrus in the ordinary position, that is, right

of the paroral (present in *U. ignea*), and (ii) the pattern of the midventral complex. In *U. citrina* the middle portion of the midventral complex is composed of the right cirri of the cirral pairs only (Fig. 14); the anterior and posterior portion consist of ordinary midventral pairs although, very rarely, short midventral rows occur at the end of the complex. In contrast, the anterior portion of the midventral complex of *U. ignea* is composed of midventral pairs, while the middle and posterior portion consist of midventral rows (Figs 29, 30). A more detailed analysis of the first difference shows that the buccal cirrus is not lacking in *U. citrina*, but it does not migrate posteriorly into the ordinary position; it is - in contrast to *U. ignea* - part of the bicorona even in non-dividers. This difference is of course very conspicuous and sufficient to establish a new subgenus or even genus. As mentioned above, all other species assigned to *Uroleptopsis* are not described by modern methods. However, the data available indicate that they lack a buccal cirrus in the ordinary position, that is, they are obviously more similar to *U. citrina* than to *U. ignea*. Thus, I establish a new subgenus for *U. ignea* (see below). A subgenus has the advantage that the binomen including the authorship of the species does not change again.

Interestingly, the species now assigned to *Uroleptopsis* (*Uroleptopsis*) are from marine habitats, whereas *U. ignea* - the sole species belonging to the other subgenus - was discovered in an inland saltwater. Further studies will show whether this ecological separation is confirmed or not.

### *Uroleptopsis* (*Uroleptopsis*) Kahl, 1932 stat. n.

1932 ***Uroleptopsis*** gen. n. - Kahl, *Tierwelt Dtl.*, **25:** 543 (original description). Type species (by original designation on p. 543): *Uroleptopsis citrina* Kahl, 1932.

**Diagnosis:** *Uroleptopsis* with cirrus II/2 (= buccal cirrus) not in ordinary position right of paroral, but in line with cirri of posterior corona.

**Nomenclature:** For genus-group names the principle of co-ordination applies. Thus, a name established for a taxon at either rank in the genus-group is deemed to have been simultaneously established by the same author for a nominal taxon at the other rank in the group; both nominal taxa have the same type species (ICZN 1999, Article 43.1). Consequently, Kahl (1932) is the author and *U. citrina* Kahl, 1932 the type species of the present subgenus, which is also termed the nominotypical subgenus (ICZN 1999, Article 44.1).

**Remarks:** At least in the type species, cirrus II/2 (= buccal cirrus) is formed during cell division and present in interphasic specimens; however, it does not migrate posteriorly in the ordinary position immediately right of the paroral (Figs 14, 27). *Uroleptopsis citrina* has a further highly interesting feature, namely the lack of the left cirrus in some cirral pairs of the middle region of the midventral complex. Unfortunately, we do not know whether or not this character is also present in the other species assigned to *U.* (*Uroleptopsis*). Thus, this feature - which could be a second autapomorphy for *U. (Uroleptopsis)* - is not included in the characterization.

**Species included:** *Uroleptopsis* (*Uroleptopsis*) *citrina* Kahl, 1932; *U.* (*Uroleptopsis*) *viridis* (Pereyaslawzewa, 1886) Kahl, 1932; *U.* (*Uroleptopsis*) *roscoviana* (Maupas, 1883) Kahl, 1932; *U.* (*Uroleptopsis*) *tannaensis* (Shigematsu, 1953) comb. nov. (foundation of new combination, see above).

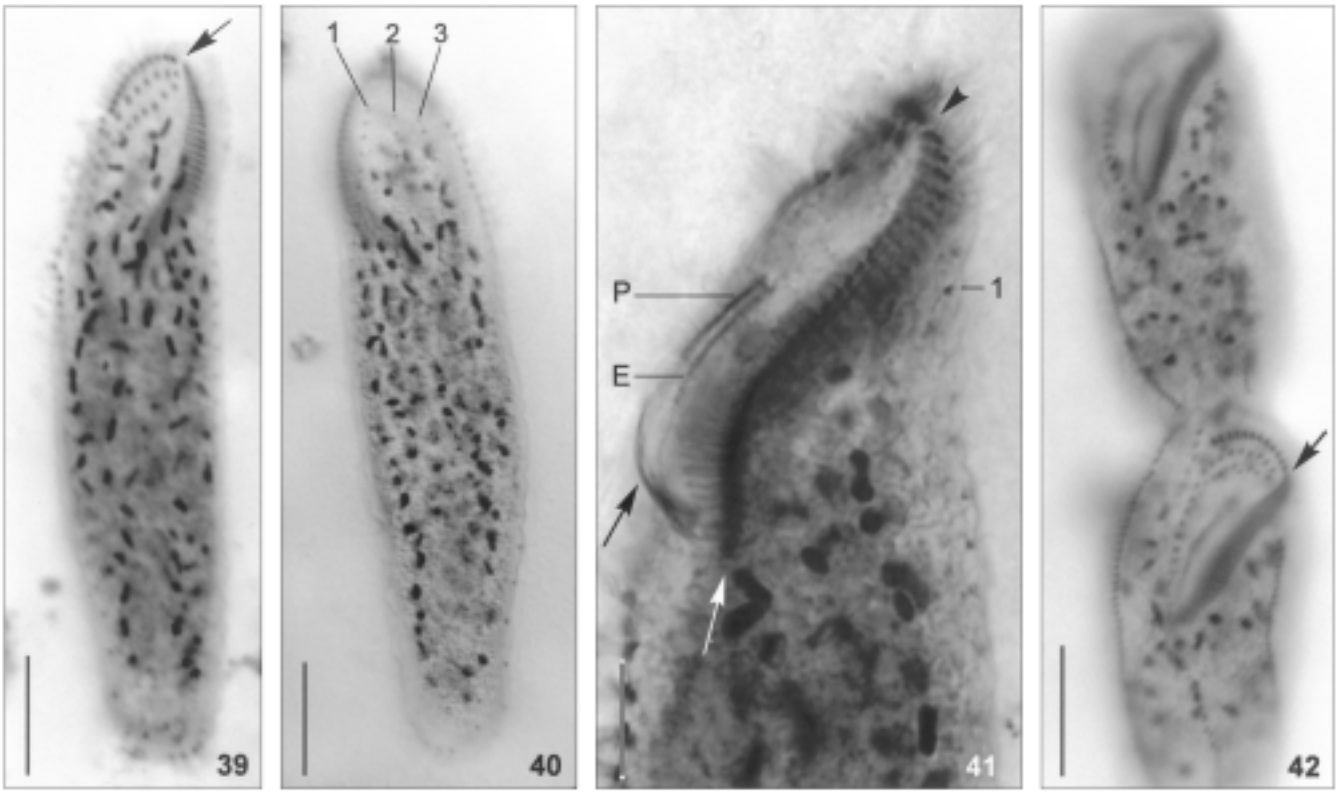
### *Uroleptopsis (Plesiouroleptopsis)* subgen. n.

**Diagnosis:** *Uroleptopsis* with midventral complex composed of midventral pairs and midventral rows.

**Type species:** *Pseudokeronopsis ignea* Mihailowitsch et Wilbert, 1990.

**Nomenclature:** *Plesiouroleptopsis* is a composite of the Greek *plesió* (near, neighbouring; Hentschel and Wagner 1996) and the existing generic name *Uroleptopsis* (see there for derivation). *Plesiouroleptopsis* alludes to the fact that the type species, *Pseudokeronopsis ignea*, has a buccal cirrus in ordinary position which is the plesiomorphic character state. In contrast, the type species of *U.* (*Uroleptopsis*), *Uroleptopsis citrina*, has no cirrus immediately right of the undulating membranes which is interpreted as apomorphic state. The subgenus *Plesiouroleptopsis* has, like *Uroleptopsis*, feminine gender because ending with *-opsis* (ICZN 1999, Article 30.1.2).

**Remarks:** As already mentioned, *Pseudokeronopsis ignea* was transferred to *Uroleptopsis* by Foissner (1995). It is the sole species in *Uroleptopsis* with a buccal cirrus in the ordinary position which is very likely the plesiomorphic state. By contrast, the midventral rows are a novelty within the Pseudokeronopsidae and therefore the autapomorphy for this species/subgenus. Midventral rows are not a very complex feature. They originate in that simply more than two cirri per streak are produced. Consequently, their convergent evolution in




**Figs 39-42.** *Uroleptopsis citrina*. Infraciliature of neotype population after protargol impregnation. **39, 40** - ventral and dorsal side. Arrow marks gap in adoral zone of membranelles. **41** - left lateral view of oral apparatus showing adoral zone with gap (arrowhead), undulating membranes, buccal lip (black arrow), nuclear apparatus, and dorsal kinety 1. White arrow marks proximal end of adoral zone of membranelles; **42** - ventral side of a very late divider. At this stage the gap in the adoral zone is not yet recognizable (arrow). E - endoral; P - paroral; 1-3 - dorsal kineties. Scale bars 30 µm (39, 40, 42) and 10 µm (41).

other urostylids - for example, *Bakuella* and *Holostichides* - is not a great surprise.

**Species included:** Only the type species - *Uroleptopsis* (*Plesiouroleptopsis*) *ignea* (Mihailowitsch and Wilbert, 1990) Foissner, 1995 - is included. For further discussion, see same chapter at genus section.

**Key to *Uroleptopsis* species**

Note that only two of the five species listed below are described after protargol preparations. Thus, for the remaining three species the features concerning the cirral pattern are rather uncertain. Further, size and shape as well as the nuclear apparatus do not allow a clear separation. Consequently, I use the colour of the cells as key character, which is admittedly a difficult feature, especially for beginners. Please be sure that the colour of your specimens is a real colour and not due to a badly adjusted optics of your microscope! However, before you use the key, you must be sure that your specimens belong to an *Uroleptopsis* population. Thus, identification needs both protargol impregnation (cirral pattern) and live observation (colour). Only very experienced workers have a chance to identify these species correctly exclusively after live observation.

1. Buccal cirrus present, that is, cirrus arranged right of paroral (Fig. 29).....*Uroleptopsis* (*Plesiouroleptopsis*) *ignea*
- Buccal cirrus lacking, that is, no cirrus immediately right of paroral (e.g., Fig. 14).....*Uroleptopsis* (*Uroleptopsis*) 2
2. Cells more or less colourless (Fig. 33).....*Uroleptopsis tannaensis*
- Cells light green, rose-carmine, or yellow.....3
3. Cells rose-carmine (Figs 31, 34).....*Uroleptopsis roscoviana*
- Cells yellow or light green.....4
4. Cells yellow (Figs 5, 13).....*Uroleptopsis citrina*
- Cells light green (Fig. 32).....*Uroleptopsis viridis*

## Phylogenetic relationships

Borror and Wicklow (1983) - basically using the system proposed by Wicklow (1981) - united *Pseudokeronopsis* (including *Uroleptopsis* as synonym; see above) and *Thigmokeronopsis* in the Pseudokeronopsidae. As unifying features they mentioned the presence of a bicorona and the far posteriorly extending distal end of the adoral zone of membranelles. Eigner and Foissner (1992) also considered *Thigmokeronopsis* and *Pseudokeronopsis* as sister groups. However, they could not provide a synapomorphy because of the lack of appropriate data on *Thigmokeronopsis*.

I agree with this grouping but provide a different and more detailed foundation of the relationships (Fig. 43). The diagram proposed is the most parsimonious one of three possible arrangements of *Pseudokeronopsis*, *Thigmokeronopsis*, and *Uroleptopsis*.

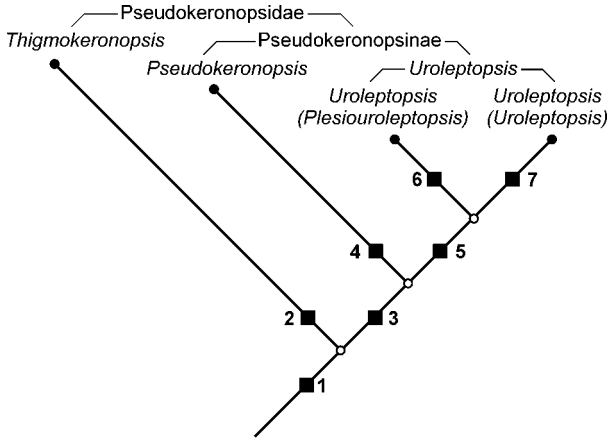



**Fig. 43.** Diagram of phylogenetic relationships within the Pseudokeronopsidae. Autapomorphies (black squares 1-7): **1** - the many macronuclear nodules fuse to some parts during division. **2** - thigmotactic field of cirri; anlagen of marginal rows and dorsal kineties originate de novo. **3** - each of the many macronuclear nodules divides individually. **4** - four or more dorsal kineties. **5** - cirral anlage I forms two cirri; transverse cirri lacking; gap in adoral zone. **6** - some midventral cirral anlagen produce midventral rows. **7** - buccal cirrus not in ordinary position; some midventral cirral anlagen produce finally only one cirrus. For detailed description and discussion of autapomorphies, see text.

## Pseudokeronopsidae (Fig. 43, autapomorphy 1)

(i) The many macronuclear nodules fuse to some parts during division.

**Remarks:** This state is realized in *Thigmokeronopsis*, at least in *T. crystallis* and *T. antarctica*, where the many nodules fuse to several parts during morphogenesis (Petz 1995). Unfortunately, nothing is known about the fate of the macronucleus during this part of the life cycle in the type species *Thigmokeronopsis jahodai* (Wicklow 1981). The plesiomorphic state of this feature is that all (two to many) nodules fuse to a single mass during division. This state is present in all non-euplotid hypotrichs, except the pseudokeronopsids. In *Metaurostylopsis marina* the macronuclear nodules fuse to a single mass too (Song *et al.* 2001). However, the mass is not globular or has another compact shape as in most species, but is a strongly branched structure. Interestingly, the formation of the proter's adoral zone proceeds very similar (identical?) as in the pseudokeronopsids (see next paragraph). Thus, *Metaurostylopsis* could be the sister group of the Pseudokeronopsidae because the macronucleus already shows the tendency not to fuse to a compact, globular mass.

So far I do not know a second autapomorphy for the Pseudokeronopsidae. The formation of a new adoral zone for the proter, as described for *Thigmokeronopsis*, *Uroleptopsis*, and *Pseudokeronopsis*, is possibly a candidate. However, a more or less identical mode is described for *Metaurostylopsis marina* (Song *et al.* 2001) and *Holosticha multistilata* (Hemberger 1982). In both species, the macronuclear nodules fuse to a single mass so that they cannot be included in the Pseudokeronopsidae (see, however, previous paragraph for *Metaurostylopsis*). Consequently this type of stomatogenesis is either a plesiomorphy in the ground plan of the Pseudokeronopsidae or this feature evolved convergently. Song *et al.* (1997) also described a total new formation of the proter's adoral zone for *Pseudoamphisiella lacazei*. However, in this species the corresponding oral primordium originates obviously behind the parental adoral zone and not in the buccal cavity as in the pseudokeronopsids. Further, the macronuclear nodules fuse to a single mass so that it cannot be included in the Pseudokeronopsidae. In the other urostylids, few parental adoral membranelles (for example, *Bakuella*; Song *et al.* 1992, Eigner and Foissner 1992) to many (for example, in *Urostyla grandis*; Ganner 1991) are reorganized. This partial reorganisation is obviously distinctly different from the total new formation discussed above.

Pseudokeronopsid species have a bicorona, a type of frontal ciliature also present in other urostylid taxa, for example, *Bicoronella* (Foissner 1995), *Keronella*

(Wiackowski 1985), *Pseudourostyla* (Jerka-Dziadosz 1964, Borror 1972), and *Neokeronopsis* (Warren *et al.* 2002). This distribution indicates that the bicorona is a plesiomorphy for the Pseudokeronopsidae, although one cannot exclude that such a frontal ciliature evolved convergently.

Borror and Wicklow (1983) characterized the Pseudokeronopsidae, inter alia, by the far posteriorly extending distal end of the adoral zone. In fact, this feature applies to *Pseudokeronopsis* and *Thigmokeronopsis*, and to a somewhat smaller extant also to *Uroleptopsis* (Figs 17-19). However, this characteristic is also known from other urostylids, for example, *Notocephalus* (Petz *et al.* 1995) and *Pseudoamphisiella* (Song *et al.* 1997), which certainly do not belong to the Pseudokeronopsidae. Since the branching pattern outside the Pseudokeronopsidae is unknown, we do not know whether this distal elongation is a symplesiomorphy or a convergence.

***Thigmokeronopsis* (Fig. 43, autapomorphies 2)**

(i) Thigmotactic field of cirri.

**Remarks:** *Thigmokeronopsis* species have a more or less large field of thigmotactic cirri (= left postoral ventral files according to Petz 1995) between the midventral complex and the left marginal row (Wicklow 1981, Petz 1995). Such a group of cirri is lacking in other hypotrichs strongly indicating that this is an autapomorphy of *Thigmokeronopsis* (Wicklow 1981, Eigner and Foissner 1992).

(ii) Anlagen of marginal rows and dorsal kineties originate de novo.

**Remarks:** Generally, new marginal rows and dorsal kineties originate within the parental structures. By contrast, in all three *Thigmokeronopsis* species the new marginal rows and dorsal kineties occur distinctly left or right of the parental structures (Wicklow 1981, Petz 1995).

**Pseudokeronopsinae (Fig. 43, autapomorphy 3)**

(i) More or less each of the many macronuclear nodules divides individually.

**Remarks:** So far, this feature is only described for several *Pseudokeronopsis* populations (for example, Gruber 1884, Rühmekorf 1935, Wirnsberger 1987) and for *Uroleptopsis citrina* and *U. ignea* (present paper, Mihailowitsch and Wilbert 1990). The plesiomorphic state is the partial fusion still present in *Thigmokeronopsis* (see Pseudokeronopsidae). It is more parsimonious to assume that the individual division has evolved *via* the intermediate state still realized in *Thigmokeronopsis* than directly from the common mode where all nodules fuse to a single mass.

Here the ring-shaped structures, which form a distinct seam in *U. citrina*, have to be discussed (Figs 7, 8, 11, 12, 36-38). These structures have also been described for some *Pseudokeronopsis* populations (Prowazek 1900, Hu and Song 2001, Song *et al.* 2002), but not for *Thigmokeronopsis* (Wicklow 1981, Petz 1995). Thus, one could suggest that this feature is an autapomorphy for the Pseudokeronopsinae. However, these structures are also described for two holostichid species (Song and Wilbert 1997, Gong *et al.* 2001) which certainly are not members of the Pseudokeronopsidae. Thus, this feature cannot be used as phylogenetic marker at the present state of knowledge.

Interestingly enough, many *Uroleptopsis* and *Pseudokeronopsis* species have a more or less distinct colour whereas all three *Thigmokeronopsis* species are colourless. However, currently too few data are available to assess the meaning of this feature for phylogenetic analysis.

***Pseudokeronopsis* (Fig. 43, autapomorphy 4)**

(i) Four or more dorsal kineties present.

**Remarks:** I do not know if the increase of the number of dorsal kineties from three to four or more is in fact a good autapomorphy for *Pseudokeronopsis*. Anyhow, it is interesting that all *Thigmokeronopsis* species and both *Uroleptopsis* species investigated in detail have invariably three dorsal kineties. This indicates that three kineties is the plesiomorphic state within the Pseudokeronopsidae. In contrast, *Pseudokeronopsis* species have four or more bristle rows (Foissner 1984, Wirnsberger *et al.* 1987, Hu and Song 2001, Song *et al.* 2002). Only *P. flava* has very rarely three kineties (Wirnsberger *et al.* 1987), which, however, must not be over-interpreted.

Eigner and Foissner (1992) used the feature "Parental basal bodies not involved in formation of ciliary structures of daughters". Likely they meant the frontal-midventral-transverse-cirri because the formation of the marginal rows and dorsal kineties proceeds in ordinary manner in *Pseudokeronopsis*, that is, within the parental structures (Wirnsberger 1987). In contrast, the parental midventral complex is obviously not involved in primordia formation. However, the data on *Thigmokeronopsis* (Petz 1995) and *Uroleptopsis* (Mihailowitsch and Wilbert 1990, present paper) indicate that this feature also applies to these taxa. Thus, it could

be an autapomorphy of the Pseudokeronopsidae. However, it is very difficult to decide whether or not parental cirri are definitely involved in primordia formation. Consequently this feature is not used further although it cannot be excluded that it is a useful marker in future when more morphogenetic data on urostylids are available.

***Uroleptopsis* (Fig. 43, autapomorphies 5)**

(i) Cirral anlage I forms two cirri.

**Remarks:** Within the pseudokeronopsids this feature only occurs in *Uroleptopsis*. In *Pseudokeronopsis*, *Thigmokeronopsis*, and most other hypotrichs, the anlage I, which produces the undulating membranes, forms only the left frontal cirrus. This state must be therefore considered as plesiomorphic. *Bicoronella costaricana* and *Caudiholosticha sylvatica* have 1-7 cirri behind the left frontal cirrus indicating that in these two species anlage I also produces more than one cirrus (Foissner 1982, 1995; Berger and Foissner 1989; Berger 2003). *Caudiholosticha sylvatica* has three frontal cirri indicating that it is not closely related to the pseudokeronopsids. In contrast, *Bicoronella costaricana* has a bicorona so that it could be a near relative of the pseudokeronopsids. However, morphogenetic data are needed to show the fate of the macronuclear nodules and the origin of the supernumerary cirri behind the left frontal cirrus.

(ii) Transverse cirri lacking.

**Remarks:** This feature was the main reason for Kahl (1932) to separate *U. citrina* from *Holosticha* (*Keronopsis*) species (now *Pseudokeronopsis*). The loss of the transverse cirri occurred undoubtedly several times independently within the hypotrichs. Other urostylid taxa which lack transverse cirri are, for example, *Australothrix* spp. (Blatterer and Foissner 1988), *Eschaneustyla* (Eigner 1994, Foissner *et al.* 2002), and *Holostichides* spp. (Foissner 1987b). However, in *Eschaneustyla* the macronuclear nodules fuse to a single mass during cell division and *Australothrix* and *Holostichides* lack, in addition, a bicorona strongly indicating that none of them is a member of the Pseudokeronopsidae.

(iii) Gap in adoral zone.

**Remarks:** Within the pseudokeronopsids, *Uroleptopsis citrina* and *U. ignea* are the sole species which have a distinct break in the adoral zone. The gap is not very distinct in life and therefore I assume that it has been overlooked in the three other *Uroleptopsis* species which are not yet described after protargol impregnation. This break, which is likely the site where the zone turns from ventral to dorsal, is possibly homologous with the interruption separating the anterior (= outer, = collar) membranelles from the ventral (= inner, = buccal) membranelles of the oligotrichs (Petz and Foissner 1992, Foissner *et al.* 1999). In most hypotrichs, this transition site is inconspicuous because not marked by a gap. Very likely such a distinct division evolved several times independently, for instance, in *Holosticha* (e.g., Petz *et al.* 1995, Berger 2003), *Afrothrix*, *Erniella*, *Etoschothrix* (for review, see Foissner *et al.* 2002), or *Parabirojimia* (Hu *et al.* 2002).

***Uroleptopsis* (*Plesiouroleptopsis*) (Fig. 43, autapomorphy 6)**

(i) Some midventral cirral anlagen produce midventral rows.

**Remarks:** A midventral complex composed of cirral pairs is undoubtedly the plesiomorphic state. Consequently the formation of more than two cirri within a streak has to be interpreted as autapomorphy of *U. ignea*, the sole species belonging to the present subgenus. Midventral rows occur in other urostylid taxa too, for example, *Bakuella*, *Eschaneustyla*, *Holostichides*, *Keronella*, *Paragastrostyla* (Wiackowski 1985, Song and Wilbert 1988, Song 1990, Song *et al.* 1992, Eigner 1994). However, in none of these taxa the macronuclear nodules divide individually so that we must postulate the convergent evolution of midventral rows. A midventral row is not a very complex feature because it is produced by a simple increase of the number of cirri formed within an anlage. Thus, the convergent evolution of midventral rows is nothing unusual.

***Uroleptopsis* (*Uroleptopsis*) (Fig. 43, autapomorphies 7)**

(i) Buccal cirrus not in ordinary position.

**Remarks:** For review on the confusing terminology of this cirrus, see Berger and Foissner (1997) and Berger (1999). The plesiomorphic state is the presence of a single cirrus (= cirrus II/2 according to Wallengren's 1900 terminology) in ordinary position which is immediately right of the paroral. Some taxa have two or more buccal cirri but only few lack such a cirrus, for example,

*Paragastrostyla* and *Periholosticha* (Hemberger 1985). However, in these taxa cirrus II/2 is indeed lacking while it is present, but not in the ordinary position in *U. citrina*. As already mentioned above, it is part of the posterior corona in interphasic specimens (Figs 14, 27). A similar situation is realized in *Neokeronopsis spectabilis*, a huge urostylid freshwater species with prominent transverse cirri, only two macronuclear nodules which fuse during morphogenesis, and fragmentation of dorsal kinety 3 (Warren *et al*. 2002, own observations). In this species cirrus II/2 is also in line with the posterior corona, but the long undulating membranes are arranged more or less as in *Cyrtohymena* so that cirrus II/2 is simultaneously positioned immediately right of the anterior portion of the paroral.

(ii) Some midventral cirral anlagen finally produce only one cirrus.

**Remarks:** This is obviously a real novelty within the urostylids. The plesiomorphic state is that a frontal-midventral anlage produces finally two cirri, a so-called midventral pair (the rearmost anlagen, of course, produce three to four cirri if they also form a transverse cirrus, respectively, a pretransverse ventral cirrus and a transverse cirrus; Figs 1, 2). At first, two cirri are produced in *U. citrina* too (Fig. 25). However, somewhat later the left cirrus of the corresponding pairs is obviously resorbed so that only the right cirrus remains in the interphasic specimen (Fig. 26). Interestingly enough, this resorption is confined to the middle portion of the midventral complex. This section of the complex therefore looks almost like a midventral row. It is unknown whether or not this feature is present in the other species assigned to *U.* (*Uroleptopsis*). It could be that this feature is only an autapomorphy of *U. citrina*. A very similar resorption of cirri is described for *Psammocephalus faurei* by Wicklow (1982) indicating a convergence.

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