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Taxonomic and Ecologic Revision of Urotrichs (Ciliophora, Prostomatida) with Three or More Caudal Cilia, Including a User-Friendly Key

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With 170 Figures and 3 Tables

Key words: Ecology, plankton, protozooplankton, revision, taxonomy, Urotricha

Abstract

Four species of Urotricha with more than three caudal cilia, namely U. apsheronica, U. castalia, U. pelagica, and U. matthesi tristicha nov. subspec. were studied using live observation, morphometry, silver impregnation and scanning electron microscopy. These investigations served as guideline for a partial revision of the genus, i.e. of those species having three or more caudal cilia. The following characters were selected for species distinction: size, body shape (with or without posterior plug), macronucleus shape (ellipsoidal or distinctly elongate), location of excretory pore of contractile vacuole (within or outside circle formed by caudal cilia), somatic trichocysts (present/absent, size and shape), number of somatic and brosse kineties, number and arrangement of caudal cilia, symbiotic algae (present/absent), and biotope (freshwater, terrestrial or marine). Based on these features and the reinvestigation of the type slides of U. matthesi and U. puytoraci, 14 out of 23 nominal Urotricha species with three or more caudal cilia were recognized: U. alveolata, U. apsheronica, U. baltica, U. castalia, U. cyrtonucleata, U. faurei, U. matthesi, U. matthesi tristicha nov. subspec., U. multisetosa, U. pelagica, U. pusilla, U. terricola, U. tricha, and U. venatrix. Urotricha rotunda FERNANDEZ-LEBORANS & NOVILLO, 1994 was synonymized with U. castalia Muñoz et al., 1987, U. valida SONG & WILBERT, 1989 was synonymized with U. venatrix KAHL, 1935, and U. puytoraci DRAGESCO et al., 1974 was transferred to the genus Longitricha GAJEWSKAJA, 1933: Longitricha puytoraci nov. comb. Some other nominal species were also transferred or remained in uncertain systematic position. A simple key, usable also for ecologists, has been prepared. The faunistic and ecological literature available on each species was compiled and reviewed. The data show that most species are widely distributed and have peak abundances in late spring at water temperatures around 10 °C.

Introduction

Species of the prostomatid genus Urotricha CLAPARÈDE & LACHMANN, 1859 are among the most common ciliates

in pond and lake plankton. Usually, they are easily recognized by their fast and jumping movement. In spite of this, urotrichs are poorly explored and listed in many ecological papers as "*Urotricha* sp." (e.g. CARRIAS et al. 1994; CARRICK & FAHNENSTIEL 1990; MÜLLER et al. 1991; ŠIMEK et al. 1995; SIME-NGANDO et al. 1992). In fact, most species of this genus are difficult to determine not only because they are very agile but also due to the insufficient original descriptions and the lack of a modern genus revision.

We have thus undertaken a revision of the genus by reinvestigating common species and, where available, the type slides of described species. The first part of the study deals with the "multitrichate" members of the genus, i.e. those having three or more caudal cilia. Some of these species are rather voluminous and abundant in small and large lakes, and may thus significantly contribute to biomass and energy turnover.

Material and Methods

Urotricha apsheronica, U. castalia, U. matthesi tristicha, and U. pelagica were found in spring 1993 in the plankton of the pond at the University of Salzburg (N $47^{\circ}47'/E \ 13^{\circ}40'$). The artificial basin was built about 10 years before the samples were taken; it is a small (about 50×20 m), shallow (max. depth 1 m), highly eutrophic pool fed by a clean brook, the Hellbrunner Bach.

Cells were studied in vivo using a high-power oil immersion objective and differential interference contrast. Characteristics subject to change under cover-glass pressure, like cell shape and movement, were of course studied in uncovered, swimming specimens using magnifications between X 100-X 400. The infraciliature (ciliary pattern), the silverline system and various other cytological details were revealed with protargol, silver carbonate, silver nitrate, and scanning electron microscopy. See FOISSNER (1991) for a detailed description of all methods used.

Counts and measurements on silvered specimens were performed at a magnification of X 1,000. In vivo measurements were conducted at a magnification of X 100–X 1,000. Although these provide only rough estimates, it is convenient to give such data as specimens usually shrink in preparations and/or become distorted during fixation. Standard deviation and coefficient of variation were calculated according to statistics textbooks. Drawings of live specimens were based on free-hand sketches and micrographs, those of impregnated cells were made with a camera lucida. Terminology is according to CORLISS (1979), FOISSNER (1984a), HIL-LER & BARDELE (1988), and KAHL (1930).

Results

1. Genus *Urotricha* CLAPARÈDE & LACHMANN, 1859

- 1859 Urotricha CLAPARÈDE & LACHMANN, Mém. Inst. natn. génev., 6:314. Type species (by monotypy): Urotricha farcta CLAPARÈDE & LACHMANN, 1859.
- 1886 Balanitozoon STOKES, Ann. Mag. nat. Hist., 17:109. Type species (by monotypy): Balanitozoon agilis STOKES, 1886.

Diagnosis: Plagiocampidae with direct and indirect connecting silverline system and somatic ciliary rows distinctly shortened posteriorly, leaving blank a more or less wide area occupied by a single caudal cilium or by many caudal cilia in posterior pole region. Circumoral kinety (paroral membrane) circular and closed, i.e. not interrupted by brosse (adoral membranelles). Brosse close underneath circumoral kinety, usually enklitoloph-dexiotrop and composed of less than five short, oblique rows arranged one after the other. Most species swim fast and can perform conspicuous jumps.

Remarks: For family characterization, see FOISSNER (1978, 1984b). SMALL & LYNN (1985) separate Plagiocampa (circumoral kinety semicircular) and Urotricha (circumoral kinety circular) at family level. Genus synonymy is according to KAHL (1930). The genus diagnosis is based on the present investigations and literature data (FOISSNER 1983, 1984a, b; KAHL 1930). The characters used separate Urotricha from Plagiocampa (circumoral kinety semicircular, brosse kineties side by side; FOISSNER 1978, 1984b), Chilophrya (very similar to Plagiocampa; FOISSNER 1984b), Balanion (syn. Pseudobalanion FOISS-NER et al., 1990; brosse within circle formed by circumoral dikinetids, see FOISSNER et al. 1994), Dissothigma JAN-KOWSKI, 1976 (syns. Urotrichopsis FOISSNER, 1983 and Patschia SMALL & LYNN, 1985; many short, transverse brosse kineties inserted one after the other between two somatic kineties), and *Longifragma* FOISSNER, 1984a (brosse aklitoloph and consisting of three long, vertical kineties side by side).

Nominal species excluded: Some species, although having several caudal cilia, were excluded from the revision because they have either been transferred to other genera or are of uncertain affinity; most are poorly known and need redescription before they can be placed properly.

Urotricha atypica ALEKPEROV, 1993 (Figs. 1–3): A terrestrial species with brosse kineties very small and side by side, similar to *Plagiocampa*; about 10 caudal cilia, but kineties unshortened posteriorly, as in *Holophrya*.

Urotricha biconica SAUERBREY, 1928 (Figs. 4–8): Transferred to *Holophrya* by KAHL (1930). We agree because this marine (interstitial) species is completely ciliated and does not jump like most other urotrichs. BUR-KOVSKY (1970) reported *U. biconica* from the interstitial of the White Sea, Kandalaksha Gulf.

Urotricha hexatricha SAVI, 1913 (Figs. 9, 10): Transferred to *Holophrya* by KAHL (1930). We agree; very likely it is a junior synonym of *H. discolor*.

Urotricha lemani FOISSNER et al., 1994 (Fig. 11): Established by FOISSNER et al. (1994) for *U. armata* DRAGESCO, 1960, a junior, primary homonym of *U. armata* KAHL, 1927. Here, this species is transferred to *Holophrya* (*H. lemani* nov. comb.) because the ciliary rows are unshortened and the brosse extends longitudinally on the anterior body third.

Urotricha obliqua KAHL, 1926 (Figs. 25–33): Now type species of genus *Longifragma* FOISSNER, 1984 (see above).

Urotricha saprophila KAHL, 1930 (Figs. 34–36): Now type species of genus *Dissothigma* JANKOWSKI, 1976 (see above).

Urotricha puytoraci DRAGESCO, IFTODE & FRYD-VERSA-VEL, 1974 (Figs. 13-24, Table 1): Described from silver nitrate-impregnated specimens only and without detailed morphometry. We reinvestigated the type slides (see below). This largely confirmed the description by DRAGESCO et al. (1974). However, one important character was not mentioned, viz. that U. puytoraci is slightly broader than long (Table 1), which is very unusual in prostome ciliates. This peculiarity and the lack of caudal cilia match the genus Longitricha GAJEWSKAJA, 1933. to which U. puytoraci thus is transferred: Longitricha puytoraci (DRAGESCO, IFTODE & FRYD-VERSAVEL, 1974) nov comb. Longitricha puytoraci differs from the type species, L. flava (Fig. 12), at the present state of knowledge in body size (about 50 µm vs. 100 µm) and, possibly, by the lack of a brown pigmentation. No data on the infraciliature of L. flava are available. Thus, the transfer of U. puytoraci cannot be substantiated by a comparison of the infraciliatures. However, if the transfer is correct, then the somatic and oral infraciliatures of Longitricha and Ur-



Figs. 1–16. Nominal species of *Urotricha* excluded from the revision because of systematic problems or transfer to other genera. 1–3: *Urotricha atypica* (from ALEKPEROV 1993), anterior (1) and posterior (2) polar view after CHATTON-LWOFF silver nitrate impregnation (bar 10 µm), and nuclear apparatus (3) stained by the Feulgen reaction. 4–8: *Urotricha biconica* from life (4–7, from SAUER-BREY 1928; 8, from KAHL 1930 after SAUERBREY 1928); anterior end with lip-like plasm projection (4), contracted specimen (5), extended specimen 115 µm long (6, 8), and anterior end with oral basket (7). 9, 10: *Urotricha hexatricha* from life (9, from SAVI 1913; 10, from KAHL 1930 after SAVI 1913), size not given in original publication. 11: *Urotricha lemani* FOISSNER, 1984a (from DRAGESCO 1960) from life, length about 80 µm. 12: *Longitricha flava* (from GAJEWSKAJA 1933) from life, bar 50 µm. Arrow marks macronucleus. 13–16: *Longitricha puytoraci* nov. comb., infraciliature after CHATTON-LWOFF silver nitrate impregnation (13, 14, from DRAGESCO et al. 1974; 15, 16, originals from type slides); ventral view (13) and anterior polar views (14–16), bar division 10 µm. B = brosse, CK = circumoral kinety, CY = cytopyge, DG = double granules at anterior end of ciliary rows, E = extrusomes, EP = excretory pore of contractile vacuole, IS = indirect silverline system, P = pores.

otricha are very similar, except for the caudal cilia, which are lacking in *Longitricha*. This has been emphasized also by GAJEWSKAJA (1933).

Description according to DRAGESCO et al. (1974): All data are from silver nitrate-impregnated specimens (CHAT-

TON-LWOFF technique, Figs. 13, 14). Length $50-60 \,\mu\text{m}$, rarely cells with less than $30 \,\mu\text{m}$ occur. Shape according to Fig. 17A in DRAGESCO et al. (1974) almost globular with posterior quarter indistinctly set off from rest of cell. Macronucleus sausage-shaped ("forme de boudin"). Excre-





Figs. 17–24. *Longitricha puytoraci* nov. comb., micrographs from type slides of somatic and oral infraciliature after silver nitrate impregnation. **17:** Ventrolateral view to show that specimens usually are slightly broader than long. **18–22:** Anterior polar views, figures 20 and 21 show same specimen at two focus levels. Asterisk marks oral aperture, arrowhead denotes ring of pores (cp. Fig. 16). **23:** Transverse view in mid-body showing kinety number. **24:** Posterior polar view. Although there are some granules in and near the silverlines, caudal cilia complexes, as found in *Urotricha* (Figs. 76, 77, 80, 82, 144), are lacking. B = brosse, CK = circumoral kinety, DG = double granules at anterior end of ciliary rows, ES = posterior end of ciliary rows, FV = food vacuoles, IDG = inner ring of double granules, N = nematodesmata.



Figs. 25–36. Nominal species of *Urotricha*, which were transferred to other genera. **25–33:** *Longifragma obliqua* from life (25–28, 33) and after CHATTON-LWOFF silver nitrate impregnation (29–32), bar division 10 μ m (25–32, from FOISSNER 1984a; 33, from KAHL 1926). 25, 33: Lateral and oblique anterior polar view of typical specimens. 26: Anterior polar view showing oral opening covered by oral flaps. 27: Somatic extrusome, 3 μ m. 28: Transverse view showing brosse ridges. 29: Silverline system. 30: Ventral view showing brosse to be distinctly different from that of *Urotricha* (Figs. 37, 41). 31, 32: Anterior and posterior polar view. Note that basal bodies of caudal cilia form distinct complexes and are scattered in whole posterior pole region. **34–36:** *Dissothigma saprophila* from life (34, 35) and after protargol impregnation (36), bar 10 μ m (34, from KAHL 1930; 35, from VUXANOVICI 1962; 36, from PÄTSCH 1974). 34, 35: Lateral views, length 45 μ m and 38 μ m. 36: Ventral view. Note that brosse extends along whole length of ciliary rows. B = brosse, CC = caudal cilia, CK = circumoral kinety, EP = excretory pore of contractile vacuole, FV = food vacuole, MA = macronucleus, MI = micronucleus.

tory pore of contractile vacuole slightly out of centre of posterior pole. DRAGESCO et al. (1974) distinguished *U. puytoraci* from their *U. venatrix* (a misidentified *U. apsheronica*, see there) by the absence of extrusomes; however, the lack of extrusomes in *U. puytoraci* is questionable because DRAGESCO et al. (1974) did not observe live specimens, and extrusomes, even if present, are often not recognizable in silver slides.

48-51 (50 on average, n = ?) somatic kineties extending meridionally from anterior end to posterior quarter of cell; each kinety commences with a pair of basal bodies connected by a tiny fibre. Posterior quarter occupied by many irregularly distributed argyrophilic granules, interpreted as basal bodies, but not as caudal cilia, by DRAGESco et al. (1974). In fact, photograph 19 K in DRAGESCO et al. (1974) shows these minute granules (Fig. 24) to appear very different from the large caudal cilia complexes found, for instance, in *U. pelagica* and *U. apsheronica* (Figs. 80, 82, 113). FERNANDEZ-LEBORANS & NOVILLO (1994) incorrectly ascribed a single caudal cilium to *U. puytoraci*, whereas ALEKPEROV (1993), also incorrectly, stated a tuft of caudal cilia. Silverline system consisting of rectangular to slightly hexagonal meshes, forms irregular network in posterior region.

Oral opening apical, cytopharyngeal basket inconspicuous. Circumoral ciliature, according to Fig. 19J in DRA-GESCO et al. (1974), very similar to that of *U. pelagica* and *U. apsheronica*, i.e. consisting of two narrowly spaced circles each composed of 26-27 oblique dikinetids, those of inner circle associated with distinct fibres extending to mouth centre, which is surrounded by a circle of about 32 argyrophilic granules. Three small, oblique brosse kineties each consisting of 4-5 paired basal bodies.

Description of morphogenesis in DRAGESCO et al. (1974).

Data obtained by the reinvestigation of the type slides (kindly supplied by Mme. IFTODE, Paris University, Centre d'Orsay, where the slides are deposited): The two type slides, prepared by the CHATTON-LWOFF silver nitrate method, contain several hundred specimens, many of which are excellently prepared. Thus, we could undertake detailed morphometry (Table 1) and look for characters not contained in the original description. As mentioned above, our observations largely agree with those by DRA-GESCO et al. (1974). Thus, mainly supplementary observations and some refined figures are provided. The slides also contain some conjugating and dividing cells. These, as well as apparent postconjugates and postdividers, were excluded from all analyses. Likewise, a single, small (width 37 µm) specimen having only 42 kineties was excluded.

The following details were observed (Figs. 15-24): (1) The size is considerably smaller than indicated by DRAGESCO et al. (1974), viz. $44 \times 48 \,\mu\text{m}$ (Table 1). The very small specimens with a size of less than 30 µm mentioned by DRAGESCO et al. (1974) are degenerating postconjugates and young postdividers. (2) The shape is almost globular. However, on average cells are a little broader than long (Table 1). The posterior, unciliated portion is broadly rounded and, except for a few specimens, not distinctly narrowed, i.e. set off from the ciliated part. The anterior region is flat or, in about half the specimens, even slightly concave. (3) We could not unambiguously identify the macronucleus because all cells contained large food vacuoles with flagellates. (4) The excretory pore of the contractile vacuole is situated as shown in Fig. 17A of DRAGESCO et al. (1974), i.e. slightly out of pole centre (Fig. 13). Two specimens have two excretory pores side by side. (5) No extrusomes are recognizable in bright field and interference contrast, indicating that they are lacking or inconspicuous. Likewise,

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cilia are not recognizable, thus their length could not be determined. (6) The posterior quarter is very likely unciliated because the recognizable argyrophilic granules are very irregularly distributed, highly variable in number (about 100-200) and considerably different in size, rarely appearing large and paired. Such granules, probably marking extrusome attachment sites, are also present in Urotricha spp. (Figs. 76, 77, 82). Urotricha puytoraci entirely lacks the typical, large caudal cilia complexes found, e.g., in U. pelagica and U. castalia. Such complexes would be recognizable if present because the specimens are excellently prepared. (7) The oral basket is a broad cone extending to the posterior third of the cell. It is surrounded by two distinct circles of paired granules, very likely dikinetids (or a single circle with associated parasomal sacs), the inner pairs probably giving rise to distinct fibres (nematodesmata).

Occurrence and ecology: Locus typicus of *U. puytoraci* is "d'une pièce d'eau de Ballancourt", a suburb of Paris, France. It was cultivated for one year on Eau de Volvic with *Cryptomonas* sp. as food. Later, it was found by MIRABDULLAEV (1988, 1989) in fish ponds of Tashkent, with peak abundances in late spring.

Remarks: Described from silver nitrate-impregnated specimens only. Thus, redescription from live material is necessary, especially to obtain more detailed data about shape, colour, extrusomes and caudal cilia.

2. General morphology and species characters of urotrichs with three or more caudal cilia (Figs. 37–45)

Body size and shape: The taxa recognized split into two rather distinct size groups, viz. small species (length $30-50 \ \mu\text{m}$) and large species (length $50-100 \ \mu\text{m}$). Likewise, the body shape may be either rather evenly ellipsoidal or narrowed posteriorly, causing the unciliated body portion to be more or less distinctly set off, plug-like, from the rest of the cell (Figs. 37, 38). However, the narrowing is often inconspicuous and rather variable and hence used sparsely in the key. All species are almost or completely circular in transverse view, but symmetry is not radial because of the brosse and the contractile vacuole which define a ventral side (Figs. 37, 152, 162).

The small species have fewer ciliary rows and caudal cilia than the large ones. Interestingly, such a correlation is not found with the number of brosse kineties. Vermiform macronuclei occur only in the small-sized group, whereas conspicuous, fusiform extrusomes occur only in large-sized species.



Figs. 37–45. General morphology and main species characters of urotrichs with three or more caudal cilia. **37:** Ventral view of species with narrowed, unciliated posterior body portion (plug). **38:** Species with different body and macronuclear shape. **39, 40:** The excretory pore (arrow) of the contractile vacuole is either within or outside the circle formed by the caudal cilia. **41, 45:** Anterior polar view (original) and ultrastructure (from PUYTORAC & GRAIN 1972) of oral infraciliature. **42:** Shapes of somatic (left two) and oral extrusomes. **43:** Silverline system (from FOISSNER 1979). **44:** The ciliary rows commence either with a pair of granules or with a single granule (arrows). B = brosse kineties 1-3, BB = basal body, C = cilia, CC = caudal cilia, CK = circumoral kinety, CR = ciliary rows, CV = contractile vacuole, DS = direct connecting silverline system, E = extrusomes, EP = excretory pore of contractile vacuole, ES = end of somatic ciliary rows (kineties), FR = microfibrillar ring, IS = indirect connecting silverline system, MA = macronucleus, MI = micronucleus, N = nematodesma, OA = oral aperture, OB = oral basket, OF = oral flaps, P = pore, PS = parasomal sac.

Nuclear apparatus: The nuclear apparatus invariably consists of a single macronucleus to which a micronucleus is closely attached (Figs. 37, 147). The macronucleus is globular or ellipsoidal in all freshwater species and vermiform in *U. cyrtonucleata*, a marine species, and *U. terricola*, a soil inhabitant. Thus, the shape of the macronucleus is an important species character.

Contractile vacuole and its excretory pore: These structures are near the posterior end of the organism, usually neighbouring the ventral (brosse) side. Only the location of the excretory pore, i.e. within (Fig. 39) our outside (Fig. 40) the circle formed by the caudal cilia, is of alpha-taxonomic significance.

Extrusomes: There are urotrichs with or without somatic extrusomes (trichocysts, toxicysts and/or mucocysts), at least in the light microscope and according to literature data. Both the presence/absence and the shape and size of the extrusomes are important species characters which must be analyzed in live specimens because these tiny organelles disappear and/or alter shape and length when prepared. The extrusomes are either rodshaped or fusiform, only the latter produce conspicuous, peripheral fringes (Figs. 42, 106, 107,139, 142).

Oral extrusomes within the cytopharyngeal basket occur at least in some species. They are numerous but small and thus inconspicuous (Figs. 42, 94).

Symbiotic algae: These occur only in *U. alveolata*, a species of rather doubtful systematic position. See FOISS-NER & WÖLFL (1994) for a brief discussion of "zoochlorellae" as species character.

Somatic infraciliature and caudal cilia: Urotricha is covered by meridional, rather closely spaced ciliary rows which are, however, shortened posteriorly by 10-20%. Thus, a more or less large, blank posterior pole area is formed, the centre of which is occupied by one or many caudal cilia. Depending on species, the kineties either commence with a single basal body or with a granule pair having only the posterior granule ciliated (Figs. 44, 125). It is not known whether this pair is a dikinetid sensu stricto or a monokinetid with a parasomal sac, as indicated by the (sometimes) smaller size of the anterior granule (Fig. 170). In *Holophrya* (formerly *Prorodon*), which is closely related to *Urotricha*, both granules are ciliated, i.e. are basal bodies (HILLER 1993 a, b).

The numbers of somatic kineties and caudal cilia are rather important species characters because they are easily recognized and have low coefficients of variation (Table 1). By comparison, the numbers of basal bodies (cilia) within the ciliary rows are rather variable, especially between populations (Table 2). As concerns the caudal cilia, which usually are about twice as long as normal body cilia, their arrangement is also important: in most species they form a distinct circle, only in *U. terricola* and *U. faurei* are they scattered. The basal bodies of the caudal cilia are very distinct in silver nitrate slides because they are surrounded at a rather wide distance by a silverline, producing a so-called "caudal cilium complex" (Figs. 76, 77, 82, 144).

Brosse: The brosse defines the ventral side of the organism because it is very likely a highly modified part (adoral membranelles) of the oral apparatus (HILLER 1993a, b). Usually, the brosse consists of 3 short, oblique rows composed of narrowly spaced dikinetids having only the anterior basal body ciliated. However, some species have 4-6 brosse kineties, and the length of the kineties is rather different in certain species. Thus, both the number and length of the brosse kineties have some, although admittedly limited, value in distinguishing species because they can be recognized with sufficient clarity only in excellent slides.

Our scanning electron micrographs show the brosse extending in deep furrows separated by conspicuous ridges (Figs. 83, 122-125). Frequently, one gets the impression that some brosse bristles perforate the brosse ridges, which often appear tile-like and fused (Figs. 84, 126).

Typically, the brosse of Urotricha is enklitoloph-dexiotrop [terminology after HILLER & BARDELE (1988)], i.e. some somatic kineties are slightly shortened and abut at acute angles on its right side and posterior end (U. cyrtonucleata, Fig. 46; U. terricola, Fig. 50; U. venatrix, Fig. 53; U. matthesi, Fig. 154). However, some species (U. castalia, Figs. 131, 133, 134, 136, 150; Longitricha puytoraci, Figs. 14, 15) have one or two shortened kineties also on the left side of the brosse, producing a more or less distinct enklitoloph-syntropic pattern. Other species, viz. U. pelagica (Figs. 73, 74), U. apsheronica (Figs. 91, 93, 103, 104, 108), U. matthesi tristicha (Figs. 161, 162), and U. faurei (Fig. 170), may or may not have shortened kineties on the left side of the brosse. Obviously, there is some variation, indicating that not too much weight should be put on this character.

Biotope: Most *Urotricha* species were described from freshwater biotopes. Interestingly, the few reliable species reported from marine and terrestrial habitats have an unusual, vermiform macronucleus. The restricted distribution can be used to support identification, but with some caution because faunistic data are still very sparse.

Oral apparatus, cortex and silverline system: These organelles are very similar in the species investigated so far. It is not known whether the minor differences recognizable are caused by variations in the observation and preparation procedures or have a real structural basis. See Figures 37, 41, 43–45 and species descriptions, especially *U. apsheronica*, for a detailed presentation of these organelles. Ultrastructural data on *Urotricha* are sparse, the most detailed studies being those by PUYTORAC & GRAIN (1972) and the scanning electron micrographs in the present study.

A specific problem is posed by the oral flaps, which originate from and/or near the circumoral dikinetids and

are thus very likely modified, short cilia. They appear as single, navicular lobes in U. apsheronica and as short, paired rods in U. matthesi tristicha according to our very thorough in vivo observations (Figs. 100, 101, 157). However, in scanning electron microscopic preparations the navicular lobes of U. apsheronica are paired like those of U. matthesi (Figs. 122-125). As we are quite sure that the flaps of U. apsheronica are unpaired in live condition, although the transverse view is dumb-bell shaped indicating that two cilia (?) are contained, the separation into pairs of rods must be a preparation artifact, at least in this species. Furthermore, some scanning electron micrographs (Fig. 125) indicate that the flaps are composed of three finger-like structures, possibly two cilia and one cortical palp, as in Plagiocampa (FAURÉ-FRE-MIET & ANDRÉ 1965).

The silverline system of *Urotricha* is composed, like that of e.g. *Paramecium*, of a direct connecting and an indirect connecting system (Fig. 43). The direct system consists of longitudinal silverlines connecting the basal bodies of the cilia; short horizontal silverlines, which contain granules and/or minute rings (very likely repre-

senting attachment sites of extrusomes), branch off from the longitudinal silverlines at rather regular intervals. The indirect system forms a very regular, honey-combed pattern with cilia slightly right of centre of the individual meshes. This system is congruent with the cortical alveoli recognizable in live specimens (Fig. 146) and in scanning electron micrographs (Figs. 119–121). The unciliated posterior pole region contains a rather irregular silverline network, possibly belonging to the indirect system.

Key to urotrichs with three or more caudal cilia and description of species

Some important characters (e.g. brosse structure, number and arrangement of caudal cilia) of the urotrichs are difficult to recognize in vivo even with interference contrast. Thus, reliable identification often needs silver impregnation although some species and/or species groups can be correctly identified by careful inspection of live cells. We recommend that ecologists use silver carbonate, a fast

1	Marine or brackish
_	Freshwater or terrestrial
2	Length 38-53 µm, macronucleus distinctly elongate, 46-56 ciliary rows, about 3 caudal cilia, brosse row (kinety) 3 with
	8-9 dikinetids (paired basal bodies)
_	Length 69-80 µm, macronucleus probably ellipsoidal, brosse row 3 with 3 dikinetids U. baltica (no figure available)
3	Terrestrial. Macronucleus distinctly elongate, 30-32 ciliary rows, about 13 caudal cilia U. terricola (Figs. 48-50)
_	Freshwater. Macronucleus ellipsoidal or globular
4	With somatic trichocysts (extrusomes; observe carefully because inconspicuous in some species!)
_	Without somatic trichocysts
5	Trichocysts conspicuous, about 5 μ m long and \pm fusiform, produce distinct peripheral fringe. Length of cells usually
	50–100 μm
_	Trichocysts inconspicuous, usually less than 5 µm long and slender, do not form distinct peripheral fringe. Length of cells
	usually 30–50 μm
6	Ellipsoidal to globular, i.e. posterior, unciliated portion evenly rounded and indistinctly set off from rest of cell.
	60-100 µm long, about 80 ciliary rows and 12 caudal cilia. Brosse rows of same length, each consisting of about 10
	dikinetids (paired basal bodies)
_	Champagne cork shaped, i.e. posterior, unciliated portion narrowed and set off plug-like from rest of cell
7	Less than 8 caudal cilia
_	10–20 caudal cilia forming distinct tuft at posterior end
8	$42-50$ ($\bar{x} = 46$) ciliary rows, $14-18$ ($\bar{x} = 16$) caudal cilia, excretory pore of contractile vacuole outside circle formed by
	caudal cilia; brosse rows very short, each consisting of 2–4 dikinetids U. pelagica (Figs. 67–85)
-	$51-62$ ($\bar{x} = 58$) somatic kineties, $12-16$ ($\bar{x} = 13$) caudal cilia, excretory pore of contractile vacuole within circle formed
	by caudal cilia; brosse kineties distinct, each consisting of about 7 dikinetids U. apsheronica (Figs. 88–126)
9	Distinctly cylindroid, 3 widely set and obliquely spread caudal cilia U. pusilla (Figs. 58–66)
_	Ellipsoidal or globular, 4–10 caudal cilia
10	Two size types of rod-shaped trichocysts, somatic ones about 3 µm long, those in posterior plug about 6 µm long. About
	35–50 ciliary rows
-	Trichocysts of same length $(2.5-4 \mu\text{m})$ throughout. About 28–38 ciliary rows
11	5–6 brosse rows; trichocysts 4 µm long; body shape ellipsoidal U. matthesi (Figs. 151–154)
-	3 brosse rows; trichocysts 2.5 µm long; body shape conical U. matthesi tristicha (Figs. 155–163)
12	Body length $< 60 \mu\text{m}$
-	Length about 90 µm
13	With symbiotic algae (zoochlorellae). Cortex distinctly vacualated U. alveolata (Figs. 165–167)
	Without symbiotic algae. Cortex of usual structure. 55–60 ciliary rows, 4 minute brosse rows U. faurei (Figs. 168–170)

Body, length Body, width	F, PW F, PW C, PF F, PW F, PW C, S F, PW F, PW C, PF E, PW F, PW	UA UP UCC UCS UV LP UA UP	48.2 47.4 29.0 32.2 55.6 44.2 40.8	46 47 29 32 2 42	8.5 6.3 2.5 4.5 3.7 65	1.6 1.4 0.5 0.9	17.5 13.4 8.7 13.9	35 37 24	63 60 35	27 22 30
Body, width	F, PW C, PF F, PW F, PW C, S F, PW F, PW C, PF E, PW F, PW	UP UCC UCS UV LP UA UP	47.4 29.0 32.2 55.6 44.2 40.8	47 29 32 ? 42	6.3 2.5 4.5 3.7	1.4 0.5 0.9	13,4 8,7 13,9	37 24	60 35	22 30
Body, width	C, PF F, PW F, PW C, S F, PW F, PW C, PF E, PW F, PW	UCC UCS UV LP UA UP	29.0 32.2 55.6 44.2 40.8	29 32 ? 42	2.5 4.5 3.7	0.5 0.9	8.7 13.9	24	35	30
Body, width	F, PW F, PW C, S F, PW F, PW C, PF E, PW F, PW	UCS UV LP UA UP	32.2 55.6 44.2 40.8	32 ? 42	4.5 3.7	0.9	13.9	100		200
Body, width	F. PW C. S F. PW F. PW C. PF E. PW F. PW	UV LP UA UP	55.6 44.2 40.8	? 42	3.7	1. 11		24	33	22
Body, width	C, S F, PW F, PW C, PF F, PW F PW	LP UA UP	44.2 40.8	42	65	1.4	6.7	52	63	7
Body, width	F, PW F, PW C, PF F, PW F, PW	UA UP	40.8	10	4.2	1.6	14.6	36	60 35 33 63 59 59 55 28 38 55 62 52 51 29 35 ? 46 12 8 6 8 ? 9 24 22 14 17 33 ? 12 10 0	17
	F, PW C, PF F, PW F, PW	UP	10.0	40	8.1	1.2	19.8	31	59	43
	C, PF E, PW E PW	LICC	40.9	40	6.2	1.1	15.2	30	55	32
	F, PW	ULL	25.0	25	1.4	0.3	5.7	22	28	30
	E PW	UCS	28.7	28	3.8	0.7	13.4	23	38	31
		UV	50.4	2	2.6	1.0	5.1	43	55	7
	C, S	LP	47.6	46	5,6	1.0	11.8	39	62	32
Somatic kineties	F PW	UA	39.5	38	6.8	1.6	17.4	31	52	18
length	E PW	UP	39.1	38	7.0	1.7	18.0	30	51	17
in the second se	C PF	UCC	73.9	24	23	0.4	97	18	29	30
	F PW	UCS	26.0	26	4.6	1.0	17.6	20	35	20
	E PW	UV	20.0	9	2	2	-9	20	2	
	C, S	LP	34.3	32	4.9	1.2	14.3	29	46	16
Anterior and to and of	F PW	TIA	8.4	o	1.8	0.4	22.0	6	12	25
brosse distance	E PW	LIP	5.0	6	1.0	0.4	24.4	3	8	11
brosse, distance	CPE	LICC	12	5	1.1	0.2	25.7	2	6	25
	E DW	LICS	5.0	6	1.2	0.2	21.6	Â	ů.	1.1
	E DW	UVS	2.0	-0	1.0	9	21.0		2	-9
	C, S	LP	7.6	8	1.0	0.3	13.4	6	9	12
Manager and American	F 1944		17.1	17	2.0		16.7	12	24	24
Macronucleus, length	F, PW	UA	17.4	17	2.9	0.5	10./	15	24	34
	F, PW	UP	10.5	17	4.0	1.0	27.7	12	22	22
	C, PF	UCC	11.5	12	1.4	0.5	12.0	8	14	28
	F, PW	UCS	12.1	12	1.7	0.5	15.8	9	17	24
	F. PW	UV	30.0	1 August	2.2	0.8	1.2	26	35	1
	C, \$	LP	Ŷ.	3	1	3	3	2	2	3
Macronucleus, width	F. PW	UA	8.9	9	1.6	0.3	17.8	6	12	39
	F, PW	UP	8.0	8	1.6	0.3	20.6	6	12	24
	C, PF	UCC	8.2	9	1.0	0.2	11.9	6	10	29
	F, PW	UCS	6.4	6	1.2	0.2	18.7	5	9	30
	F. PW	UV	13.4	2	1.4	0.5	10.4	12	16	7
	C, S	LP	2	2	2	2	2	2	2	2
Micronucleus, length	F, PW	UA	4.2	4	1.1	0.2	25.5	3	7	22
	F. PW	UP	3.1	3	0.7	0.2	22.9	2.5	5	10
	C. PF	UCC	1.7	1.5	0.3	0.1	19.9	1.5	2.5	11
	F. PW	UCS	2.6	2.5	0.5	0.1	19.7	2	3.5	18
	F. PW	UV	2	2	2	2	?	2	2	1
	C, S	LP	?	2	2	2	2	2	2	2
Micronucleus width	E. PW	UA	2.6	2.5	0.7	0.1	27.1	1.5	3.5	24
and a state of the	F. PW	UP	27	2.5	0.3	0.1	11.9	2.5	2.5	11
	C PE	UCC	15	15	0.2	0.1	12.0	13	2	IT.
	F.PW	UCS	2.2	2	0.4	0.1	18.6	15	3	22
	F PW	UV	2	2	9	9.	2	2	2	
	C S	LP	9	7	9	2	2	17	2	0

Table 1. Morphometric characteristics from Urotricha apsheronica (UA), Urotricha pelagica (UP), Urotricha castalia (UCC; Lake Constance population), Urotricha castalia (UCS; Salzburg population), Urotricha venatrix (UV; from Song & WILBERT 1989), and Longitricha puytoraci (LP).

	A DESCRIPTION OF A DESC
Ishle	(continued)
Table L.	(commucu)

Character ¹)	Method ²)	Species	\bar{x}	М	SD	SD _x	CV	Min	Max	n
Oral opening, diameter	F, PW	UA	10.2	10	1,1	0.2	10.5	8	13	38
	F, PW	UP	7.7	7	1.3	0.2	16.5	6	12	32
	C, PF	UCC	6.2	6	-	-		6	7	30
	F, PW	UCS	7.4	7	0.9	0.2	12.7	6	11	30
	F. PW	UV	2	?	?	?	2	2	2	?
	C, S	LP	11.2	11	1.4	0.3	12.4	9	$\begin{array}{c} 13\\ 12\\ 7\\ 11\\ 2\\ 14\\ 4.5\\ 2.5\\ 3\\ 2\\ 4\\ 4.5\\ 2.3\\ 2\\ 3.2\\ 3.2\\ 3.2\\ 3.2\\ 3.5\\ 1.5\\ 1.5\\ 1.5\\ 1.5\\ 1.5\\ 2\\ 2\\ 2\\ 2\\ 8\\ 6\\ 5\\ 5\\ 2\\ 6\\ 8\\ 4\\ 4\\ 5\\ 2\\ 5\\ 7\\ 6\\ 8\\ 4\\ 4\\ 5\\ 2\\ 5\\ 7\\ 7\\ 7\\ 7\\ 7\\ 7\\ 7\\ 7\\ 7\\ 7\\ 7\\ 7\\ 7\\$	29
Brosse kinety 1, length	F. PW	UA	3.9	4	0.5	0.1	13.8	3.0	4.5	31
	F. PW	UP	2.2	2	0.5	0.1	20.9	1.5	2.5	16
	C, PF	UCC	2.6	2.5	0.4	0.1	13.9	1.7	3	23
	F. PW	UCS	2.1	2	0.4	0.1	19.7	1.5	3	14
	F, PW	UV	?	?	?	?	?	2	2	2
	C, S	LP	3.1	3	0.4	0.1	13.0	2.8	4	26
Brosse kinety 2, length	F. PW	UA	3.5	3.5	0.5	0.1	13.9	3	4.5	32
	F. PW	UP	1.5	1.5	0.2	0.0	10.9	1.2	2	18
	C. PF	UCC	1.7	1.5	0.3	0.1	17.2	1.3	2.3	16
	F. PW	UCS	1.8	1.5	0.3	0.1	19.0	1.4	2	14
	F. PW	UV	2	2	7	2	2	2	2	2
	C, S	LP	2.5	2.5	0.3	0.1	12.9	1.8	3.2	26
Brosse kinety 3. length	E PW	ŪA	3.0	3	0.3	0.1	11.1	1.8	3.5	31
alonda musif of the Bur	E PW	UP	0.9	ĩ	0.2	0.1	22.5	0.7	1.5	15
	C. PF	UCC	1.1	1	0.2	0.1	17.7	1	1.5	18
	F PW	UCS	1.0	î	03	0.1	24.7	0.7	1.5	14
	F PW	UV	7	.,	2	2	7	7	2	2
	C, S	LP	1.9	2	0.4	0.1	18.2	1.5	2.6	26
Excretory pore	F PW	UA	23	2.2	04	0.1	17.9	15	3	38
diameter	F. PW	UP	1.8	1.7	0.3	0.1	18.1	13	2.5	26
unineter	C. PF	UCC	1.5	1.5	0.1	0.0	8.7	1.3	2	23
	E PW	UCS	1.5	1.5	0.2	0.1	14.6	1.2	2	16
	F PW	UV	7	2	7	9	7	7	2	2
	C. S	LP	2.1	2	0.5	0.1	22.1	1.5	2.8	24
Dikinatide in brosse	F PW	TIA	75	7				7	8	28
kinety 1 number	F PW	LIP	45	à	1.1		1.1	4	6	13
Rulety 1, Italiber	CPF	UCC	4.6	5		-		4	5	33
Brosse kinety 2, length Brosse kinety 3, length Excretory pore, diameter Dikinetids in brosse kinety 1, number Dikinetids in brosse kinety 2, number	E PW	UCS	43	4	-	-	-	4	5	15
	E PW	UV	7	2	17	9	7	9	2	2
	C, S	LP	5,9	6	-	-	-	5	6	18
Dikinetids in brosse	E PW	UA	7.0	7	1	-	-	6	8	29
kinety 2. number	F. PW	UP	3.4	3	-	-	-	3	4	12
andy to annot	C. PF	UCC	3.8	4	-	_	_	3	4	23
	E PW	UCS	3.6	4	-	-	-	3	5	14
	F. PW	UV	7	2	7	2	2	2	2	2
	C. S	LP	4.9	5	-	-	-	4	5	17
Dikinetids in brosse	F, PW	UA	6.2	6	-	-	-	5	7	23
kinety 3, number	F, PW	UP	2.3	2	-	-	-	2	3	0
A CONTRACTOR OF A CONTRACTOR	C, PF	UCC	2.7	3	-	-	-	2	3	29
	F. PW	UCS	2.2	2	-	-	-	2	3	14
	F, PW	UV	2	2	?	2	?	2	2	2
	C, S	LP	4.0	4	0.0	0.0	0.0	4	4	16

	/ / 1
Table I	(continued)
rable 1.	(continueu)

Character ¹)	Method ²)	Species	\overline{X}	М	SD	$SD_{\bar{x}}$	CV	Min	Max	n
Somatic kineties,	F, PW	UA	57.7	58	2.9	0.5	5.0	51	62	39
number	F, PW	UP	45.9	46	2.7	0.6	6.0	42	50	23
	C, PF	UCC	37.6	38	1.4	0.2	3.8	34	41	36
	F, PW	UCS	40.4	40	3.1	0.6	7.8	35	46	31
	F, PW	UV	81.0	?	3.8	1.4	4.7	76	87	7
	C, S	LP	49.2	49	0.5	0.1	1.0	48	50	27
Somatic kineties	F, PW	UA	5.4	5	1.0	0.2	19.4	4	8	20
abutting to brosse,	F, PW	UP	3.2	3	_	_	_	2	4	9
number	C, PF	UCC	4.0	4	0.0	0.0	0.0	4	4	10
	F, PW	UCS	3.0	3	_	_	_	2	4	9
	F, PW	UV	?	?	?	?	?	?	?	?
	C, S	LP	4.6	5	-	_	_	4	5	21
Cilia in a somatic	F, PW	UA	36.3	36	5.3	1.3	14.7	28	49	16
kinety, number	F, PW	UP	32.7	32	3.9	0.9	11.8	28	38	19
	C, PF	UCC	20.1	20	2.7	0.4	13.3	14	28	39
	F, PW	UCS	24.3	25	2.6	0.6	10.7	20	28	21
	F, PW	UV	?	?	?	?	?	?	?	?
	C, S	LP	21.2	20	3.8	0.9	18.1	16	31	18
Caudal cilia, number	F, PW	UA	13.5	13	0.9	0.1	7.0	12	16	41
	F, PW	UP	16.0	16	1.0	0.2	6.1	14	18	23
	C, PF	UCC	6.7	7	1.0	0.2	15.3	4	9	45
	F, PW	UCS	8.8	9	0.5	0.1	5.9	8	10	26
	F, PW	UV	$\sim 10 - 10$	4 ?	?	?	?	?	?	?
	C, S	LP	lacking							
Circumoral dikinetids,	F, PW	UA	33.8	33	2.7	0.5	7.9	30	40	24
number	F, PW	UP	23.3	22	2.3	0.5	10.1	21	30	26
	C, PF	UCC	19.4	19	1.8	0.3	9.1	17	24	32
	F, PW	UCS	20.8	21	2.4	0.6	11.6	16	25	18
	F, PW	UV	~ 50	?	?	?	?	?	?	?
	C, S	LP	26.1	26	1.7	0.4	6.6	23	29	17

¹) All data from randomly selected cells. Measurements in μ m. CV = coefficient of variation in %; M = median, Max = maximum; Min = minimum, n = number of cells investigated; SD = standard deviation; SD_x = standard deviation of mean; \bar{x} = arithmetic mean.

²) C = cultured material; F = field material; PF = protargol impregnation, FOISSNER method (protocol 1 in FOISSNER 1991); PW = protargol impregnation, WILBERT method (protocol 2 in FOISSNER 1991); S = silver nitrate after CHATTON-LWOFF.

method that works well with urotrichs (Figs. 143, 144; FOISSNER 1991). However, it has to be emphasized that live observation is indispensable in identifying urotrichs because one of the most important characters, the trichocysts (presence/absence, size and shape), is usually recognizable with sufficient clarity only in live specimens.

Urotricha cyrtonucleata MARTIN & MONTAGNES, 1993 (Figs. 46, 47)

1993 Urotricha cyrtonucleata MARTIN & MONTAGNES, J. Euk. Microbiol., 40:544. Type slide with protargol-impregnated

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specimens deposited in the U.S. Natural History Museum, Smithsonian Institution, Washington, DC, USA, no. USNM 43113.

Description: All data are from protargol-impregnated specimens (n = more than 30, but no detailed morphometric analysis was performed). Ellipsoidal, $45 \,\mu\text{m}$ (38–53) × 32 μm (27–43). Macronucleus elongate, 35–50 μm long when extended, curving around cytopharyngeal basket in mid-body. 46–52 ciliary rows terminating in posterior fifth, consist of 35–40 cilia each; 3 rows abut to brosse kineties at acute angles. About 3 caudal cilia. Cytopharyngeal basket conspicuous, extends to mid-



Figs. 46–66. Morphology and infraciliature of *Urotricha cyrtonucleata* (46, 47), *U. terricola* (48–50), *U. venatrix* (51–56), *U. tricha* (57), and *U. pusilla* (58–66). **46, 47:** *U. cyrtonucleata*, oblique ventral view and lateral view after protargol impregnation, bar 25 μ m (from MARTIN & MONTAGNES 1993). **48–50**: *U. terricola*, posterior (48) and anterior (50) polar view after silver nitrate impregnation, and nuclear apparatus (49) stained by the Feulgen reaction, bar 10 μ m (from ALEKPEROV & MUSAYEV 1988). **51–56**: *U. venatrix* from life (51, 54), after protargol impregnation (52, 53, 55), and silver nitrate impregnation (56). Figures 51–53, 55, 56 show *U. valida* from SoNG & WILBERT (1989), figure 54 is from KAHL (1935). 51, 54: Lateral views, length 60 μ m and 80 μ m. The conical inclusions in KAHL's figure are ingested rotifers. 52: Main cell organelles. 53: Infraciliature of ventral anterior body portion. 55: Extrusomes. 56: Silverline system. **57:** *U. tricha* from life, length about 60 μ m (from WANG & NIE 1933). **58–66**: *U. pusilla* from life. Figures 58–60 from PENARD (1922), figure 61 from KAHL (1930) after PENARD (1922), figure 62 from CHORIK (1968), figures 63–65 from VUXANOVICI (1962), figure 66 from BIERNACKA (1967). 58, 59: Broad and narrow side view, length 30–40 μ m. 61–63, 66: Broad side views, length 35 μ m, 40 μ m, 28 μ m, 40 μ m. 60: Feeding specimen. 64: Anterior region at high magnification. 65: Transverse view. B = brosse, CC = caudal cilia, CK = circumoral kinety, CV = contractile vacuole, E = extrusomes, MA = macronucleus, MI = micronucleus, OB = oral basket, OF = oral flaps.

body, anteriorly surrounded by 32-36 oblique circumoral dikinetids. Three oblique brosse kineties, kinety 1 composed of 5-6 paired basal bodies, kineties 2 and 3 each composed of 8-9 paired basal bodies.

Occurrence and ecology: Locus classicus is shallow marine water (top 5 m, salinity 22–25‰) of Indian Arm, British Columbia, Canada (N 49°22'/W 122°55'). Found only once in very sparse number (14 ind./l) in February 1990. No other records known.

Remarks: Described from protargol-impregnated specimens only. Thus, redescription from life is necessary, especially to obtain data on shape, extrusomes and caudal cilia. *Urotricha cyrtonucleata* has a conspicuous, elongate macronucleus distinguishing it from all congeners, except for *U. terricola* ALEKPEROV & MUSAYEV, 1988, a species obviously overlooked by MARTIN & MONTAGNES (1993). However, *U. terricola* is a soil species which is smaller (35 µm), has less (30–32) ciliary rows and many more (16) caudal cilia.

Urotricha baltica CZAPIK & JORDAN, 1976

1976 Urotricha baltica CZAPIK & JORDAN, Acta Protozool., 15:424. Type slides were not sent on request by Dr. A. CZAPIK.

Description: All data are from an unknown number of silver nitrate-impregnated (CHATTON-LWOFF technique) specimens. Furthermore, this species was only documented by four micrographs, which were not reproduced here because of their poor quality. Length 65-80 µm; broadly ellipsoidal. Data on nuclear apparatus, contractile vacuole, extrusomes, and movement are lacking. Cortex with rectangular silverline meshes. Food vacuoles dark, probably containing bacteria. 32-36 somatic kineties in three quarters of perimeter (thus, about 40-45 in total), each kinety commences with 2 dikinetids; basal bodies loose regular arrangement in posterior quarter of cell (caudal cilia?). Oral opening apical, surrounded by about 25 dikinetids (nematodesmal bundles). Three brosse kineties, kinety 1 composed of six, kinety 2 of five, and kinety 3 of three dikinetids.

Occurrence and ecology: As yet known only from type location, i.e. the Gdańsk Bay in the Baltic Sea, where it occurred in sand polluted by organic wastes of a village.

Remarks: Very superficially described, thus needing complete redescription. Differs from *U. cyrtonucleata*, the only other marine species, in size $(65-80 \text{ vs. } 38-53 \mu\text{m})$, number of dikinetids at anterior end of kineties (2 vs. 1), number of circumoral dikinetids (25 vs. 32–36), and in the number of dikinetids composing brosse kinety 3 (3 vs. 8–9). Unfortunately, the macronucleus, which would probably distinguish *U. baltica* from *U. cyrtonucleata* unequivocally, was not described by CZAPIK & JORDAN (1976).

Urotricha terricola ALEKPEROV & MUSAYEV, 1988 (Figs. 48–50)

1988 Urotricha terricola ALEKPEROV & MUSAYEV, Zool. Zh. 67:1904. Type slide with 26 CHATTON-LWOFF silver nitrateimpregnated specimens deposited at the Institute of Zoology, Academy of Sciences of Azerbaijan, Baku, Russia; slide designation A-4W.

Description: All data are from silver nitrate-impregnated (CHATTON-LWOFF technique) specimens. Length up to 35 μ m; globular. Macronucleus elongate with large nucleoli; single micronucleus. Contractile vacuole in posterior end with single excretory pore outside circular patch formed by caudal cilia. Ciliated part of cortex with hexagonal silverline meshes, posterior pole region with irregular meshes. Cytoplasm strongly vacuolated; cells appear blackish in vivo.

30-32 somatic ciliary rows, 3 abutting to brosse kineties, leave blank rather small zone on posterior pole bearing tuft of 16 scattered caudal cilia. Oral opening apical, surrounded by about 15 dikinetids (nematodesmal bundles). Brosse composed of 3 relatively long, oblique kineties consisting of ciliated dikinetids, kinety 1 smaller than kineties 2 and 3, intersects circle formed by basal bodies at anterior end of ciliary rows.

Occurrence and ecology: As yet known only from type location, i.e. rhizosphere soil of an orchard near Kaili-Gel, Apsheron peninsula, USSR.

Remarks: Described from silver nitrate-impregnated specimens only and without detailed morphometry. Thus, redescription is necessary, especially to obtain data on shape, size, extrusomes, and variability. *Urotricha terrico-la* is the only species in the genus, except for *U. cyrtonucleata*, with a long, vermiform macronucleus. However, both species are easily distinguished by the number of caudal cilia (16 vs. 3), the number of somatic kineties (30-32 vs. 46-52), and their habitat (soil vs. marine plankton).

Urotricha venatrix KAHL, 1935 (Figs. 51–56, Table 1)

- 1935 Urotricha venatrix KAHL, Tierwelt Dtl., 30:807.
- 1989 Urotricha valida SONG & WILBERT, Lauterbornia, 3:14. Type slides with protargol (WILBERT technique) and silver nitrate-impregnated (CHATTON-LWOFF technique) specimens deposited in the College of Fisheries, Ocean University of Qingdao, China.

Synonymy: The descriptions of the main characters of *U. venatrix* and *U. valida* not only largely agree but also sound very similar. Thus, these species are very likely synonymous. SONG & WILBERT (1989) mentioned *U. venatrix* in the species comparison but did not definitely state any difference. In fact, they compared their new species not with the original description of *U. venatrix* but with the

redescription by DRAGESCO et al. (1974). However, the population studied by DRAGESCO et al. (1974) has a distinctly set off posterior body portion and long caudal cilia. Thus, it cannot be identical with KAHL's species, but is very likely *U. apsheronica* (see there for details).

Description: To make the suggested synonymy distinct, the descriptions are reproduced in the original wording (both, however, translated from German). Description by KAHL (1935): "Length $60-100 \,\mu\text{m}$; broadly ovoid; posteriorly with rather many (about 12) caudal cilia. Distinct trichocysts in ectoplasm. Moves straight ahead very quickly and performs sharp turns" (Fig. 54).

Description by SONG & WILBERT (1989): "Length in vivo $55-70 \,\mu$ m; spherical to slightly ovoid, ametabolic, posterior end slightly transverse truncate; about 10-14 caudal cilia $10-13 \,\mu$ m long. Extrusomes distinct, $5-6 \,\mu$ m long and fusiform, narrowly spaced, serrate pellicle. Movement as in other members of genus, i.e. with alternating gliding and accelerating phases. Macronucleus bean-shaped to prolate ellipsoidal, about $30 \times 14 \,\mu$ m, occasionally in two pieces. Contractile vacuole terminal. Body colourless, frequently greyish-yellow by numerous small granules. Very densely ciliated, 76-87 kineties extend almost to posterior pole leaving blank a comparatively small field, do not commence with a dikinetid. Oral flaps $2-3 \,\mu$ m long, pharyngeal basket conspicuous" (Figs. 51-53, 55, 56, Table 1).

Occurrence and ecology: Locus classicus of *U. venatrix* is the pelagial of a moorland pond, probably near Hamburg, Germany. KAHL (1935) found *U. venatrix* only once, but in considerable number. It fed only on rotifers whose indigestible remnants were defecated through the oral opening. *Urotricha venatrix* has been reported only once since the original description, viz. by SHEN YUNFEN & GU MANRU (1965), who found it rather frequently in Lake Donghu, China. Later, when the lake eutrophied, it disappeared (GONG XUNJU 1986). Locus classicus of *U. valida* is a pond (Poppelsdorfer Weiher) in Bonn, Germany, where SONG & WILBERT (1989) found few specimens in the autumn plankton.

Urotricha tricha WANG & NIE, 1933 (Fig. 57)

1933 Urotricha tricha WANG & NIE, Contr. biol. Lab. Sci. Soc. China, 10:7.

Description: In vivo $60-62 \times 48-50 \,\mu\text{m}$. Ovoid (obovoid according to figure), evenly rounded at anterior end, posterior portion gradually narrowed and rather distinctly set off, gets as round as anterior end under cover glass pressure. Macronucleus large, spherical, centrally located. One contractile vacuole in posterior end. Cortex longitud-inally striated. Extrusomes (trichocysts) long (about 8 μm according to figure) and numerous, attached to cortex, in some specimens even longer than shown in Figure 57, with interior extremities deeply imbedded in cytoplasm to

give an appearance of a bundle of fine rods radiating from centre to periphery of cell. Cytoplasm palish, granular, usually containing some vacuoles without solid content. Feeds voraciously on diatoms, *Euglena* and *Gymnodinium*. Moves swiftly by rotation, describing circles of considerable diameter; jumps in various directions at irregular intervals using caudal cilia as agent.

Cilia short, evenly distributed throughout body (obviously, WANG & NIE overlooked that plug is barren), those encircling oral opening a little elongated. Number of ciliary rows not known. Usually 4, rarely 5 or 6 caudal cilia, about a quarter or fifth the length of body, when there are four caudal cilia, they are regularly and equidistantly projected from the four corners of the plug, giving body quadruped appearance should the cell stand on these bristles.

Oral opening more or less subterminal, pharynx short and tubular, surrounded by many elongate rods (trichites) directed slightly obliquely to midline.

Occurrence and ecology: As yet found only at type location, i.e. Lake Ho Hu and in ponds near by the National Central University Farm at Nanking, China. Frequent between December and March. Possibly, *U. tricha* has been lumped with the much better known *U. pelagica* KAHL, 1935 by several authors, simply because they were unaware of WANG & NIE's paper.

Remarks: This species highly resembles *U. apsheronica*, *U. pelagica* and *U. venatrix*, all having large size and conspicuous extrusomes (cp. Figs. 51, 57, 67, 92, 94). However, WANG & NIE (1933) very definitely state that the caudal cilia of *U. tricha* "are in most cases four in number, while, in some individuals, they may be five or six", which is distinctly different from the numbers found in *U. apsheronica* (12–16), *U. pelagica* (14–18) and *U. venatrix* (10–14). Thus, *U. tricha* is very likely a distinct species needing, however, redescription with modern methods.

Urotricha pelagica KAHL, 1935 (Figs. 67–85, Table 1)

- 1935 Urotricha pelagica KAHL, Tierwelt Dtl., 30:807. No type material of *U. pelagica* has been mentioned in the literature. Thus, we have deposited eight neotype slides with specimens from Salzburg, four prepared with silver nitrate (CHATTON-LWOFF technique) and four with protargol (WIL-BERT technique), in the Oberösterreichische Landesmuseum in Linz (LI), Austria.
- 1986 Urotricha pelagica KAHL, 1932 WILBERT, Arch. Protistenk., 131:63 (partim).

Synonymy: WILBERT (1986) obviously mixed three species (Figs. 70, 71). The number of ciliary rows (45-50) matches *U. pelagica*, the number of brosse dikinetids (6-8) matches *U. apsheronica*, and the number of caudal cilia (up to 10) and the location of the excretory pore match *U. castalia*. K.-H. KRAINER (Diss. Univ. Graz) had



Figs. 67–77. Urotricha pelagica from life (67–70), after protargol impregnation (70, 74), and after CHATTON-LWOFF silver nitrate impregnation (71–73, 75–77); bar division 10 μ m. **67:** Lateral view, length 45 μ m (from KAHL 1935). **68:** Lateral view, length 20–50 μ m (from MAMAEVA 1979). The great size range indicates that several species were confused. **69:** Lateral view, length 40 μ m (from LOKOT 1987). **70, 71:** Ventral and posterior polar view (from WILBERT 1986), figure 70 is a composite from life observation and protargol – impregnated cells. Note that WILBERT mixed three species, viz. U. pelagica (number of somatic kineties), U. apsheronica (brosse), and U. castalia (number of caudal cilia, location of excretory pore of contractile vacuole). **72–77:** Somatic and oral infraciliature (originals). 72–74: Oblique anterior polar views showing details of somatic and oral infraciliature. Note variability in number of brosse kineties; three are common. 75, 76: Anterior and posterior polar view. Note excretory pore of contractile vacuole *outside* circle formed by caudal cilia. 77: Caudal cilia complexes at high magnification. B = brosse, CC = caudal cilia, CK = circumoral kinety, CV = contractile vacuole, DG = double granules at anterior end of ciliary rows, E = extrusomes, EP = excretory pore of contractile vacuole, G = argyrophilic granules possibly belonging to extrusomes, MA = macronucleus, N = nematodesmata, OA = oral aperture, P = pores.



Figs. 78–85. Urotricha pelagica (originals), infraciliature after CHATTON-LWOFF silver nitrate impregnation (78–82) and in the scanning electron microscope (83–85). **78:** Lateral view of typical specimen. **79:** Anterior polar view. Arrows mark brosse kineties, which are smaller than those of *U. apsheronica* (cp. Figs. 108, 114). **80, 85:** Posterior polar views showing excretory pore (arrow) of contractile vacuole *outside* the circle formed by the caudal cilia. **81:** Details of oral infraciliature. **82:** Posterior body portion showing conspicuous caudal cilia complexes and rather irregular silverline system. **83, 84:** Anterior polar views. Asterisk marks oral opening. Note paired oral flaps and short brosse cilia emerging between distinct ridges. B = brosse, BC = brosse cilia, CC = caudal cilia, CK = circumoral kinety, DG = double granules at anterior end of ciliary rows, EP = excretory pore of contractile vacuole, ES = end of somatic ciliary rows, G = argyrophilic granules possibly belonging to extrusomes, IDG = inner ring of double granules, OF = oral flaps.



Figs. 86, 87. Abundances of *U. pelagica* and other ciliates in lakes of the central Baikal area (from LOKOT 1987). **86:** Seasonal abundances (abscissa: ind./l; ordinate: months) in lakes Arakhlyey (1), Ivan (2), Shaksha (3), and Irgyen (4). **87:** Mean numbers (ordinate: billion ind./m³) of dominant planktonic ciliates at various stations of lake Arakhlyey. 1 - Holophrya simplex, 2 - Urotricha pelagica, 3 - Lembadion lucens, 4 - Halteria grandinella, 5 - Strobilidium velox, 6 - Strobilidium viride, 7 - total.

the same bad luck. In fact, these three species are easily confused, although *U. castalia* is distinctly apart by its comparatively inconspicuous, rod-shaped extrusomes.

Redescription (Figs. 72–85, Table 1). The original description is very brief and incomplete, hardly separating *U. pelagica* from *U. apsheronica* and *U. castalia*: "Length 40–50 μ m; very similar to *U. farcta* but with several conspicuous caudal cilia and distinct ectoplasmatic trichocysts 5–6 μ m long".

In vivo, *U. pelagica* is hardly distinguishable from *U. apsheronica*, the best characters being the shorter brosse kineties and the different location of the excretory pore of the contractile vacuole. In fact, we noted *U. pelagica* only in the silver slides, where it was, however, much less numerous than *U. apsheronica*. Thus, live observations are lacking. The in vivo observations on *U. apsheronica* were repeated later when only this species was present. The infraciliature is also very similar in both species. Thus, we refer the reader to the thorough description of *U. apsheronica* and to the detailed figures of both species. Here, we discuss only the distinguishing characters, all of which, except one, relate to morphometrics (Table 1).

The location of the excretory pore of the contractile vacuole is the sole morphological character distinguishing *U. pelagica* from *U. apsheronica*: outside the circle formed by the caudal cilia in the former (Figs. 76, 80, 85), within in the latter (Figs. 90, 105, 113, 117). This character is very constant in our material and should thus be preferred in separating these species, especially so in conjunction with the number of dikinetids comprising each brosse kinety: 2-4 in *U. pelagica*, 6-8 in *U. apsheronica*. Further, minor differences occur in the diameter of the oral aperture (7 vs. $10 \,\mu$ m), the number of circumoral dikinetids (22 vs. 33), the number of ciliary rows (46 vs. 58), and the number of caudal cilia (16 vs. 13). Thus, the proportion of somatic kineties to caudal cilia is distinctly narrower in *U. pelagica* (2.9:1) than in *U. apsheronica* (4.4:1).

Occurrence and ecology: Locus classicus not known, very likely near Hamburg, Germany. We found a weak population of *U. pelagica* in an artificial, heavily eutrophic pond in April 1993 (see Material and Methods). There are numerous records of *U. pelagica* in the literature. However, very likely it has often been confused with, or at least not separated from *U. apsheronica*, *U. castalia*, and *U. tricha*, all being superficially rather similar to *U. pelagica*.

Urotricha pelagica has been recorded from the plankton of oligo-, meso- and polytrophic ponds, reservoirs, and lakes in Germany (KAHL 1935; PACKROFF 1992; PACK-

ROFF & WILBERT 1991; WILBERT 1969), Austria (MACEK et al. 1996; own observ.), China (PAI KAO-TUNG 1962), and the former Soviet Union (ALEKPEROV 1983, 1984a, 1990; KUSTOVLYANKINA 1990; LOKOT 1987; MAMAEVA 1967a, b; OLEKSIV 1985a, b; OLEKSIV & YALYNSKAYA 1984; OLEKSIV et al. 1986; TROSHINA 1984; ŽHARI-KOV & ROTAR 1992), as well as from brackish waters in Finland (KIVI 1986).

A brief, alphabetical compilation of autecological data mentioned in the literature cited above follows. ALEKPE-ROV (1983): in the upper, middle and bottom zone (100 m) of a reservoir, with up to 850 ind./l in the upper 40 m; ALEKPEROV (1984a): up to 100 ind./l, mainly in the upper and middle (up to 15 m) zone of a shallow (max. depth 30 m) reservoir; ALEKPEROV (1990): migrates from the epilimnion to the metalimnion during daytime; KIVI (1990): °C 0-20, salinity 4.5-7%; LOKOT (1987): late spring and autumn maxima with up to 5740 ind./l in several lakes of the central Baikal area (Figs. 86, 87); MACEK et al. (1996): cell volume (Lugol-formaldehyde fixed) $6770 \pm 2620 \,\mu\text{m}^3$ (very likely distinctly underestimated; authors), up to 12% of total ciliate biomass, max. growth rate in situ 0.35/dav (mean 0.19/dav); MAMAEVA (1976a): 180-2053 ind./l in the shore zone of a reservoir; MAMAEVA (1976b): 0 (October) to 247 (May) ind./l in a reservoir, mainly in the metalimnion and in late spring; OLEKSIV (1985a, b): dominating (up to 1.200,000 ind./m³) in Ukrainian ponds, mainly in spring and early summer, when water temperature rose over 12 °C abundances of U. pelagica decreased, generation time 15 h (18-20 °C) to 27 h (8-12 °C), biomass/cell 17 (18-20 °C) to 24 $(8-12 \degree C) \text{ mg } 10^{-6}$ (very likely miscalculated; authors); OLEKSIV et al. (1986): up to 4.225,000 ind./m³ in fishponds; PACKROFF & WILBERT (1991): found in oligotrophic, mesotrophic, and eu-polytrophic lakes; WILBERT (1969, 1986): °C 2-18.4, pH 7.5-8.9, O₂ (mg/l) 0.9-16.2, NH₄-N (mg/l) 0-1.2, NO₂-N (mg/l) 0-0.2, NO₃-N (mg/l) 2.8-10.4, peak abundances (up to 40 ind./ml) in a highly eutrophic pond were observed in summer (remember, however, that WILBERT mixed three species; see above); ŽHARIKOV & ROTAR (1992): biomass (mg)/cell 0.02×10^{-3} (very likely miscalculated; authors), feeds on bacteria, detritus and diatoms.

These data indicate that *U. pelagica* is a euplanktonic ciliate preferring water temperatures <12 °C. Thus, peak abundances are usually encountered in late spring and in autumn. It occurs at all trophic levels, possibly preferring polytrophic conditions.

Urotricha apsheronica ALEKPEROV, 1984 (Figs. 88–126, Table 1)

1984 Urotricha apsheronica ALEKPEROV, Zool. Zh., 63:1417. One holotype slide and several syntype slides with CHAT- TON-LWOFF silver nitrate-impregnated specimens deposited at the Institute of Zoology, Academy of Sciences of Azerbaijan, Baku, Russia; slide designations DBW 21–26. Four CHATTON-LWOFF silver nitrate and five protargol-impregnated (WILBERT technique) voucher slides of our population have been deposited in LI.

1974 Urotricha venatrix KAHL, 1935 – DRAGESCO, IF-TODE & FRYD-VERSAVEL, Protistologica, 10:70 (misidentification).

Synonymy: We found large numbers of this species and could thus study it in detail. We separate our observations from those of ALEKPEROV (1984b) and DRAGESCO et al. (1974) who described U. apsheronica rather superficially, i.e. without detailed morphometry and live morphology. However, the main characteristics of ALEKPEROV's and our population match so well that conspecificity is beyond doubt. ALEKPEROV (1984b) compared his new species with two rather distant taxa, viz. U. ovata and Longifragma obliqua, obviously overlooking or neglecting U. pelagica which is so similar to U. apsheronica that live specimens are almost indistinguishable. Thus, subspecies rank would probably be more appropriate for U. apsheronica.

The U. venatrix population investigated by DRAGESCO et al. (1974) differs markedly from the original description, especially in having a large, narrowed, distinctly set off posterior body portion and long caudal cilia (Fig. 92). Thus, it is a misidentification (cp. Fig. 54). The characters provided by DRAGESCO et al. (1974) largely match those of U. apsheronica, although the number of somatic kineties (65-70) and circumoral dikinetids (44 according to Fig. 93), but not of caudal cilia (10-15), slightly exceeds the upper limits found by us (Table 1) and by ALEKPEROV (see below). Specifically, Fig. 19E (a micrograph and thus not reproduced here) in DRAGESCO et al. (1974) shows that the excretory pore of the contractile vacuole is within the circle formed by the caudal cilia, as is typical for U. apsheronica. Furthermore, Figs. 15B (reproduced here as Fig. 93) and 19F (a micrograph) in DRAGESCO et al. (1974) show about 6 dikinetids in each brosse kinety, which also matches U. apsheronica better than U. pelagica (Figs. 73-75, Table 1) and U. venatrix (Fig. 53).

Description by ALEKPEROV (1984b, translated from Russian; Figs. 88–91): "Living cells cinnamic brown (possibly by ingested algae; revisers) and up to 75 μ m long. Fixed specimens 55–60 μ m long and ovoid. Mouth apical with 30–35 pharyngeal rods, surrounded by dikinetids. 56–60 somatic kineties which commence near oral opening and terminate at posterior end, where 18 (16 according to Fig. 90) caudal cilia and a complex system of argyrophilic fibres are found. Macronucleus spherical, 18 μ m across; 1 micronucleus. Hexagonal silverline meshes between somatic kineties. Contractile vacuole in posterior end".



Figs. 88–93. Urotricha apsheronica from life (92), after CHATTON-LWOFF silver nitrate impregnation (89–91, 93), and after Feulgen reaction (88). **88–91:** Nuclear apparatus (18 μ m), lateral (length 60 μ m), posterior polar (length 70 μ m), and anterior polar (55 μ m) view of infraciliature (from ALEKPEROV 1984b). Arrow marks excretory pore of contractile vacuole *within* the circle formed by the caudal cilia. **92, 93:** Lateral and anterior polar view (from DRAGESCO et al. 1974, named *U. venatrix*). B = brosse.

Description by DRAGESCO et al. (1974, translated from French; Figs. 92, 93): "Fixed specimens 66 μ m long on average. Elongate ellipsoidal with posterior body portion distinctly set off and barren, except for 10–15 caudal cilia. Macronucleus sausage-shaped, 19 μ m long on average. Trichocysts distinct, fusiform, in rows. 65–70 meridional somatic kineties, each commencing with a dikinetid. Silverline meshes rectangular. Cytopharyngeal basket rather indistinct and with peribuccal granules. Circumoral kinety composed of about 44 (according to Fig. 93) oblique dikinetids. Three oblique brosse kineties, each composed of about 6 dikinetids (according to Fig. 93), in small subapical depression".

Redescription (Figs. 94–126, Table 1): In vivo about $40-70 \times 30-40 \mu m$, unflattened. Shape fragile, i.e. easily becoming globular or irregular when cell is stressed, undisturbed specimens ellipsoidal to cylindrical with unciliated posterior body portion distinctly narrowed and set off plug-like from rest of cell (Figs. 94, 99, 116); rarely, almost globular, possibly slightly distorted, specimens occur. Macronucleus distinctly (about 2:1) ellipsoidal, rarely

usually in distinct indentation of macronucleus. Contractile vacuole in posterior end, slightly eccentric, with single (very rarely two), cylindrical excretory pore in circle formed by caudal cilia (Figs. 105, 111, 117). Cortex rigid, rectangularly to slightly hexagonally patterned with longitudinal ridges slightly thicker than transverse ones and thus more distinct in vivo as well as after silver nitrate and protargol impregnation; meshes irregular and weakly stained with silver nitrate in posterior pole area, which has very small (<0.5 µm) pores, possibly representing attachment sites of trichocysts or other extrusomes (Figs. 110, 118-121). Two kinds of extrusomes, both very numerous (about 1000 each) and clearly recognizable only in live specimens: type 1 inconspicuous, 2.5-3 µm long, slightly fusiform and curved, found exclusively within pharyngeal basket (Figs. 94, 95); type 2 produces very conspicuous peripheral fringe in live specimens (Figs. 94, 106), $4.5-5 \times 0.8 \,\mu\text{m}$, fusiform, inserted right of ciliary rows and in posterior body area (Figs. 95, 107, 120, 121). Cyto-

reniform, eccentric in mid-body, after protargol impregna-

tion with globular nucleoli. Micronucleus ellipsoidal,



Figs. 94–105. Urotricha apsheronica (originals) from life (94–102) and after protargol (103, 105) and silver nitrate (104) impregnation; bar division 10 μ m. **94:** Lateral view of typical specimen containing two ingested pollen grains. Note distinct fringe formed by the extrusomes. **95:** Somatic (left two, 5 μ m) and oral (right one, 2.5 μ m) extrusomes. **96:** Pharyngeal rod. **97:** Oral area, composite from life and scanning electron microscopical observations. **98:** Brosse cilia, length 5 μ m. **99:** Shape variant. **100:** Margin of oral aperture. **101:** Oral flap in side and transverse view. Note that flaps are single structures in life, but paired after preparation for scanning electron microscopy (cp. Figs. 97, 122–125). **102:** Cortical pattern recognizable with interference contrast under optimal conditions. **103:** Oblique anterior polar view showing details of oral infraciliature and brosse. Note that brosse kineties are longer than in *U. pelagica* (cp. Figs. 74, 79). **104, 105:** Anterior and posterior polar view. Note excretory pore of contractile vacuole within circle formed by caudal cilia, as indicated by single, displaced caudal cilium. B = brosse, C = cilia, CK = circumoral kinety, DG = double granules at anterior end of ciliary rows, EP = excretory pore of contractile vacuole, OF = oral flaps, PG = pollen grain, R = ridges.

plasm colourless, usually containing some food vacuoles up to 40 μ m across (see ecology), many 2–5 μ m sized fat globules in anterior and about 1 μ m sized fat globules in posterior half, and some 5 μ m long crystals around contractile vacuole. Swims fast, jumping conspicuously at irregular intervals. Somatic cilia $8-10 \,\mu\text{m}$ long and with parasomal sac right of basal body, inserted right of centre of cortical hexagons (Figs. 119, 120); arranged in equidistant, longitudinal rows extending about 80% of body length, 4-8rows, usually 5 (Table 1), abut to right side and posterior end of brosse, all other kineties commence around oral



Figs. 106–115. Urotricha apsheronica (originals) from life (106, 107) and after protargol (108–111) and CHATTON-LWOFF silver nitrate impregnation (112–115). 106, 107: Slightly flattened specimen showing distinct fringe formed by long, fusiform extrusomes, 108, 114: Lateral views showing brosse. 109: U. apsheronica can ingest large food items by its wide oral basket. 110: Cortical pattern. 111, 113: Posterior polar views. Arrow marks two caudal cilia displaced by the excretory pore. 112, 115: Anterior polar views. Asterisk marks oral aperture. B = brosse, CC = caudal cilia, CK = circumoral kinety, DG = double granules at anterior end of ciliary rows, E = extrusomes, EP = excretory pore of contractile vacuole, FR = microfibrillar ring, FV = food vacuoles, N = nematodesmata, OA = oral aperture, OB = oral basket, P = pores.



Figs. 116–121. Urotricha apsheronica in the scanning electron microscope (originals). **116:** Oblique anterior polar view. For details of oral apparatus see Figs. 122–126. Note metachronal ciliary waves: **117:** Posterior polar view. Note excretory pore (EP) of contractile vacuole within circle formed by caudal cilia; in *U. pelagica*, a very similar species, the excretory pore is *outside* the circle formed by the caudal cilia (Fig. 85). **118:** Part of posterior pole area showing many tiny pores (arrows), possibly marking sites where extrusomes are anchored. **119, 120:** Partially and completely demembranated cells showing cortical sculpturing very similar to the pattern sometimes seen after protargol impregnation (Fig. 110). **121:** Demembranated posterior pole showing reticulate pattern formed by cortical alveoli. BB = basal bodies, CC = caudal cilia, CR = ciliary rows, E = extrusomes, EP = excretory pore of contractile vacuole, OA = oral apparatus.



Figs. 122–126. Urotricha apsheronica in the scanning electron microscope (originals). The figures are polar and oblique anterior polar views showing oral and brosse structures. Asterisk marks centre of pharyngeal basket. Arrowheads denote unciliated basal body at anterior end of somatic kineties; this unciliated and the following ciliated basal body appear as dikinetid in silver slides (Figs. 108, 112, 114). Note high variability of brosse ridges and oral flaps composed of two or three rod-shaped structures each, although they appear as single palp in live cells (Figs. 100, 101). When contracted, the pharyngeal wall forms four lobes producing a cruciform pattern (104, 122, 124). B = brosse, OF = oral flaps, P = pores, R = ridges.

opening with a dikinetid having a slightly shortened, about $6 \,\mu\text{m}$ long posterior cilium (Figs. 104, 105, 112, 116, 122). Caudal cilia about 15 μm long, originate from small pits each surrounded by a flat ridge, arranged in rather wide, regular circle, except for 1–3 cilia, usually 1, displaced centripetally at excretory pore of contractile vacuole (Figs. 105, 110, 111, 113, 117, 121).

Oral opening slightly projecting from body proper, circular, in or slightly out of centre of anterior end (Figs. 94, 97, 99, 112, 116). Pharyngeal basket conspicuous, especially in protargol slides (Fig. 109), conical, extends almost to posterior body end, anteriorly with distinct microfibrillar ring connecting pharyngeal rods, filled with viscous plasm and fine extrusomes described above (Figs. 94, 103, 108, 109); lined by distinctly ribbed membrane having evenly spaced pores subapically, which appear as ring of granules in silver nitrate-impregnated specimens (Figs. 97, 100, 115, 125); ribbed membrane frequently with four lobes, at least in fixed specimens, producing cruciform pattern (Figs. 104, 122, 124). Pharyngeal rods thick, bifurcated in posterior half, at anterior end with small tooth covered by pharyngeal or, respectively, cell membrane; rod-teeth produce minute crown around oral opening and are continuous with ribs of membrane lining pharyngeal basket (Figs. 96, 124, 125).

Oral flaps at base of pharyngeal teeth, originate from circumoral dikinetids, can swing there and back oral opening, unpaired, i.e. navicular with slightly brighter midline due to dumb-bell shaped outline clearly recognizable in top view (Figs. 97, 100, 101); in scanning electron micrographs, however, invariably paired or triplicate, i.e. composed of two or three closely spaced, individual processes forming dense fringe around oral aperture (Figs. 97, 116, 122-126). Brosse enklitolophdexiotrop to enklitoloph-syntrop, upper kinety intersects circle formed by dikinetids at anterior end of ciliary rows, invariably composed of 3 oblique rows slightly decreasing in length and kinetid number from anterior to posterior; brosse rows composed of oblique dikinetids having only anterior basal body ciliated, implanted between minute, proximally fusing cortical ridges appearing as compact, elongate tile in side view; brosse cilia slightly flexible, inflated and hyaline distally, appear very short, although about 5 µm long, because posterior, more compact half covered by brosse ridges (Figs. 97, 98, 103, 104, 108, 112, 114, 122-126).

Occurrence and ecology: Locus classicus of *U. apsheronica* is the Djeiranbaten reservoir on the Apsheron peninsula of Azerbaijan. It occurred in the plankton with a maximum abundance of about 20 ind./l and did not show distinct diurnal migration (ALEKPEROV 1990). We found *U. apsheronica* in large numbers (>1000 ind./l) in late spring in the pond at Salzburg University. Most cells had ingested at least one pollen grain (up to 40 μ m across) and several algae (dinoflagellates, diatoms), rarely

also some ciliates. DRAGESCO et al. (1974) found their *U. venatrix* in a pond near Paris.

Remarks: Very likely, *U. apsheronica* has often been confused with *U. pelagica* (see there) and *U. castalia* due to its numerous caudal cilia. However, *U. castalia* is easily distinguished from *U. pelagica* and *U. apsheronica* by its inconspicuous, rod-shaped trichocysts.

Urotricha pusilla PENARD, 1922 (Figs. 58-66)

1922 Urotricha pusilla PENARD, Études Infusoires: 18.

- 1930 Urotricha pusilla PENARD, 1922 KAHL, Tierwelt Dtl., 18:59.
- 1962 Urotricha pusilla PENARD, 1922 VUXANOVICI, Studii Cerc. Biol., 14:197.
- 1967 Urotricha pusilla PENARD, 1922 BIERNACKA, Wiss. Z. Univ. Greifswald, 16:244.
- 1968 Urotricha pusilla PENARD, 1922 CHORIK, Planktonwimpertiere: 46.

Taxonomy: KAHL (1930) suggested transferring *U. pusilla* to *Pithothorax*, if a reinvestigation confirmed the lack of oral flaps. However, VUXANOVICI (1962) observed that the circumoral cilia form a small dome, indicating the presence of oral flaps (Fig. 64). Thus, we keep it with *Urotricha*. In contrast to PENARD (Figs. 58, 59), all later students figured, but did not describe, the ciliary rows as extending onto the posterior pole of the organism (Figs. 62, 63, 66). Certainly, this species needs careful redescription from live and silver-impregnated specimens. For the present, *U. pusilla* is easily distinguished from the congeners by its slender shape and the widely spaced, obliquely spread caudal cilia.

Description: $30-40 \times 10-15 \,\mu\text{m}$, shape rather constant, cylindroid with slight equatorial constriction, both ends broadly rounded, almost circular in transverse section (Fig. 65), slightly asymmetrical anteriorly (Fig. 59). Macronucleus globular to slightly ellipsoidal, in middle third of body. Contractile vacuole in posterior end slightly out of midline (PENARD 1922; BIERNACKA 1967). Cortex firm and flexible, distinctly furrowed by ciliary rows, contains very fine extrusomes recognizable, however, only when extruded in strongly squeezed specimens (PENARD 1922); VUXANOVICI (1962) observed a dense granulation between the ciliary rows, possibly mucocysts (Fig. 64). Cytoplasm colourless with some refractile, small inclusions either around contractile vacuole (PENARD 1922) or in anterior end (BIERNACKA 1967). PENARD (1922) observed some coloured food vacuoles, and a feeding specimen with greatly extended anterior end (Fig. 60).

Somatic and oral infraciliature insufficiently known. About 6-7 ciliary rows per side terminate near posterior end of cell, where usually 4, rarely 2 or 6-8 long caudal cilia emerge from minute cortical pits; caudal cilia often difficult to recognize because obliquely spread and thus out of focus when cell is viewed laterally. Oral opening at anterior end, surrounded by closely spaced cilia (oral flaps?) forming small dome (Fig. 64). Cytopharyngeal basket not recognizable; however, VUXANOVICI (1962) observed a minute $(1-1.5 \,\mu\text{m})$, central depression (Fig. 64).

Occurrence and ecology: Locus classicus is a pond near Geneva, Switzerland, where PENARD (1922) found huge numbers of *U. pusilla* in August and September. BIERNACKA (1967) reported *U. pusilla* from a brackish coastal pond at Hiddensee, a small island at the north coast of Germany, where it was very abundant; she classified *U. pusilla* as euryhaline. VUXANOVICI (1962) found many specimens in the sapropelic mud of Lake Fundeni near Bucharest, Rumania. CHORIK (1968) observed some specimens in the plankton of small water bodies in Moldavia. LIEPA (1983, 1990) and VEYLANDE & LIYEPA (1985) found *U. pusilla* on the sediment surface of small and large Latvian rivers between 18 °C and 23 °C.

Urotricha castalia MUÑOZ, TÉLLEZ & FERNÁNDEZ-GALIANO, 1987 (Figs. 127–150, Tables 1, 2)

- 1987 Urotricha castalia MUÑOZ, TÉLLEZ & FERNÁNDEZ-GALIANO, Acta Protozool., 26:200. No type material of *U. castalia* has been mentioned in the literature. Thus, we have deposited eight neotype slides with specimens from Salzburg, four prepared with silver nitrate (CHATTON-LWOFF technique) and four with protargol (WILBERT technique), in the Oberösterreichische Landesmuseum in Linz (LI), Austria.
- 1994 Urotricha rotunda FERNANDEZ-LEBORANS & NOVILLO, Proc. biol. Soc. Wash., 107:231. Type slides with silver carbonate-impregnated cells deposited in the Departamento de Biologia Animal I (Zoologia), Universidad Complutense, Madrid, Spain, no. 2788a–1. However, none of the type slides was sent on request by FERNANDEZ-LEBORANS because "they were sent provisionally to another laboratory"; possibly, no type slides exist or the author had reservations about our checking his description.

Synonymy: Both species were poorly described, i.e. from squashed silver carbonate-impregnated specimens only, and lack accurate figures. Thus, we provide a full redescription. The main characteristics (number of somatic and brosse kineties, number of caudal cilia and circumoral dikinetids, presence of extrusomes) of U. castalia and U. rotunda are identical and match our data from the Salzburg population (Table 2). Thus, these three populations, although differing in some details (number of kinetids comprising somatic and brosse kineties), are considered as conspecific. There is, however, a main character which does not agree, viz. the location of the contractile vacuole, which supposedly is near mid-body in U. rotunda. Unfortunately, the authors neither document this unusual location by a photograph nor comment on it. Thus, we interpret it as misobservation because all other urotrichs have the contractile vacuole near the posterior end. Furthermore, morphometry is incomplete in both species, i.e does not indicate the source of the metric data (very likely from more or less heavily squashed silver carbonate preparations and thus useless), and many of the measurements from U. rotunda look unreliable because of their low variation. For instance, a range of only 3 µm is reported for the width of 80 specimens, which is unbelievably small.

Very recently, we studied a population of this species from Lake Constance (Germany), obtained by H. MULLER and cultured on *Rhodomonas* sp. It was very similar to the Salzburg population in most characters, especially in having two size-types of extrusomes, however, the number of caudal cilia was closer to the type population (Tables 1, 2). Furthermore, the cultured specimens showed considerable variation in body shape, although it was very similar to the Salzburg population in some specimens, most had the posterior unciliated body portion indistinctly set off or evenly rounded (Fig. 127).

Table 2. Comparison of main characters in *U. castalia*, type population (n = ?; from MUNOZ et al. 1987), *U. castalia*, Salzburg population (for details see Table 1), *U. castalia*, cultured population from Lake Constance (for details see Table 1), and *U. rotunda* (from FERNANDEZ-LEBORANS & NOVILLO 1994, n = 80), a junior synonym of *U. castalia*.

Character ¹)	U. castalia	U. castalia					
	Туре	Salzburg	Lake Constance				
Somatic kineties, number	47-50	35-46(40)	34-41(38)	45-48			
Cilia in a somatic kinety, number	16-18	20-28(24)	14 - 28(20)	30-36(33)			
Caudal cilia, number	5-7	8-10(9)	4 - 9(7)	6 - 8(7)			
Circumoral dikinetids, number	20-25	16 - 25(21)	17 - 24(19)	22 - 24(23)			
Brosse kineties, number	3	3(3)	3(3)	3(3)			
Dikinetids in brosse kinety 1	5 - 9	4 - 5(4)	4 - 5(5)	7 - 10(8)			
Dikinetids in brosse kinety 2	4-6	3 - 5(4)	3 - 4(4)	6 - 7(6)			
Dikinetids in brosse kinety 3	3-5	2 - 3(2)	2 - 3(3)	3 - 4(3)			
Extrusomes	abundant	abundant	abundant	footnote 2			

1) Arithmetic means, if available, in brackets.

²) Not mentioned but recognizable in Fig. 13 of FERNANDEZ-LEBORANS & NOVILLO'S paper.



Figs. 127–138. Urotricha castalia (127–135, originals; 136, Spanish type population from MUÑOZ et al. 1987) and its synonym U. rotunda (137, 138, from FERNANDEZ-LEBORANS & NOVILLO 1994) from life (127–130), after protargol (131–133, 135), CHATTON-LWOFF silver nitrate (134), and silver carbonate (136–138) impregnation; bars 10 μ m. **127, 128:** General view and extrusomes of cultured specimens from Lake Constance. **129, 130:** General view and extrusomes of field specimens from pond in Salzburg. Note that both populations have long extrusomes only in posterior plug. **131, 132, 135:** Anterior and posterior polar views. **133, 134:** Oblique ventral views showing details of oral structures and brosse variability. **136:** Ventral view of type population (from squashed preparation). **137, 138:** General and ventrolateral view (squashed preparations). B = brosse, C = cilia, CC = caudal cilia, CK = circumoral kinety, DG = double granules at anterior end of ciliary rows, EP = excretory pore of contractile vacuole. FR = microfibrillar ring, KD = kinetodesmal fibres, OF = oral flaps.



Figs. 139–147. Urotricha castalia (originals) from life (139, 142, 145, 146) and after silver carbonate (140, 141, 143, 144) and protargol (147) impregnation. **139–142, 145:** Flattened specimens showing main cell organelles and extrusomes, some of which seen in top view (arrowheads). Note that *U. castalia* is studded with short extrusomes in the ciliated body portion and with long extrusomes in the unciliated plug (139, 142); a single circle surrounds the oral aperture (141). **143, 144:** Oblique anterior and posterior polar view of same specimen showing somatic and oral infraciliature. Asterisk marks oral aperture, arrow denotes faintly stained excretory pore. **146:** Cortical pattern and extrusomes (arrowheads) in surface view. **147:** Main cell organelles: B = brosse, CC = caudal cilia, E = extrusomes, FG = fat globules, MA = macronucleus, MI = micronucleus, OA = oral aperture, OB = oral basket.



Figs. 148–150. Urotricha castalia (originals), somatic and oral infraciliature after silver carbonate (148, 150) and protargol (149) impregnation. **148:** Lateral view showing the characteristic bipartition of the urotrich infraciliature in a densely ciliated main portion and an unciliated, narrowed posterior fifth bearing a circle of elongated caudal cilia. **149:** Ventrolateral view with brosse kineties marked by arrowheads. **150:** Oblique anterior view showing brosse kineties (arrowheads) and deeply impregnated extrusomes around pharyngeal opening (asterisk). CC = caudal cilia, DG = double granules at anterior end of ciliary rows, E = extrusomes, ES = end of somatic ciliary rows, FV = food vacuole, OA = oral aperture, OF = oral flaps.

Description by Muñoz et al. (1987; Fig. 136, Table 2; very likely solely based on squashed silver carbonate-impregnated cells): Size $44-67 \times 39-65 \,\mu\text{m}$, spherical. Macronucleus $11-19 \,\mu\text{m}$, micronucleus $3.5-4.5 \,\mu\text{m}$ in diameter. Abundant somatic toxicysts. 47-50 meridional somatic kineties and a tuft of 5-7 long caudal cilia; kineties composed of 16-18 kinetosomes each, except of 5-7 rows which abut to the brosse and are thus shortened, each consisting of only 12-15 kinetosomes. Three brosse kineties rectangular in shape and obliquely disposed, decrease in size posteriorly, kinety 1 composed of five to nine dikinetids, kinety 2 of four to six, kinety 3 of three to five. Circumoral kinety made of 20-25 oblique dikinetids.

Redescription (Figs. 127–135, 139–150, Table 1): Size in vivo about $30-40 \times 20-30 \,\mu\text{m}$. Ellipsoidal to slightly fusiform because oral opening rather distinctly projecting and unciliated posterior portion narrowed pluglike, remaining conspicuous even after protargol impregnation (Fig. 147). Macronucleus in mid-body slightly out of midline, distinctly ellipsoidal, in vivo with reticulate nucleolus, shrinking to globular aggregates in prepared specimens. Micronucleus slightly ellipsoidal, in small indentation of macronucleus (Figs. 130, 139, 147). Contractile vacuole in posterior end between body margin and midline; excretory pore usually in, rarely outside circle formed by caudal cilia (Figs. 127, 132, 135, 144). Cortex thick, longitudinally striated by serially arranged pentagonal meshes becoming polygonal in unciliated posterior region (Fig. 146). Silverline system as described in U. apsheronica. Two types of extrusomes: type 1, very

numerous and found in and around (possibly between or within oral flaps) oral opening and in longitudinal rows between somatic kineties, $2.5-3 \mu m$ long and slightly fusiform; type 2, found only in unciliated posterior body portion, $5-6 \mu m$ long and rod-shaped (Figs. 127–130, 139–142, 145, 146, 150). Cytoplasm colourless, with some 1–3 μm sized crystals, few to many 2–5 μm sized fat globules, and some large (up to 20 μm) food vacuoles containing *Peridinium* sp. and *Chlamydomonas* sp. Rotates about longitudinal body axis, performing fast jumps at irregular intervals.

Ciliary rows extend over about 80% of body length. All kineties, except those abutting to brosse, commence with a single dikinetid having only the posterior basal body ciliated (Figs. 127, 129, 131–134, 143, 148–150). Caudal cilia form narrow circle in centre of posterior pole (Figs. 127, 129, 132, 144, 148), occasionally rather irregularly arranged (Fig. 135). Left of brosse small, blank area due to one to two shortened ciliary rows (Figs. 131, 134, 150).

Pharyngeal opening in centre of anterior pole, surrounded by an average of 21 oblique dikinetids having about 2 μ m long cilia forming indistinct oral flaps. Pharyngeal basket conical, extends to posterior third of cell (Figs. 127, 129, 131, 134, 139, 145, 147). Brosse usually composed of 3, rarely (in 2 out of 40 specimens) of 4–5 short kineties, upper kinety intersects circle formed by dikinetids at anterior end of ciliary rows; distinctly enklitoloph-syntrop, i.e. shortened ciliary rows occur at both sides of the brosse kineties (Fig. 131, 134, 149, 150), as



Figs. 151–154. Urotricha matthesi (from KRAINER 1995) from life (151) and after protargol impregnation (152–154); bars 10 μ m. 151: General view of specimen with large food vacuoles. 152: Infraciliature of ventral side. Arrowhead marks brosse, arrow denotes cortical meshes. Note irregular arrangement of basal bodies in somatic kineties. 153, 154: Posterior and anterior polar view. Arrow marks circumoral kinety. B = brosse, EP = excretory pore of contractile vacuole, FV = food vacuole, NA = nuclear apparatus.

also recognizable in the figures from the type population (Fig. 136) and the synonym *U. rotunda* (Fig. 138); brosse kineties occasionally rather irregularly arranged (Fig. 133).

Occurrence and ecology: Locus classicus of *U. castalia* is an artificial pond in the "Parque de Berlin", Madrid, Spain, where it occurred in large numbers from October to May. It could be cultivated with small flagellates as food organisms. Locus classicus of the synonym, *U. rotunda*, is a reservoir at La Jarosa, about 60 km out of Madrid (N 40°12'/W 4°10'). We also found *U. castalia* in a pond, mainly in late spring. It occurred in low numbers feeding on *Peridinium* sp. and *Chlamydomonas* sp. Other records or detailed ecological data not known.

Remarks: *U. castalia* is distinguished from *U. pelagica* and *U. apsheronica*, with which it is easily confused due to the numerous caudal cilia, by the smaller size (length $30-40 \mu m$ vs. $40-70 \mu m$) and the less conspicuous, rod-shaped extrusomes. It is also easily confused with *U. matthesi* and *U. matthesi* tristicha which, however, lack elongated extrusomes in the posterior body portion and have fewer ciliary rows (28–35 vs. 35–50).

Urotricha matthesi KRAINER, 1995 (Figs. 151–154, Table 3)

1995 Urotricha matthesi KRAINER, Lauterbornia, 21:43. One holotype and one syntype slide, both with protargol-impregnated specimens (FOISSNER technique), deposited in LI.

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Description: In vivo $30-45 \times 20-40 \,\mu\text{m}$. Ovoid (ellipsoidal according to figure), posterior unciliated portion indistinctly narrowed and set off. Macronucleus ellipsoidal, slightly eccentric in mid-body, with numerous nucleoli. One globular micronucleus in indentation of macronucleus. Contractile vacuole in posterior end, excretory pore slightly out of pole centre. Cortex serrated, with argyrophilic, rectangular meshes. Extrusomes rare and tiny, rod-shaped, about 4 μ m long. Cytoplasm hyaline, with some bright fat globules and crystals and $6-8 \,\mu\text{m}$ sized food vacuoles containing yellowbrown remnants. Rotates slowly about main body axis, interrupted by quick jumps and periods of fast forward swimming.

Ciliary rows almost as long as body, 5 abut to brosse kineties at acute angles, all others commence, as usual, with a dikinetid followed, however, by basal bodies not evenly spaced but singly or in pairs and triplets, each ciliary row having a slightly different pattern. 4-5 caudal cilia about half as long as body, distal portion spread outwards.

Oral opening apical and circular, pharyngeal basket terminates in mid-body. Oral dikinetids connected by two closely spaced argyrophilic rings. Five minute brosse kineties, anterior rows composed of 4 dikinetids each, middle of 3-4, last of 2.

Occurrence and ecology: As yet known only from type location, i.e. the plankton of a dreggered groundwater pond in Styria, Austria (N $46^{\circ}50'/E \ 15^{\circ}30'$).

Remarks: The reinvestigation of the type slides resulted in several major discrepancies to KRAINER's description and figures: (1) some specimens have a distinctly setoff posterior body portion, indicating that the plug is more distinct in vivo than described and figured by KRAINER; (2) the excretory pore is not within but distinctly outside the area occupied by the caudal cilia as, e.g., in *U. pelagica*; (3) the ciliary rows are shorter than described, i.e. terminate in the posterior quarter, as is usual; (4) in 3 out of 9 specimens the basal bodies are as regu-

Table 3. Morphometric characteristics from Urotricha matthesi (upper line; from KRAINER 1995) and Urotricha matthesi tristicha (lower line).

Character ¹)	\overline{X}	М	SD	$\mathrm{SD}_{ar{x}}$	CV	Min	Max	n
Body, length	28.8	?	3.9	1.2	13.5	24	36	10
	32.4	33	3.8	0.8	11.6	26	38	20
Body, width	26.4	?	3.9	1.2	14.8	19	31	10
	25.8	26	2.9	0.6	11.4	18	31	28
Somatic kineties, length	?	?	?	?	?	?	?	?
	25.6	26	3.4	0.8	13.1	20	32	19
Anterior end to end of brosse, distance	?	?	?	?	?	?	?	?
	5.1	5	1.4	0.5	26.5	3	7	8
Macronucleus, length	9.1	?	1.4	0.4	15.4	7	12	10
	10.1	10	1.4	0.3	14.1	7	13	24
Macronucleus, width	7.5	?	0.6	0.2	8.0	7	8	10
	6.5	7	1.3	0.3	20.6	4	9	26
Micronucleus, length	2.6	?	0.5	0.1	18.4	2	4	11
	2.3	2	0.5	0.1	23.5	1.7	3.5	16
Micronucleus, width	2.3	?	0.6	0.2	27.9	1	4	11
	2.1	2	0.5	0.1	25.3	1.5	3.5	16
Oral opening, diameter	?	?	?	?	?	?	?	?
	6.8	7	0.5	0.1	7.6	6	9	28
Brosse kinety 1, length	?	?	?	?	?	?	?	?
	2.3	2.5	_	_	_	2	2.8	8
Brosse kinety 2, length	?	?	?	?	?	?	?	?
	1.8	2	_	_	_	1.5	2	8
Brosse kinety 3, length	?	?	?	?	?	?	?	?
	0.8	1	_	_	_	0.5	1	6
Excretory pore, diameter	?	?	?	?	?	?	?	?
	1.4	1.4	_	_	_	1.3	1.7	13
Brosse kineties, number	5 - 6	?	?	?	?	?	?	?
	3.0	3	_	_	_	2	3	40
Dikinetids in brosse kinety 1, number	about 4	?	?	?	?	?	?	?
	5.0	5	0.0	0.0	0.0	5	5	5
Dikinetids in brosse kinety 2, number	3-4	?	?	?	?	?	?	?
	4.0	4	0.0	0.0	0.0	4	4	7
Dikinetids in brosse kinety 3, number	about 2	?	?	?	?	?	?	?
	2.0	2	0.0	0.0	0.0	2	2	5
Somatic kineties, number	31.6	?	2.0	0.6	6.2	28	35	12
	31.3	32	2.4	0.5	7.6	28	38	25
Somatic kineties abutting to brosse.	about 5	?	?	?	?	?	?	?
number	2.7	3	0.8	0.3	27.8	2	4	7
Cilia in a somatic kinety, number	15.5	?	1.6	0.4	10.4	13	18	13
,	19.2	18	3.7	0.8	19.3	15	28	21
Caudal cilia, number	3.5	?	0.8	0.2	22.6	2	4	12
	4.0	4	_	_	_	4	5	22
Circumoral dikinetids, number	13.0	?	1.8	0.5	14.1	11	17	13
	16.7	16	1.7	0.5	9.9	15	20	13

¹) All data from randomly selected, protargol-impregnated cells. Measurements in μ m. CV = coefficient of variation in %; M = median; Max = maximum, Min = minimum, n = number of cells investigated; SD = standard deviation; SD_{x̄} = standard deviation of mean; \bar{x} = arithmetic mean.



Figs. 155–163. Urotricha matthesi tristicha (originals) from life (155-160) and after protargol impregnation (161-163); bars $10 \mu m$. 155, 158: General view of typical specimen. The extrusomes (158) are slender and short ($2.5 \mu m$), thus the fringe formed is inconspicuous. 156: Shape variants. 157: Anterior polar view showing oral flaps composed of two short processes. 159: A ridge extends right of each ciliary row. 160: Posterior polar view. Usually, *U. matthesi tristicha* has 4 caudal cilia. 161: Ventrolateral view showing details of somatic and oral infraciliature. In contrast to *U. matthesi matthesi*, the brosse of *U. matthesi tristicha* invariably consists of 3 kineties. Note that brosse kinety 3 (arrowhead) is distinctly smaller than brosse kineties 1 and 2. 162, 163: Oblique anterior and posterior polar view showing general organization of somatic and oral infraciliature. B = brosse, CC = caudal cilia, CK = circumoral kinety, CP = cortical pattern, CV = contractile vacuole, EP = excretory pore of contractile vacuole, FV = food vacuole, MI = micronucleus, OF = oral flaps.

larly spaced as in other *Urotricha* species; (5) there are not 4-5 or 2-4 caudal cilia, as stated in KRAINER's diagnosis and, respectively, morphometric table, but 3-4; (6) there are not 5 brosse kineties, as diagnosed and described, but 5-6 as also shown in one of KRAINER's figures (Fig. 154). Furthermore, the length of the extrusomes (unfortunately not recognizable in type slides) differs greatly in the figure (1.3 µm; Fig. 151) and description (4 µm).

Easily confused with *U. matthesi tristicha* (5–6 vs. 3 brosse kineties; shape ellipsoidal vs. conical) and *U. castalia* (extrusomes 4 μ m vs. 2.5–3 μ m, no elongated (6 μ m) extrusomes in posterior end; 3–4 vs. 4–10 caudal cilia; 28–35 vs. 34–50 somatic kineties).

Urotricha matthesi tristicha nov. subspec. (Figs. 155–163, Table 3)

Diagnosis: Conical to broadly fusiform. Extrusomes numerous but inconspicuous because rod-shaped and only $2.5 \,\mu\text{m}$ long. Basal bodies evenly spaced in ciliary rows. Brosse composed of 3 kineties.

Type location: Plankton of an artificial pond at Salzburg University (N 47°47′/E 13°40′).

Type material: A holotype slide and three syntype slides with protargol-impregnated (WILBERT technique) specimens have been deposited in the Oberösterreichische Landesmuseum in Linz (LI), Austria.

Etymology: *tristicha* refers to the 3 brosse kineties, the main distinctive character to the nominate species, which has 5-6.

Description: In vivo about $35-45 \times 25-35 \,\mu\text{m}$. Very fragile and thus frequently distorted when transferred to slide, overall appearance conical to broadly fusiform or almost globular, oral area often slightly rostrate, accentuating fusiform shape, unciliated posterior portion gradually but distinctly narrowed and thus set off plug-like (Figs. 155, 156). Macronucleus distinctly ellipsoidal (about 2:1), eccentric in mid-body, with conspicuous, double-layered membrane and reticulate nucleolus disintegrated to globular pieces in fixed specimens. Micronucleus globular, in vivo about $3 \times 2.5 \,\mu\text{m}$, attached to outer surface of nuclear membrane. Contractile vacuole and excretory pore distinctly subterminal in rather variable position outside area occupied by caudal cilia (Figs. 155, 160, 162, 163). Cortex with distinct longitudinal ridge left of ciliary rows, rectangularly meshed in some protargol preparations (Figs. 159, 161). Extrusomes easily overlooked because inconspicuous and often extruded when specimens become distorted under cover glass (Figs. 155, 158). Cytoplasm colourless, contains small and large coloured food vacuoles with green algae (Chlamydomonas sp.), dinoflagellates and diatoms, as well as colourless and orange-coloured fat globules, 1-6 µm across, making, if abundant,

cells dark under low (X 40) magnification. Swims very fast performing long jumps from time to time.

Ciliary rows extend over about 80% of body length, 2-4, usually 3, abut to right side and posterior end of brosse, all other commence with a dikinetid followed by rather evenly spaced monokinetids. Caudal cilia arranged in rather narrow circle, approximately twice as long as body cilia, i.e. about 15 μ m, distal third spread outwards, distal quarter narrowed (Figs. 155, 160, 163).

Oral opening apical and slightly rostrate, circular, pharyngeal basket terminates in mid-body. Oral flaps paired, about 2 μ m long (Figs. 155, 157). Oral infraciliature without peculiarities, pharyngeal microfibrillar ring distinct. Brosse usually composed of 3, rarely of 2 kineties (the minute third row was lacking in 2 out of 40 specimens), upper kinety intersects circle formed by dikinetids at anterior end of ciliary rows; brosse rows consist of dikinetids having only anterior basal body ciliated, as also indicated by smaller size of posterior granule; brosse cilia about 5 μ m long and motionless (Figs. 161, 162).

Occurrence and ecology: As yet found only at type location in low numbers in April 1993 and July 1995.

Comparison with related species: See U. matthesi.

Urotricha multisetosa WANG & NIE, 1933 (Fig. 164)

1933 Urotricha multisetosa WANG & NIE, Contr. biol. Lab. Sci. Soc. China, 10:9.

Description: In vivo $90 \times 70 \,\mu\text{m}$ on average. Globular to somewhat ovoid, evenly rounded at anterior end, posterior fifth rather abruptly narrowed to broad plug which disappears under cover glass pressure. Macronucleus spherical, central or lateral in position. One contractile vacuole in midline of posterior end. Cortex smooth, longitudinally striated. No extrusomes. Cytoplasm granular, greyish yellow, usually with many food vacuoles chiefly containing diatoms and *Cryptomonas*. Movement as in *U. tricha*, i.e. forward swimming interrupted by conspicuous jumps.

Cilia fine, rather short, evenly distributed throughout body (obviously, WANG & NIE overlooked that plug is barren), those encircling oral opening slightly elongated. Number of ciliary rows not known. Caudal cilia numerous, never less than 10, long, viz. about third or fourth of body length.

Oral opening terminal, bordered by simple, conical pharynx; pharyngeal rods not recognizable.

Occurrence and ecology: As yet found only at type location, i.e. Lake Ho Hu and in ponds near by the National Central University Farm at Nanking, China. Found from December to March.

Remarks: *U. multisetosa* is the largest known species of the genus. See *U. faurei*, possibly a junior synonym, for comparison with related species. The lack of extrusomes is striking in such a large species and should be confirmed; possibly, they are as thin as in *U. matthesi tristicha* and have thus been overlooked. However,

WANG & NIE (1933) definitely stated: "The trichocysts and pharyngeal trichites so characteristic to *U. tricha* are totally absent in *U. multisetosa*".

Urotricha alveolata KAHL, 1926 (Figs. 165-167)

1926 Urotricha alveolata KAHL, Arch. Protistenk., 55:209.

1930 Holophrya (Urotricha) alveolata KAHL, 1926 – KAHL, Tierwelt Dtl., 18:51.

Taxonomie: General characteristics very much like in typical *Urotricha* species, oral flaps, however, indistinct or lacking and thus transferred to *Holophrya* by KAHL (1930). We retain it in the original genus because the oral

flaps are often difficult to recognize and KAHL, being less experienced in 1926 than in 1930, might simply have overlooked them. The figures and descriptions provided by KAHL (1926, 1930) differ slightly, mainly in body shape and extrusomes. Needs redescription from live (oral flaps) and silver-prepared (infraciliature) specimens. Obviously, *U. alveolata* is a distinct species easily recognized, even alive, by the symbiotic algae, the distinct cortical alveolation, and the caudal cilia.

Description: $30 \times 20 \,\mu\text{m}$ according to KAHL (1926), about 40 μm long in KAHL (1930). Shape tetragonal, i.e. rounded triangular both in lateral and transverse view, obliquely truncate anteriorly, rather distinctly narrowed pos-



Figs. 164–170. Urotricha multisetosa (164), U. alveolata (165–167), and U. faurei (168–170). **164:** U. multisetosa from life, length about 90 μ m (from WANG & NIE 1933). **165–167:** U. alveolata from life, lateral (165, 167) and frontal (166) views, length 30–40 μ m (165, 166, from KAHL 1926; 167, from KAHL 1930). **168–170:** U. faurei (from DRAGESCO et al. 1974). 168: General view from live and protargol-impregnated specimens, length about 45 μ m. 169, 170: Posterior and anterior polar view of infraciliature after CHATTON-LWOFF silver nitrate impregnation, bar 20 μ m. B = brosse, CC = caudal cilia, CP = cortical pattern, EP = excretory pore of contractile vacuole.

teriorly but not set off plug-like. Macronucleus globular in cell centre. Contractile vacuole and cytopyge in posterior end. Cortex bright, colourless, deeply furrowed by ciliary rows, with conspicuous alveolar layer, but apparently without extrusomes. Cytoplasm colourless but with some green symbiotic algae (zoochlorellae). Rotates slowly, does not jump like many other members of genus.

Somatic and oral infraciliature insufficiently known. KAHL (1926) figured slightly shortened ciliary rows and mentioned 3–5 distinctly elongated, soft caudal cilia. Somatic cilia closely spaced, long and flexible. Cytopharyngeal basket indistinct, anteriorly surrounded by thick layer of compact plasm containing one (KAHL 1930) or several (KAHL 1926) wreaths of very thin, short extrusomes.

Occurrence and ecology: Locus classicus is a moorland pond near Hamburg, Germany, where KAHL (1926) discovered *U. alveolata* in sapropelic mud. It was rare and fed on purple bacteria. One specimen was covered with bacterial rods about 3 µm long. Not found since.

Urotricha faurei DRAGESCO, IFTODE & FRYD-VERSAVEL, 1974 (Figs. 168–170)

1974 Urotricha faurei DRAGESCO, IFTODE & FRYD-VERSAVEL, Protistologica, 10:69. Type slides with CHATTON-LWOFF silver nitrate-impregnated cells deposited at Paris University, Centre d'Orsay.

Description: Silver nitrate-prepared specimens $35-46 \,\mu\text{m}$ (41 μm on average, n = ?) long. Ellipsoidal with posterior fifth set off plug-like. Macronucleus globular, $14-22 \,\mu\text{m}$ in diameter; micronucleus 2.7 μm . Excretory pore of contractile vacuole distinctly out of pole centre and caudal ciliary tuft (Fig. 169). No trichocysts but inconspicuous mucocysts.

55-60 somatic kineties extending meridionally from anterior end to posterior fifth of cell, about 6 of them abut to right side of brosse kineties in acute angles; each kinety commences with a pair of granules the anterior granule being smaller and/or less distinctly impregnated. Posterior pole region occupied by 12-15 paired, irregularly arranged granules giving rise to distinct tuft of caudal cilia; irregular arrangement of caudal cilia (granule complexes) documented by micrograph in DRAGESCO et al. (1974). Silverline system forms rectangular meshes in ciliated body portion and irregular pattern in posterior pole region (Figs. 169, 170).

Oral opening apical, cytopharyngeal basket conical, conspicuous, i.e. extending almost to posterior end of cell. About 27 circumoral, oblique dikinetids and an equal number of argyrophilic granules around mouth centre according to Fig. 13B in DRAGESCO et al. (1974), reproduced here as Fig. 170. Four brosse kineties, kinety 1 intersects circle formed by dikinetids at anterior end of ciliary rows and is composed of five dikinetids, kinety 2 composed of six dikinetids, kinety 3 of four, and kinety 4 of three dikinetids, according to Fig. 170.

Occurrence and ecology: As yet found only at type location, i.e. "une pièce d'eau du C. N. R. S. à Gif-sur-Yvette", France. *Urotricha faurei* was cultivated for some weeks on Eau de Volvic with *Cryptomonas* sp. as food.

Remarks: Lack of extrusomes (trichocysts) should be confirmed in live specimens, and more detailed morphometric data should be provided. *Urotricha faurei* differs from *U. multisetosa* only by the much smaller size (45 μ m vs. 90 μ m) and might thus be a junior synonym. The number of somatic kineties and caudal cilia is very similar to those of *U. apsheronica* and *U. pelagica*, which, however, have conspicuous extrusomes and circularly arranged caudal cilia.

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