

Revision of *Lamlostyla* Buitkamp, 1977 and Description of *Territricha* nov. gen. (Ciliophora: Hypotrichida)

By HELMUT BERGER and WILHELM FOISSNER

Hydrologische Untersuchungsstelle Salzburg und Institut für Zoologie der
Universität Salzburg (Austria)

With 47 Figures and 2 Tables

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Abstract

The genus *Lamlostyla* Buitkamp, 1977 is revised and the morphology of *Territricha stramenticola* nov. gen., nov. spec. is described. The oxytrichid genus *Lamlostyla* comprises 7 soil-dwelling species: *L. lamottei* (Type-species), *L. edaphoni*, *L. hyalina*, *L. islandica* nov. spec., *L. kirkeniensis* nov. spec., *L. longa* nov. comb., and *L. perisincirra*. The urostylid genus *Territricha* nov. gen. is mainly characterized by a restriction of the typical midventral pattern to the postoral area and a distinct reduction of the number of midventral cirri. It probably links the urostylids with the oxytrichids.

Introduction

Lamlostyla Buitkamp, 1977 was a monotypical genus for several years. Recently, however, some species of *Tachysoma* were transferred to it (BERGER and FOISSNER 1987). On the occasion of the discovery of 2 new species, we present a revision of this genus, which now contains 7 species restricted to soil.

In the second part a new hypotrichous genus is described which shows the relationship of the urostylids with many midventral cirri to the oxytrichids s. str. with usually only 18 cirri on the ventral surface.

Materials and Techniques

Lamlostyla islandica occurred on August 8, 1985 in the litter and upper soil layer of a heath with dwarf shrubs (dominated by *Betula nana*, *Empetrum nigrum*, *Vaccinium uliginosum*, *Arctostaphylos uva-ursi*) in Gooa Foss, Bardárdalur, North-Iceland (120 m sea-level; pH = 5.5). *Lamlostyla kirkeniensis* was found on August 19, 1985 in the litter and upper layer of a tundra soil (with lichen, moss, *Vaccinium myrtillus*, and *Betula nana*) near the airport of Kirkenes, Norway. *Territricha stramenticola* occurred on April 19, 1987 in the litter of a beechforest on the Gaisberg, Salzburg, Austria.

The culture and staining methods were done according to FOISSNER (1979, 1982). The body shape of the living specimens was drawn from slides without cover glasses. Details were studied on slightly to heavily squeezed individuals using the oil immersion objective (100×; eyepiece, 10×) and bright

field technique. The drawings of the protargol impregnated specimens were made with a camera lucida. All countings and measurements were performed at a magnification of $1000\times$ (1 unit = 1 μm).

All statistical procedures follow methods described in SOKAL and ROHLF (1981). The terminology is according to KAHL (1932), BORROR and WICKLOW (1983), and CORLISS and LOM (1985).

Revision of the Genus *Lamtostyla* Buitkamp, 1977

- 1977 *Lamtostyla lamottei* n. gen. n. spec. — BUITKAMP, Acta Protozool. **16**: 270
 1979 *Lamtostyla* Buitkamp, 1977 — CORLISS, The ciliated protozoa. 2nd ed.: 309
 1985 *Lamtostyla* Buitkamp, 1977 — SMALL and LYNN, Illustrated guide to the protozoa: 419, 456
 1986 *Lamtostyla* Buitkamp, 1977 — DRAGESCO et DRAGESCO-KERNEIS, Fauna tropicale **26**: 456
 1986 *Lamtostyla* Buitkamp, 1977 — TUFFRAU, Ann. Sci. nat., Zool. **8**: 116
 1987 *Lamtostyla* Buitkamp, 1977 — BERGER and FOISSNER, Zool. Jb. Syst. **114**: 216, 217

Diagnosis: Small to medium sized Oxytrichidae. Frontoventral infraciliature restricted to the area right of the buccal cavity and at most 2 cirri adjacent to the transverse cirri. 1 frontal row which originates from 2 streaks. Number of transverse cirri usually reduced (<5). Infraciliature of the dorsal surface consists of dorsal kineties only (Caudal cirri absent).

Type-species: *Lamtostyla lamottei* Buitkamp, 1977

Additional characters: Terricolous. Body margins nearly parallel (except *L. perisincirra*). Both ends rounded, about 2:1 flattened dorso-ventrally. Cytoplasm colourless, subpellicular granules absent. 2 macronuclear segments slightly left of the median. Contractile vacuole about in the middle of the cell on the left-hand side, during diastole without distinct channels. Adoral zone of membranelles 20–30% of body length. Buccal area flat and narrow. Undulating membranes nearly parallel, slightly bent. Buccal cirrus small, usually near the anterior end of the undulating membranes. Frontal cirri slightly enlarged (except *L. hyalina*). Frontal row terminates at about the level of the cytostome. Marginal rows with about the same number of cirri, rows widely open posteriorly, terminate at about the level of the transverse cirri, marginal cirri c. 10 μm long. Bases of the transverse cirri not enlarged, cirri about 12 μm (*L. hyalina*) to c. 15 μm (remaining species, *L. lamottei*?) long, protruding distinctly beyond the posterior edge. Dorsal cilia in vivo c. 3 μm long.

Discrimination from related Genera: BUITKAMP (1977) characterized the genus *Lamtostyla* insufficiently and supposed that it is in the holostichid lineage. However, some morphogenetic stages of *L. perisincirra* indicate a classification within the family Oxytrichidae; 6 typical fronto-ventral-transverse primordia occur (Fig. 13; BERGER et al. 1984, BERGER and FOISSNER 1987).

Lamtostyla is difficult to separate from *Hemisincirra* Hemberger, 1985. The most important discriminating characteristic is very probably the rather irregular arrangement of the cirri in the frontal row of *Hemisincirra* (FOISSNER 1982). Supporting characteristics exist probably a) in the origin of the oral primordium, viz. near the transverse cirri in *Lamtostyla* (Figs. 8–12) and near the peristome in *Hemisincirra* (HEM-

BERGER 1985), b) in the body shape, viz. wide to long ellipsoid and stretched to vermicular, respectively, and c) in the number of macronuclear segments, namely 2 in *Lamtostyla* and more than 2 in *Hemisincirra*. The few exceptions in *Hemisincirra* can be very likely explained in that these species do not belong to this genus.

Gonostomum Sterki, 1878 is distinct from *Lamtostyla* in that it has caudal cirri and the location of the adoral zone of membranelles is at the left lateral margin (FOISSNER 1982).

Tachysoma Stokes, 1887 and *Oxytricha* Bory De St. Vincent, 1824 differ from *Lamtostyla* in that they have postoral ventral cirri and in the arrangement of the cirri in the frontal area. Additionally, *Oxytricha* is separated by the presence of caudal cirri.

Lamtostyla has probably evolved from *Oxytricha* by a resorption of the caudal cirri and an anteriad displacement of the typical postoral ventral cirri. This plesiomorphic state is well represented by *L. longa* (Fig. 1) where the elongated posteriormost dorsal cilia are still reminiscent of the oxytrichid caudal cirri. Subsequently, the number of transverse cirri and adjacent ventral cirri and dorsal kineties are less and the number of cirri in the streaks V and VI (?) which form the frontal row have increased. This type of infraciliature is characteristic for most of the other species of *Lamtostyla* (Fig. 3) and probably a adaptation to the soil habitat (FOISSNER 1987a). Furthermore, the loss of the dorsomarginal kineties is considered to be a derived character state, which is shared within the oxytrichids s. l. with *Gonostomum* only (WIRNSBERGER et al. 1986).

Key to the Species

1. Distal 3 adoral membranelles distinctly separated from the proximal part of the adoral zone of membranelles (Fig. 29, 31) *L. hyalina*
— Adoral zone of membranelles not interrupted 2
2. 1 micronucleus between the macronuclear segments (Fig. 3—12) *L. perisincirra*
— 2 or more micronuclei 3
3. 1 cirrus left of the frontal row (Fig. 22, 27) 4
— Usually 3 cirri left of the frontal row (Fig. 1, 2, 16) 5
4. 2 dorsal kineties (Fig. 28) *L. kirkeniensis*
— 3 dorsal kineties (Fig. 23) *L. edaphoni*
5. 3 dorsal kineties (Fig. 17) *L. islandica*
— 4 or 5 dorsal kineties 6
6. Usually 2 transverse cirri, frontal row with c. 10 cirri (Fig. 2) *L. lamottei*
— 5 transverse cirri, frontal row with 4 cirri (Fig. 1) *L. longa*

Description of Species

For the correct determination of the species of *Lamtostyla* the following characters are necessary: shape of the adoral zone of membranelles, number of micronuclei, cirri in the frontal row, cirri left of the frontal row, transverse cirri and adjacent ventral cirri, and number of dorsal kineties. Most of these characters can be clearly seen in protargol impregnated specimens only. Observation of live specimens alone is not sufficient.

The characters mentioned in the description of the genus and those listed in Table 1 are not repeated in this section.

The genus can be divided into 2 groups, viz. species with 3 cirri left of the frontal row comprising *L. longa*, *L. perisincirra*, *L. islandica*, and *L. lamottei* and species with only 1 cirrus left of the frontal row as *L. edaphoni*, *L. kirkeniensis*, and *L. hyalina*.

Lamlostyla longa (Hemberger, 1985) nov. comb. (Fig. 1, Tab. 1)

1985 *Tachysoma longa* n. spec. — Hemberger, Arch. Protistenkd. **130**: 412, Abb. 18

Description: *In vivo* (?) $85-130 \times 35-50 \mu\text{m}$. 2 micronuclei. Posterior cirrus of the frontal row somewhat separated from the anterior cirri. Bases of the posterior 2–3 cirri of each marginal row smaller than the other marginal cirri. 2 ventral cirri near the transverse cirri. 4 dorsal kineties of body length, 1 row distinctly shorter (not figured in the original description). Posterior basal body pair of 3 (?) dorsal kineties each with $13 \mu\text{m}$ long paired cilia (see chapter "Discrimination from related genera").

Occurrence: In the soil of a woodland, Peru.

Remarks: The new combination is mainly based on the arrangement of the cirri in the frontal area, which is similar to that of *L. perisincirra*, *L. islandica*, and the type-species *L. lamottei* (Fig. 1, 3, 6).

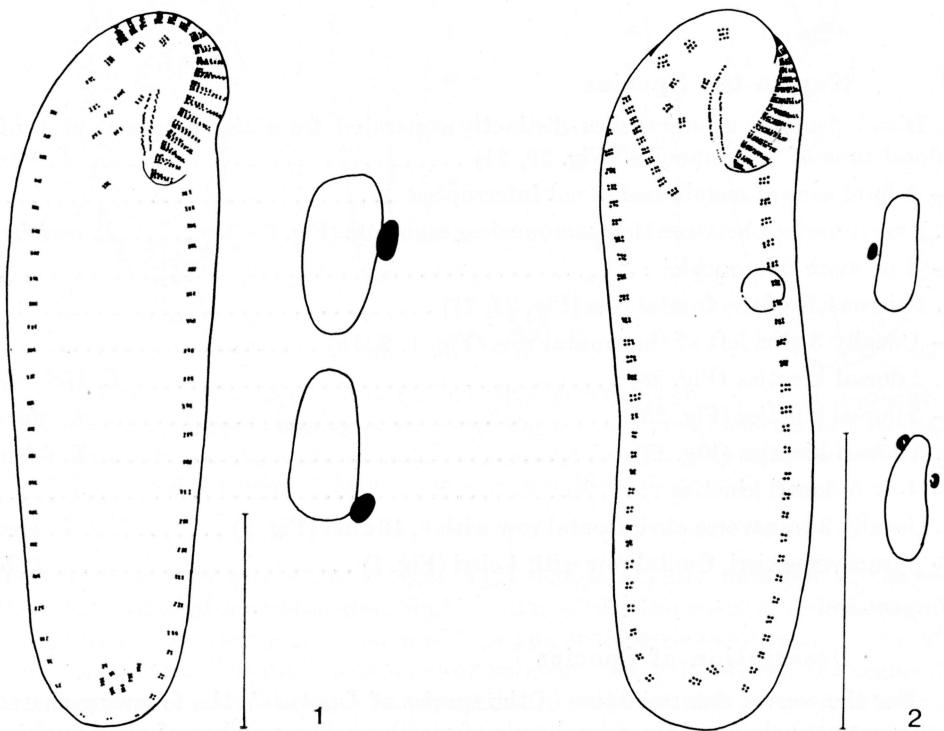


Fig. 1, 2. *Lamlostyla longa* (Fig. 1, after HEMBERGER 1985) and *L. lamottei* (Fig. 2, after BUITKAMP 1977). Infraciliature in ventral view after protargol impregnation. Scale marks = $30 \mu\text{m}$

Table 1. Biometrical characterization of *Lamostyla edaphoni* (*eda*; BERGER and FOISSNER 1987), *L. hyalina* (*hya*; BERGER et al. 1984), *L. islandica* (*isl*), *L. kirkeniensis* (*kir*), *L. lamottei* (*lam*; BUITKAMP 1977), *L. longa* (*lon*; HEMBERGER 1985), and *L. perisincirra* type material (*pe1*; HEMBERGER 1985) and an Austrian population (*pe2*; BERGER et al. 1984). All data are based on protargol impregnated specimens. All measurements in μm . $\bar{x}$, arithmetic mean; M, median; s, standard deviation; CV, coefficient of variation in %; Min, Max, minimum and maximum value; n, sample size; distance 1, distance between the macronuclear segments; distance 2, distance between the anterior end of the cell and the posterior end of the frontal row; *, these values are from the figures of the original descriptions; **, if 2 values are available they are listed as Min and Max, if only 1 value is known it is listed in the column $\bar{x}$; ?, sample size unknown

Character	Species	$\bar{x}$	M	s	CV	Min	Max	n
Body, length	<i>eda</i>	61.1	62	6.7	11.0	49	69	10
	<i>hya</i>	31.4	32	3.3	10.6	26	35	10
	<i>isl</i>	62.3	63	4.6	7.4	56	70	12
	<i>kir</i>	82.6	84	5.2	6.3	72	90	11
	<i>lam</i> **	73.0*	—	—	—	—	—	1
	<i>lon</i> **	—	—	—	—	85	130	?
	<i>pe1</i> **	—	—	—	—	60	80	?
	<i>pe2</i>	42.9	42	5.1	11.8	34	57	28
Body, width	<i>eda</i>	15.9	16	1.5	9.1	13	18	10
	<i>hya</i>	13.7	14	2.2	15.8	11	17	10
	<i>isl</i>	18.3	18	1.4	7.4	17	21	12
	<i>kir</i>	20.6	21	1.2	5.9	18	22	11
	<i>lam</i>	19.1*	—	—	—	—	—	1
	<i>lon</i>	—	—	—	—	35	50	?
	<i>pe1</i>	—	—	—	—	20	25	?
	<i>pe2</i>	25.2	15	1.7	11.4	12	18	28
Adoral membranelles, number	<i>eda</i>	16.7	17	0.7	4.1	16	18	10
	<i>hya</i>	10.7	11	0.5	4.5	10	11	10
	<i>isl</i>	15.6	16	0.5	3.3	15	16	12
	<i>kir</i>	15.3	16	1.0	6.6	13	16	11
	<i>lam</i>	19.0	—	—	—	—	—	?
	<i>lon</i>	—	—	—	—	18	19	?
	<i>pe1</i>	—	—	—	—	15	16	?
	<i>pe2</i>	16.1	16	0.8	4.9	15	18	28
Adoral zone of membranelles, length	<i>eda</i>	18.5	18	2.2	11.7	15	22	10
	<i>hya</i>	9.0	9	0.8	8.8	8	10	10
	<i>isl</i>	16.8	17	1.1	6.3	15	18	12
	<i>kir</i>	16.9	17	1.1	6.7	15	18	11
	<i>lam</i>	16.6*	—	—	—	—	—	1
	<i>lon</i>	22.6*	—	—	—	—	—	1
	<i>pe1</i>	18.7*	—	—	—	—	—	1
	<i>pe2</i>	12.8	13	0.8	6.4	11	15	25
Right marginal row, number of cirri	<i>eda</i>	18.1	18	1.7	9.2	16	20	10
	<i>hya</i>	10.7	11	0.9	8.9	9	12	10
	<i>isl</i>	14.7	15	1.2	8.4	13	16	12

Table 1 (Continued)

Character	Species	$\bar{x}$	M	s	CV	Min	Max	n
	<i>kir</i>	42.7	42	2.7	6.4	38	46	11
	<i>lam</i>	—	—	—	—	28	35	?
	<i>lon</i>	—	—	—	—	22	24	?
	<i>pe1</i>	—	—	—	—	13	15	?
	<i>pe2</i>	14.2	15	1.9	13.0	9	20	28
Left marginal row,	<i>isl</i>	14.1	14	0.8	5.6	13	15	12
number of cirri	<i>kir</i>	41.1	41	3.8	9.3	33	46	11
Frontal row,	<i>eda</i>	8.0	8	0.7	8.3	7	9	10
number of cirri	<i>hya</i>	3.0	3	0	0	3	3	10
	<i>isl</i>	5.7	6	0.5	8.7	5	6	12
	<i>kir</i>	7.2	7	1.0	13.7	6	9	11
	<i>lam</i>	10.0	—	—	—	—	—	?
	<i>lon</i>	4.0*	—	—	—	—	—	1
	<i>pe1</i>	6.0*	—	—	—	—	—	1
	<i>pe2</i>	6.5	6	0.7	10.7	6	8	28
Number of cirri	<i>eda</i>	1.0	1	0	0	1	1	10
left of the	<i>hya</i>	1.0	1	0	0	1	1	10
frontal row	<i>isl</i>	3.1	3	0.3	9.4	3	4	12
	<i>kir</i>	1.0	1	0	0	1	1	11
	<i>lam</i>	3.0	—	—	—	—	—	?
	<i>lon</i>	3.0*	—	—	—	—	—	1
	<i>pe1</i>	3.0*	—	—	—	—	—	1
	<i>pe2</i>	3.0	3	0.3	9.1	2	4	28
Number of	<i>eda</i>	4.1	4	0.6	13.8	3	5	10
transverse cirri	<i>hya</i>	5.9	5	0.4	6.5	5	6	7
(adjacent ventral	<i>isl</i>	3.1	3	0.3	9.4	3	4	12
cirri are	<i>kir</i>	3.0	3	0	0	3	3	11
included)	<i>lam</i>	2.0	—	—	—	—	—	?
	<i>lon</i>	7.0	—	—	—	—	—	?
	<i>pe1</i>	4.0	—	—	—	3	5	?
	<i>pe2</i>	3.6	4	0.9	24.3	2	5	28
Number of	<i>eda</i>	3.0	3	0	0	3	3	10
dorsal kinetics	<i>hya</i>	3.0	3	0	0	3	3	9
	<i>isl</i>	3.0	3	0	0	3	3	12
	<i>kir</i>	2.0	2	0	0	2	2	11
	<i>lam</i>	4.0	—	—	—	—	—	?
	<i>lon</i>	5.0	—	—	—	—	—	?
	<i>pe1</i>	3.0	—	—	—	—	—	?
	<i>pe2</i>	3.1	3	0.3	10.1	3	4	28
Distance 1	<i>isl</i>	4.3	4	1.4	32.9	2	7	12
	<i>kir</i>	13.4	14	3.2	24.2	6	17	11
Distance 2	<i>isl</i>	16.8	17	1.3	7.5	14	18	12
	<i>kir</i>	18.6	18	2.2	11.8	17	24	11

Table 1 (Continued)

Charakter	Species	$\bar{x}$	M	s	CV	Min	Max	n
Posterior macro-nuclear segment, length	<i>isl</i>	10.2	10	1.8	17.2	8	13	12
	<i>kir</i>	13.2	14	1.2	8.9	11	14	11
Posterior macro-nuclear segment, width	<i>isl</i>	5.3	5	0.5	8.6	5	6	12
	<i>kir</i>	6.3	6	0.7	10.3	5	7	11
Number of micronuclei	<i>isl</i>	1.8	2	0.4	21.2	1	2	12
	<i>kir</i>	2.0	2	0	0	2	2	11
Posterior micro-nucleus, length	<i>isl</i>	1.6	1.6	0.2	10.1	1.4	2	12
	<i>kir</i>	3.2	3	0.4	12.7	3	4	11
Posterior micro-nucleus, width	<i>isl</i>	1.6	1.6	0.1	7.0	1.4	1.8	12
	<i>kir</i>	1.6	1.5	0.2	9.8	1.5	2	11

Lamostyla perisincirra (Hemberger, 1985) Berger and Foissner, 1987 (Fig. 3—14, 18, Tab. 1)

- 1984
- Tachysoma perisincirra* Hemberger — BERGER, FOISSNER und ADAM, Zool. Jb. Syst. **111**: 363, Abb. 58—68, Tabelle 8
- 1985
- Tachysoma perisincirra* n. spec. — HEMBERGER, Arch. Protistenkd. **130**: 412, Abb. 20
- 1985
- Tachysoma perisincirra* Hemberger — BERGER, FOISSNER und ADAM, Veröff. Österr. MaB-Programms **9**: Tabelle 4
- 1986
- Lamostyla perisincirra* (Hemberger) — BERGER, FOISSNER, and ADAM, Pedobiologia **29**: Table 6
- 1986
- Lamostyla perisincirra* (Hemberger) — LÜFTENEGGER, FOISSNER und ADAM, Z. Vegetationst. **9**: Tabelle 2
- 1987
- Lamostyla perisincirra* (Hemberger, 1985) nov. comb. — BERGER and FOISSNER, Zool. Jb. Syst. **114**: 216

Description: *In vivo* 50—90×20—30 µm, left margin usually convex. Macronuclear segments *in vivo* c. 12×7 µm, with medium sized nucleoli. Single ellipsoid or spherical (2—3 µm in diameter), well stained micronucleus between the macronuclear segments. Contractile vacuole slightly displaced inwards. Posterior part of the cell frequently with small globules. Movement rapid, consists of very many single jerky movements.

Occurrence and Ecology: The type material was found in a mull-rendsina soil near Bonn, FRG (HEMBERGER 1985). Probably, *L. perisincirra* is the most frequent representative of the genus in European soils because it has been rediscovered by BERGER et al. (1985, 1986) and LÜFTENEGGER et al. (1986) in various alpine soils. It also occurred at the type location of *L. edaphoni* (unpubl. observ.). More detailed autecological data of the alpine populations are given by BERGER et al. (1985, 1986) and LÜFTENEGGER et al. (1986).

Remarks: BERGER et al. (1984) determined and redescribed *Tachysoma perisincirra* according to the unpublished dissertation of HEMBERGER (1982), which is based on protargol impregnated material only. Unfortunately, the valid original description was issued not until 3 years later (HEM-

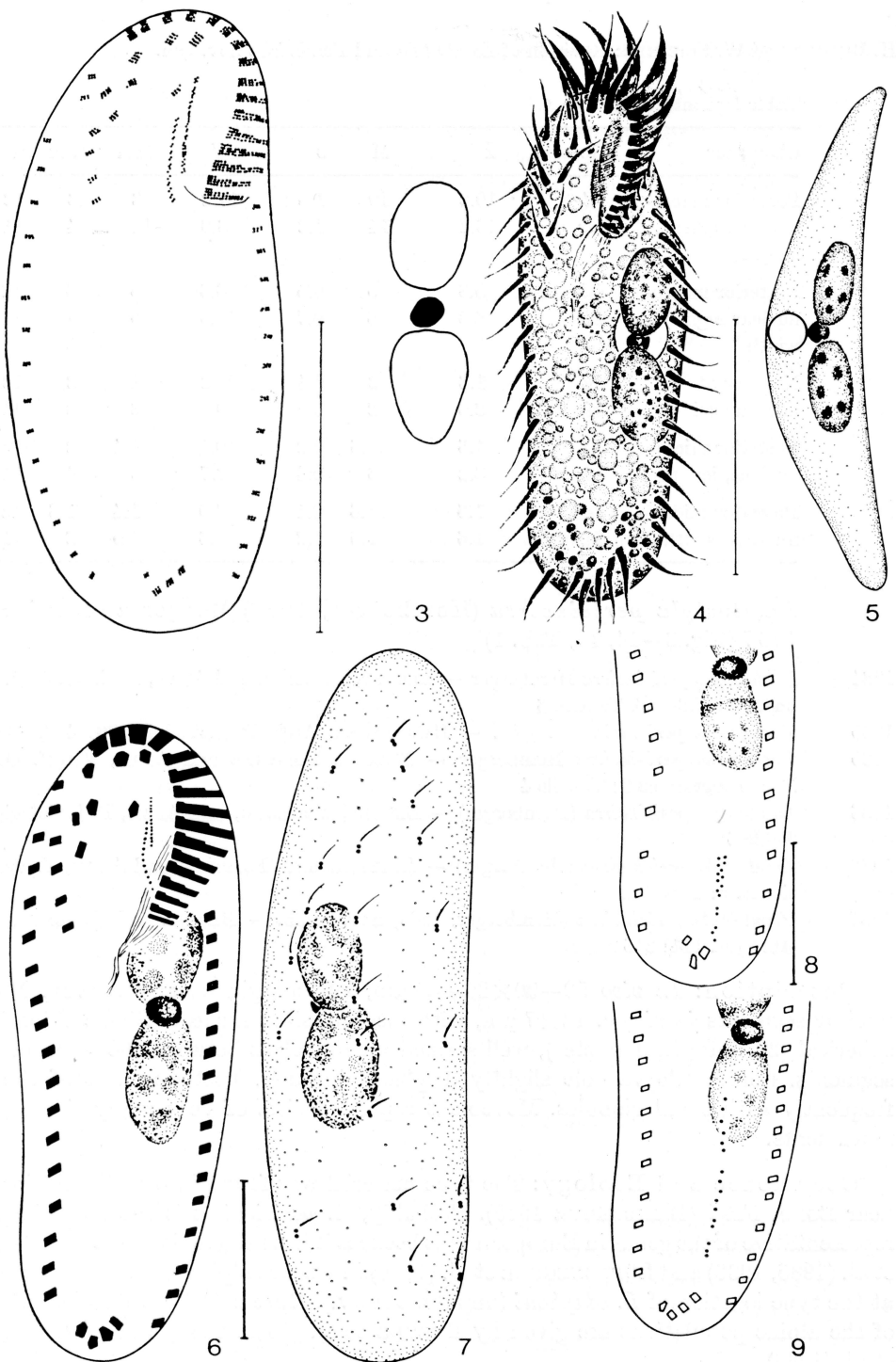


Fig. 3—9. *Lamtostyla perisincirra* from life (Fig. 4, 5) and after protargol impregnation (Fig. 3, 6—9). Fig. 3. Ventral infraciliature after HEMBERGER (1985). Scale mark = 30 μ m. Fig. 4—9. After BERGER et al. (1984). Fig. 4 and 5. Ventral and dorsal lateral view. Scale mark = 30 μ m. Fig. 6 and 7. Infraciliature of a non-dividing specimens in ventral and dorsal view. Scale mark = 10 μ m. Fig. 8 and 9. Very early morphogenetic stages in ventral view. Parental cirri are shown by outline only. Scale mark = 10 μ m

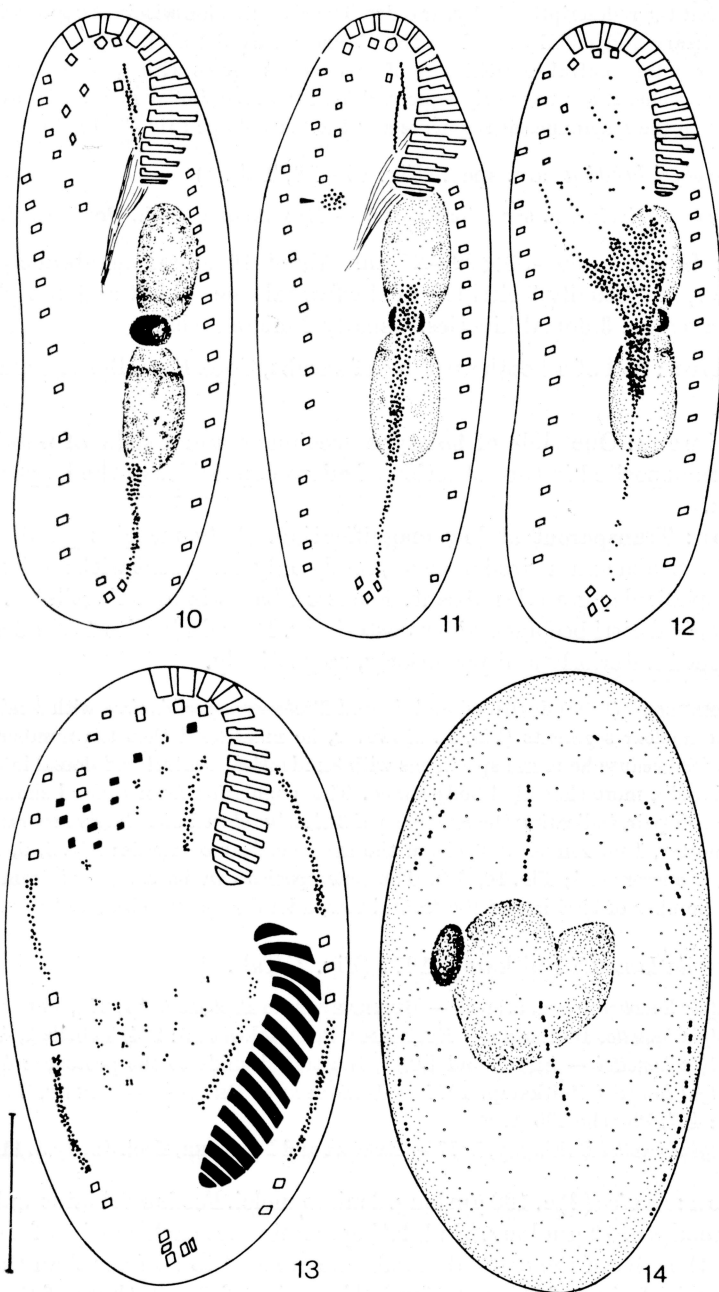


Fig. 10–14. Morphogenesis of *Lamtostyla perisincirra* after protargol impregnation. After BERGER et al. (1984). Fig. 10, 11. Early morphogenetic stages. Fig. 12. Middle morphogenetic stage. Fig. 13, 14. Late morphogenetic stages in ventral and dorsal view. Parental cirri are shown by outline only, the new ones are filled in. Scale mark = 10 μ m

ferrous tropical soil is given by RIOU (1974, cited in BUITKAMP 1979). Under experimental conditions, *L. lamottei* excysted predominantly at a temperature of c. 15°C, whereas for the other species of the community, the optimal temperature for excystment was between 20°C and 35°C (BUITKAMP 1979).

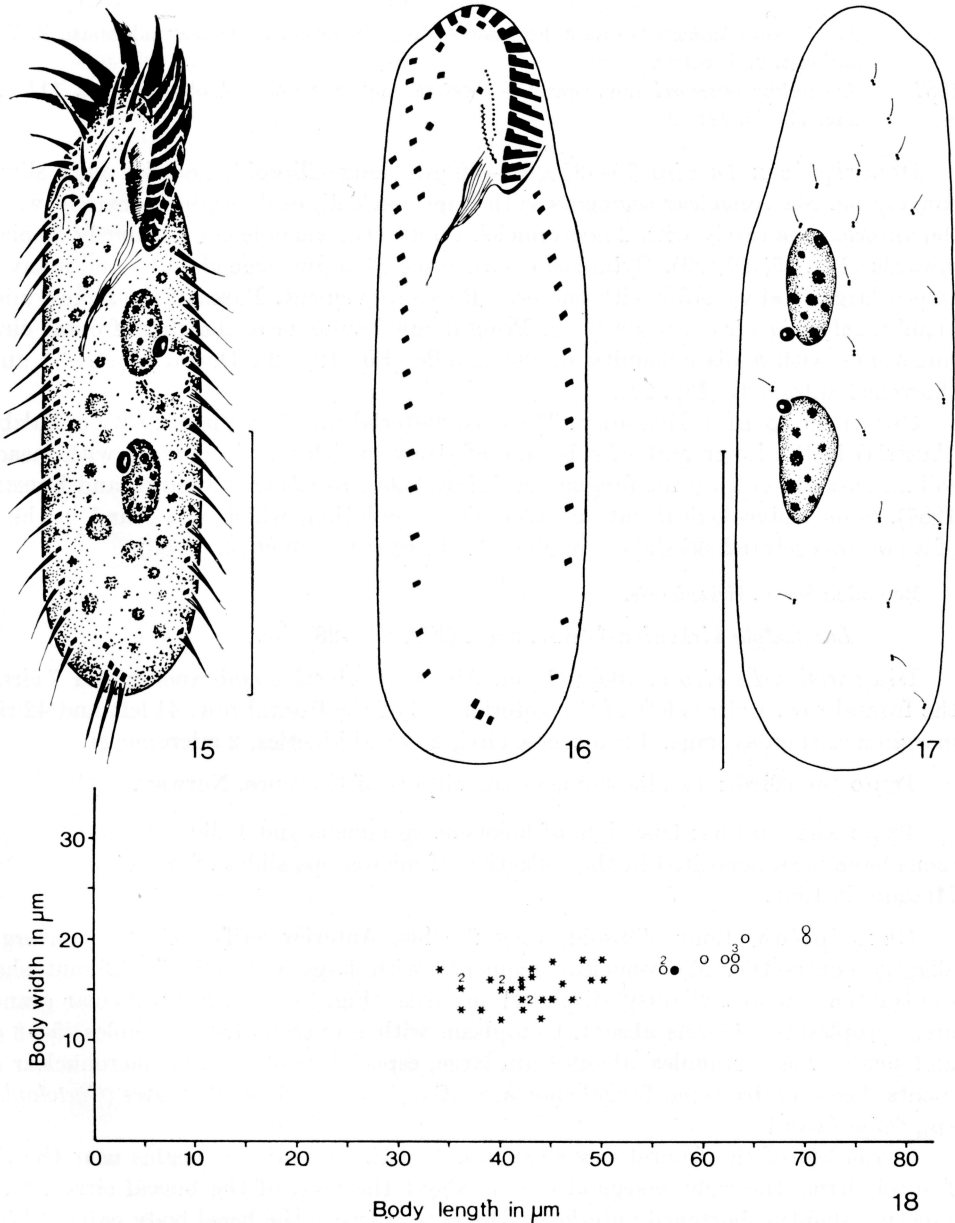


Fig. 15–18. *Lamostyla islandica* (Fig. 15–18) and *L. perisincirra* (Fig. 18). Fig. 15. Ventral view from life. Fig. 16, 17. Infaciliature in ventral and dorsal view after protargol impregnation. Scale marks = 30 µm. Fig. 18. Plot of individual measurements for specimens of *L. islandica* (o, n = 12) and *L. perisincirra* (*, n = 28, from BERGER et al. 1984)

Remarks: The type-species differs from the congeners with 3 cirri left of the frontal row (*L. perisincirra*, *L. islandica*, *L. longa*) in the number of micronuclei, dorsal kineties, transverse cirri, and cirri in the frontal row.

Lamostyla edaphoni Berger and Foissner, 1987 (Fig. 19–23, Tab. 1)

- 1986 *Lamostyla edaphoni* Berger & Foissner — LÜFTENEGGER, FOISSNER und ADAM, Z. Vegetationst. **9**: Tabelle 2
- 1987 *Lamostyla edaphoni* nov. spec. — BERGER and FOISSNER, Zool. Jb. Syst. **114**: 215, Fig. 56–60, Tab. 9

Description: *In vivo* 70–85×20–30 µm, long ellipsoid, anterior part slightly converging. Macronuclear segments with large nucleoli, each segment usually with 1, the anterior one rarely with 2 micronuclei. Contractile vacuole conspicuously displaced inwards (Fig. 19, 20, 23). Cytoplasm with some 1–3 µm large globules and many 4–10 µm large food vacuoles with bacteria. Rapid movement. Bases of the largest adoral membranelles *in vivo* c. 5 µm wide. Frontal row begins near the right frontal cirrus, sometimes with a discontinuity in the middle (Fig. 19, 22). Dorsal kineties 1 and 2 shortened anteriorly (Fig. 23).

Occurrence and Ecology: The type material was found in the City of Salzburg (Austria) in the lower part of a bundle of straw, which was in contact with meadow soil and used to culture the fungus *Leccinum testacea-scabrum* (BERGER and FOISSNER 1987). Some autecological data of an alpine population, which was found in the soil of a non-revegetated ski-slope, are given by LÜFTENEGGER et al. (1986).

Remarks: See *L. kirkeniensis*.

Lamostyla kirkeniensis nov. spec. (Fig. 24–28, Tab. 1)

Diagnosis: *In vivo* c. 100×27 µm. About 16 adoral membranelles and 7 cirri in the frontal row. 1 cirrus left of the anterior end of the frontal row. 41 left and 42 right marginal cirri on average. 3 transverse cirri, 2 dorsal kineties, 2 micronuclei.

Type location: Tundra soil near the airport of Kirkenes, Norway.

Type specimens: One slide of holotype specimens and 1 slide of paratype specimens have been deposited in the collection of microscope slides of the Upper Austrian Museum in Linz.

Description: Long ellipsoid, very flexible. Anterior half distinctly converging, slightly contractile. Macronuclear segments with large nucleoli of different shape. Contractile vacuole slightly displaced inwards (Fig. 14–16). Subpellicular granules and cytoplasmic crystals absent. Cytoplasm with numerous food vacuoles (5–8 µm) and small, greasy granules, about 1 µm large, especially around the macronuclear segments. Feeds on bacteria, fungal spores, zooflagellates, and small ciliates (*Cyrtolophosis* sp., *Colpoda* sp.).

Cirrus left of the frontal row slightly enlarged. Frontal row begins near the right frontal cirrus, the right marginal row at about the level of the buccal cirrus. Dorsal kinety 1 slightly shortened anteriorly. Distance between the basal body pairs of kinety 2 become wider from anterior to posterior (Fig. 27, 28).

Remarks: *Lamostyla kirkeniensis* can be separated from the very similar *L. edaphoni* by its having twice the number of marginal cirri and a lower number of dorsal kineties (Fig. 22, 27, Tab. 1).

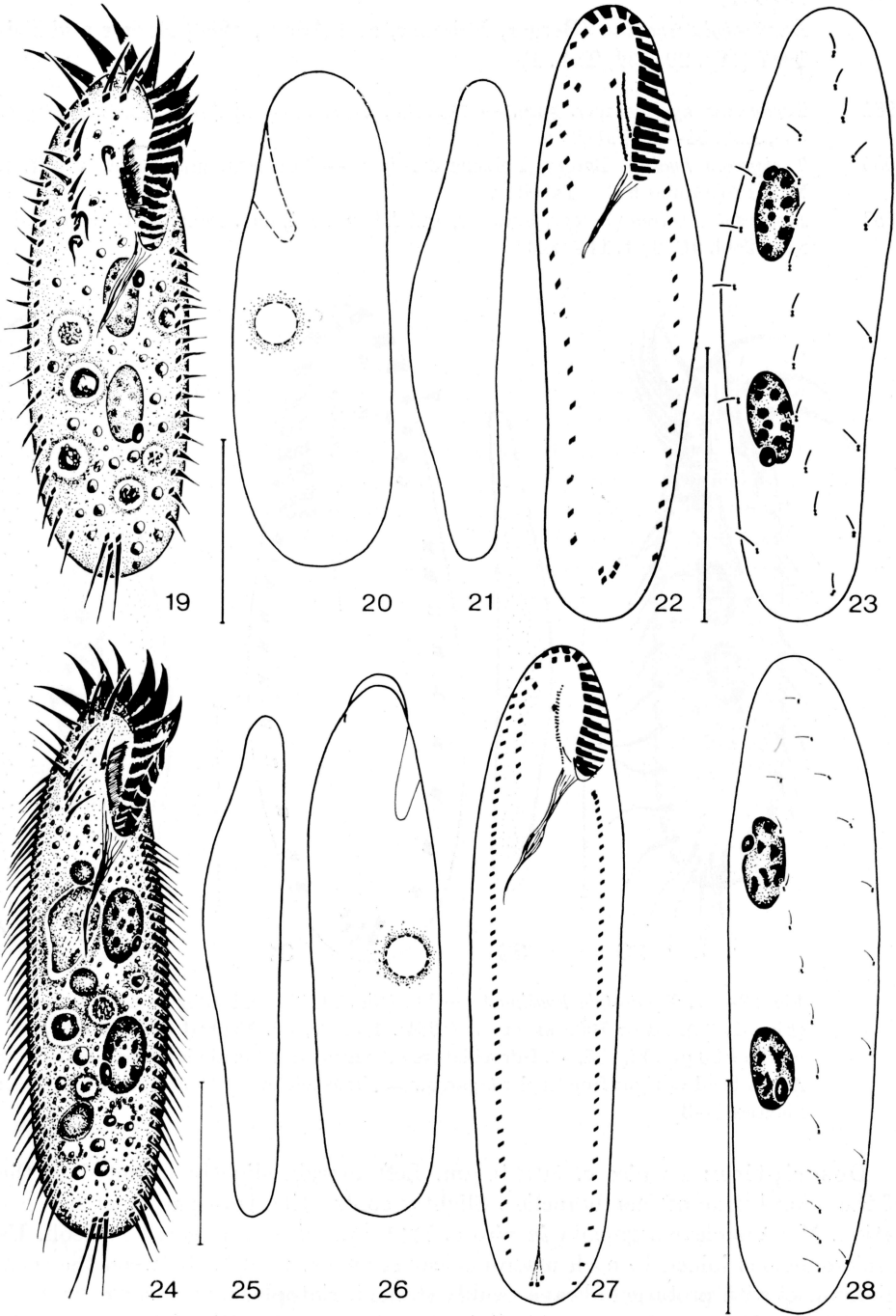


Fig. 19–28. *Lamtostyla edaphoni* (Fig. 19–23, after BERGER and FOISSNER 1987) and *L. kirkeniensis* (Fig. 24–28). Fig. 19–21, 24–26. Ventral, lateral and dorsal view from life. Fig. 22, 23, 27, 28. Infraciliature in ventral and dorsal view after protargol impregnation. Scale marks = 30 μ m

Lamtostyla hyalina (Berger, Foissner, and Adam, 1984) Berger and Foissner, 1987 (Fig. 29–32, Tab. 1)

- 1984 *Tachysoma hyalina* nov. spec. — BERGER, FOISSNER und ADAM, Zool. Jb. Syst. **111**: 359, Abb. 54–57, Tabelle 8
- 1985 *Tachysoma hyalina* Berger, Foissner & Adam — FOISSNER und PEER, Veröff. Österr. MaB-Programms **9**: 31, Tabelle 1
- 1987 *Lamtostyla hyalina* (Berger, Foissner, and Adam, 1984) nov. comb. — BERGER and FOISSNER, Zool. Jb. Syst. **114**: 216

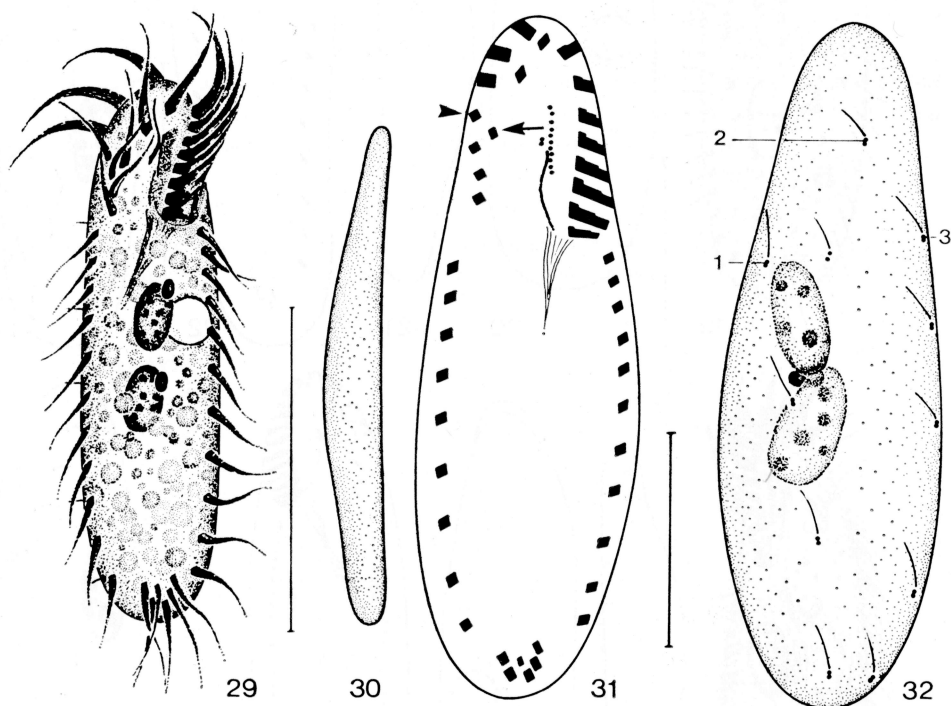


Fig. 29–32. *Lamtostyla hyalina* from life (Fig. 29, 30) and after protargol impregnation (Fig. 31, 32). After BERGER et al. (1984). Fig. 29, 30. Ventral and lateral view. Scale mark = 30 μ m. Fig. 31, 32. Infraciliature in ventral and dorsal view. Scale mark = 10 μ m. Arrow head = right frontal cirrus; arrow = cirrus left of the frontal row; 1, 2, 3 = dorsal kineties 1–3

Description: *In vivo* c. $50 \times 16 \mu$ m. Left margin slightly indented in the area of the adoral zone of membranelles. Slightly contractile, transparent at low magnification. Macronuclear segments *in vivo* c. $7 \times 4 \mu$ m, with some small nucleoli. Usually 1 micronucleus joined to each macronuclear segment, rarely 1 between the segments, micronuclei with protargol always weakly stained. Entoplasm with some small, colourless globules. Movement very rapid, sliding hastily to and fro. Distal 3 adoral membranelles distinctly separated from the proximal membranelles, conspicuously extending to the right margin (Fig. 29, 31). Frontal cirri not enlarged, the left one in the gap of the adoral zone of membranelles, the right one in front of the frontal row (Fig. 31,

arrow head). 1 cirrus left of the frontal row (Fig. 31, arrow). Buccal cirrus consists very probably of 2 cilia only. Marginal rows begin at the level of the cytostome, distance between cirri (6–8 μm long only) becomes wider posteriorly. Always 1 small cirrus (ventral cirrus?) near the transverse cirri (Fig. 31). Left and middle dorsal kinety each with 5 basal body pairs, the right one consists of a single basal body pair only (Fig. 32).

The morphogenesis commences with the formation of an oral primordium near the left transverse cirrus. Subsequently, the posterior cirrus of the frontal row is disorganized.

Occurrence and Ecology: The type material was found in the upper layer (1–5 cm) of an alpine pseudogleyic soil on the Stubnerkogel, Bad Gastein, Austrian Central Alps (*Alnetum viridis* Br. — Bl.; 1780 m above sea level). A detailed milieu-spectrum is given by FOISSNER and PEER (1985).

Remarks: This species was originally described in the genus *Tachysoma*, essentially because of the absence of caudal cirri. However, BERGER and FOISSNER (1987) transferred it to the genus *Lamlostyla* because of its ventral cirral pattern. BERGER et al. (1984) stated that the right frontal cirrus is situated left of the anterior third of the frontal row. Now we assume that this cirrus matches the cirrus left of the frontal row of *L. edaphoni* and *L. kirkeniensis* (compare Fig. 22, 27, 31). It can be separated from these species by its small size, the low number of adoral membranelles, cirri in the frontal row, and left and right marginal cirri, the interruption in the adoral zone of membranelles, and the anterior distinctly shortened right marginal row. The first stages of the morphogenesis are similar as in *L. perisincirra*.

Description of *Territricha* nov. gen.

Diagnosis: Urostylidae with transverse and caudal cirri and 1 left and 1 right marginal row. Typical midventral pattern restricted to the postoral area, number of midventral cirri distinctly less. Right of the buccal area characteristic oxytrichid cirral pattern.

Type-species: *Territricha stramenticola* nov. spec.

Systematic Position of *Territricha*: According to BORROR and WICKLOW (1983) the family Urostylidae includes genera where "frontal and midventral cirri differentiate during prefission morphogenesis from the longitudinal field of more than 5 (without streak 1) oblique ciliary streaks". If we assume that within this family a low number of ciliary streaks (e.g. 7; without streak 1) is the apomorphic character state, *Territricha* must be considered to be a derived urostylid. Very probably, it links typical urostylids such as *Holosticha* Wrzeźniowski, 1877 and *Holostichides* Foissner, 1987b with the oxytrichids s. str. such as *Oxytricha* and *Steinia* Diesing, 1866. The proposed evolutionary series (Fig. 43–47) is mainly characterized by a decrease of the number of midventral pairs, viz. many in *Holosticha*, few in *Territricha*, and only 1 in *Steinia*. Such an intermediate systematic position is indicated by the peculiarities of the dorsal infraciliature too, because a multiple fragmentation of the dorsal kinety 3 (Fig. 41) and the possession of 4 dorsomarginal kineties (Fig. 42) are considered to be ancestral within the oxytrichids (WIRNSBERGER et al. 1986). In contrast such a complicated dorsal pattern must be regarded as derived within the urostylids, because in typical members of this group dorsal primordia develop usually only within preexisting kineties (JERKA-DZIADOSZ 1972, WIACKOWSKI 1985).

These findings indicate numerous homologies in the ciliature of the urostylids and oxytrichids as already proposed by WIRNSBERGER (1987) and supports the suggestion of some other authors that a close relationship between these taxa exists (BORROR 1972, CORLISS 1979, MARTIN et al. 1983).

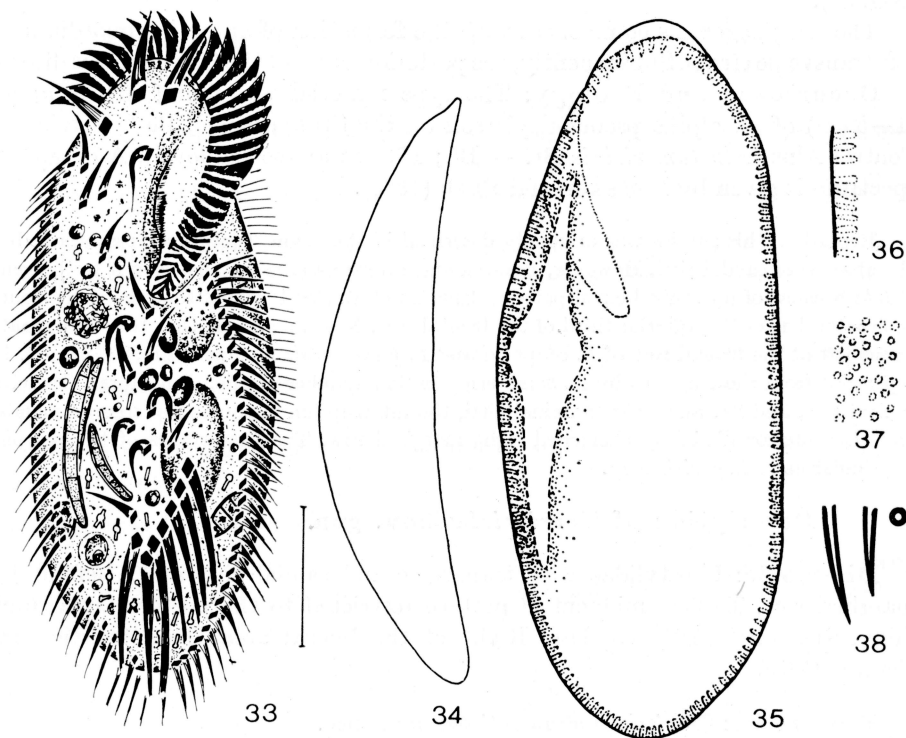


Fig. 33–38. *Territricha stramenticola* from life (Fig. 33–37) and after methyl green-pyronin staining (Fig. 38). Fig. 33–35. Ventral, lateral and dorsal view. Scale mark = 30 μ m. Fig. 36–38. Extrusomes

Comparison with other Genera: *Territricha* differs from *Holosticha* by the restriction of the midventral pairs to the postoral area and the distinctly lower number of midventral cirri (FOISSNER 1982). It can be separated from the oxytrichids s. str. by the higher number of postoral ventral cirri. *Territricha* differs from *Gastrostyla* Engelmann, 1862 by its having midventral pairs and a higher number of fronto-ventral-transverse streaks (compare Fig. 2 in WALLENGREN 1900 with Fig. 42).

Territricha stramenticola nov. spec. (Fig. 33–42, 45, 46, Tab. 2)

Diagnosis: *In vivo* 100–175 $\times$ 50–75 μ m. Usually 7 midventral cirri (3–4 pairs) and 7 distinctly anteriad displaced transverse cirri. Perpendicular to the pellicle many, c. 3 $\times$ 1 μ m large colourless subpellicular granules (extrusomes). 42 adoral membranelles on average. 5 dorsal kineties and c. 3 dorsal kinety fragments.

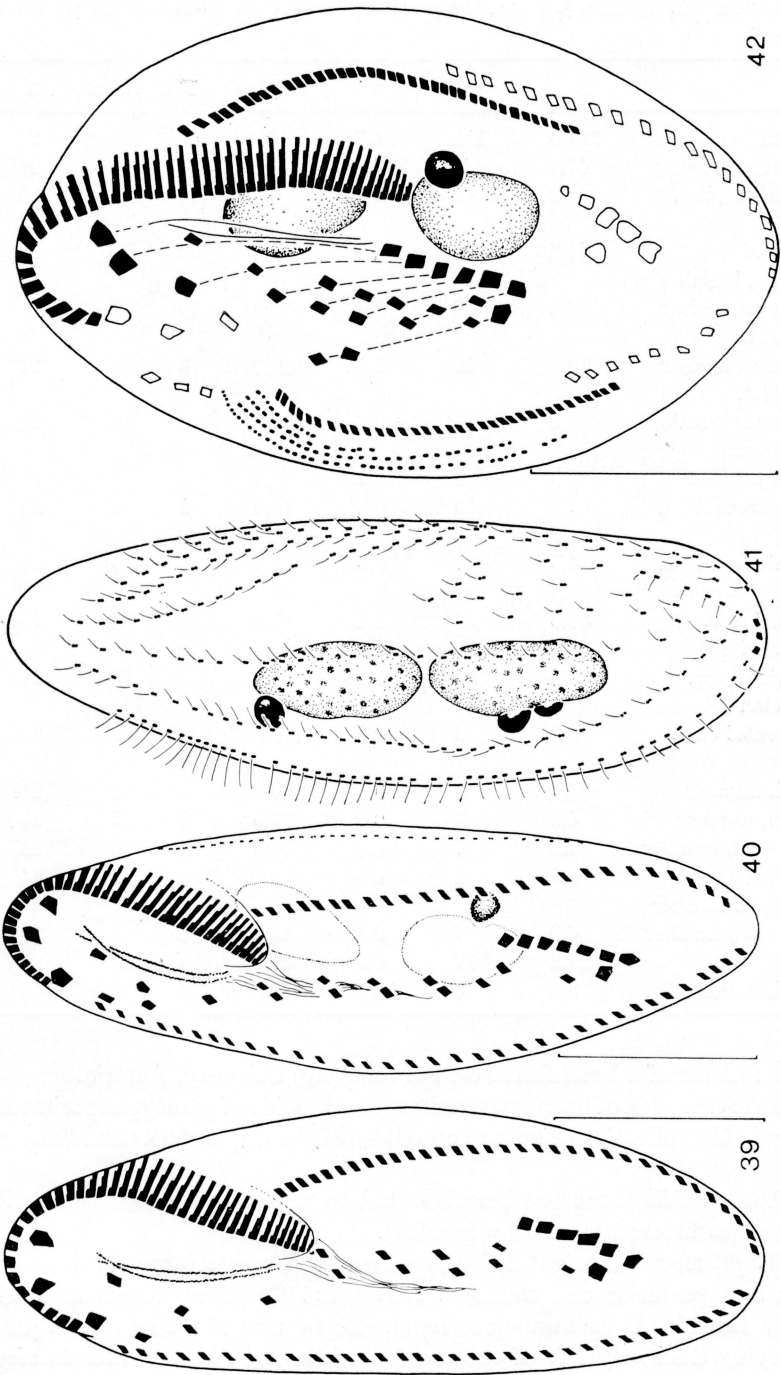


Fig. 39—42. *Territricha stramenticola* after protargol impregnation. Fig. 39—41. Infrastructure in ventral and dorsal view. Fig. 42. Late reorganization stage. Parental cirri are shown by outline, the new ones are filled in. The cirri of a primordium are connected by a dashed line. Scale marks = 30 μ m

Table 2. Biometrical characterization of *Territricha stramenticola*. All data are based on protargol impregnated specimens. All measurements in μm . For abbreviations see legend of Tab. 1. Distance 1, distance between the posterior transverse cirrus and the posterior end of the cell

Character	$\bar{x}$	M	s	CV	Min	Max	n
Body, length	111.5	111	6.7	6.0	99	126	22
Body, width	42.7	42	4.1	9.5	36	50	21
Adoral membranelles, number	42.2	42	2.5	5.8	39	47	15
Adoral zone of membranelles, length	44.8	45	3.0	6.6	39	50	21
Posterior macronuclear segment, length	18.5	18	2.0	10.9	15	22	21
Posterior macronuclear segment, width	10.0	10	1.1	10.9	8	12	21
Macronuclear segments, distance between	5.4	5	2.2	41.7	2	10	21
Micronuclei, number	2.5	2	0.7	29.2	2	4	10
Posterior micronucleus, length	5.3	5	0.6	10.8	4	6	20
Posterior micronucleus, width	4.5	4	0.5	11.5	4	5	20
Left marginal row, number of cirri	32.8	33	2.4	7.2	29	38	15
Right marginal row, number of cirri	33.4	34	3.0	9.1	27	39	18
Enlarged frontal cirri, number	3.0	3	0	0	3	3	21
Buccal cirri, number	1.0	1	0	0	1	1	21
Ventral cirri, number	4.2	4	0.7	16.5	4	7	20
Midventral cirri, number	7.3	7	0.8	10.3	7	9	13
Ventral cirri near the transverse cirri, number	2.0	2	0	0	2	2	14
Transverse cirri, number	6.8	7	0.8	12.2	4	8	19
Distance 1	17.2	17	3.6	21.1	8	23	21
Caudal cirri, number	3.0	3	0	0	3	3	9

Type location: Litter of a beechforest on the Gaisberg, Salzburg, Austria.

Type specimens: One slide of holotype specimens and 1 slide of paratype specimens have been deposited in the collection of microscope slides of the Upper Austrian Museum in Linz.

Etymology: The specific name has been selected to reflect the habitat where it lives (latin *stramentum* = litter; latin *colo* = inhabit).

Description: Right margin straight, left one convex, in the anterior part markedly indented. Anterior and posterior end rounded. About 2:1 flattened dorso-ventrally (Fig. 33–35). Body flexible. 2 macronuclear segments, *in vivo* $25-35 \times 10-17 \mu\text{m}$, finely granulated, lying distinctly left of the median of the cell. Micronuclei *in vivo* $6-8 \times 3-5 \mu\text{m}$. Contractile vacuole on the left-hand edge, about in the middle of the

cell, during diastole with channels. Extrusomes ejected after the addition of methyl green-pyronin, stain blue, corniform, c. $5-7\ \mu\text{m}$ long, do not impregnate with protargol (Fig. 35–38). Posterior part of the cell with many $1-5\ \mu\text{m}$ large, yellowish cytoplasmatic crystals and numerous homogenous $2-5\ \mu\text{m}$ large globules. Food vacuoles $10-20\ \mu\text{m}$, contain fungal spores of different shape and size and ciliates (*Colpoda* sp.). Rapid movement.

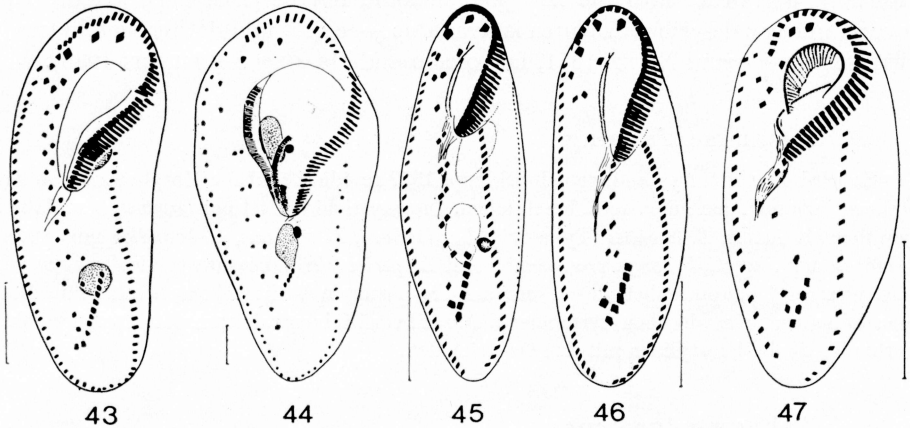


Fig. 43–47. *Holosticha cammerounensis* Dragesco, 1970 (Fig. 43, after DRAGESCO and DRAGESCO-KERNEIS 1986), *H. macrostoma* (Dragesco, 1970) BORROR, 1972 (Fig. 44, after DRAGESCO 1970), *Territricha stramenticola* (Fig. 45, 46), and *Steinia primicirrata* Berger and Foissner, 1987 (Fig. 47, after FOISSNER 1984). Ventral infraciliature after protargol impregnation. For explanation see text. Scale marks = $30\ \mu\text{m}$

Adoral zone of membranelles about 40% of body length, bases of the largest membranelles *in vivo* c. $10\ \mu\text{m}$ wide. Buccal area rather narrow, roofed by a prominent peristomial lip. Undulating membranes slightly bent, nearly the same length. Frontal cirri *in vivo* c. $25\ \mu\text{m}$ long, bases distinctly enlarged. Buccal cirrus near the anterior end of the undulating membranes. Cirri beside the adoral zone of membranelles arranged as in typical oxytrichids. Arrangement of the postoral midventral cirri (c. $20\ \mu\text{m}$ long) and transverse cirri usually as shown in Fig. 39. Bases of the c. $30\ \mu\text{m}$ long transverse cirri distinctly enlarged, only the posterior one sometimes protrude slightly beyond the posterior edge. Marginal cirri *in vivo* c. $20\ \mu\text{m}$ long. Right marginal row begins at about the level of the buccal cirrus, posteriorly only slightly separated from the left one. Complicated dorsal kinty pattern (Fig. 41). Basal body pairs, especially in dorsal kinty 1 very closely arranged. Dorsal cilia in the anterior part of the dorsal kinty 1 about $7\ \mu\text{m}$, in the posterior part and the remaining kinties c. $3\ \mu\text{m}$ long. In the posterior part of the cell, between the dorsal kinties 3 and 4 a field of about 3 short kinties. Very probably, they originate by multiple fragmentation of the posterior part of the dorsal kinty 3 (compare with *Onychodromus quadricornutus* Foissner, Schlegel, and Prescott, 1987). 3 caudal cirri, $15-20\ \mu\text{m}$ long at the posterior end of the dorsal kinties 1, 2, and presumably the leftmost row of the short kinties.

Morphogenesis: Fig. 42 shows a reorganization stage. This is indicated by the presence of both the parental fronto-terminal cirri, the parental right frontal cirrus,

and the parental transverse cirri. 8 fronto-ventral-transverse streaks occur, from which a different number of cirri develop. Right of the right marginal row the primordia of 4 dorsomarginal kineties are recognizable.

Species Comparison: Very probably, *Holosticha macrostoma* (Dragesco, 1970) Borror, 1972, with its distinctly reduced number of midventral cirri and anteriad displaced transverse cirri, is the most closely related species to *T. stramenticola* (Fig. 44). However, a transfer into the new genus should not be done until a redescription of several unclear described features is available — e.g. 3 undulating membranes, caudal cirri (DRAGESCO and NJINE 1971, DRAGESCO and DRAGESCO-KERNEIS 1986).

Zusammenfassung

Es wird die Gattung *Lamlostyla* Buitkamp, 1977 revidiert und die Morphologie von *Territricha stramenticola* nov. gen., nov. spec. beschrieben. Die oxytrichide Gattung *Lamlostyla* umfaßt 7 bodenbewohnende Arten: *L. lamottei* (Typusart), *L. edaphoni*, *L. hyalina*, *L. islandica* nov. spec., *L. kirkeniensis* nov. spec., *L. longa* nov. comb. und *L. perisincirra*. Die urostylide Gattung *Territricha* nov. gen. wird hauptsächlich durch eine auf die postorale Ventralfläche beschränkte Midventralanordnung und eine deutlich verminderte Anzahl von Midventralcirren charakterisiert. Vermutlich verbindet sie die Urostyliden mit den Oxytrichiden.

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References

- BERGER, H., and W. FOISSNER: Morphology and biometry of some soil hypotrichs (Protozoa: Ciliophora). Zool. Jahrb. Syst. **114** (1987) 193—239.
- , — und H. ADAM: Taxonomie, Biometrie und Morphogenese einiger terricoler Ciliaten (Protozoa: Ciliophora). Zool. Jahrb. Syst. **111** (1984) 339—367.
- , —, —: Protozoologische Untersuchungen an Almböden im Gasteiner Tal (Zentralalpen, Österreich). IV. Experimentelle Studien zur Wirkung der Bodenverdichtung auf die Struktur der Testaceen- und Ciliatentaxozönose. Veröff. Österr. MaB-Programms **9** (1985) 97—112.
- , —, —: Field experiments on the effects of fertilizers and lime on the soil microfauna of an alpine pasture. Pedobiologia **29** (1986) 261—272.
- BORROR, A. C.: Revision of the order Hypotrichida (Ciliophora, Protozoa). J. Protozool. **19** (1972) 1—23.
- , and B. J. WICKLOW: The suborder Urostylina Jankowski (Ciliophora, Hypotrichida): morphology, systematics and identification of species. Acta Protozool. **22** (1983) 97—126.
- BORY DE ST. VINCENT, J. B.: Essai d'une classification des animaux microscopiques. Paris 1824.
- BUITKAMP, U.: Die Ciliatenfauna der Savanne von Lamto (Elfenbeinküste). Acta Protozool. **16** (1977) 249—276.
- : Vergleichende Untersuchungen zur Temperaturadaptation von Bodenciliaten aus klimatisch verschiedenen Regionen. Pedobiologia **19** (1979) 221—236.
- CORLISS, J. O.: The ciliated protozoa. Characterization, classification and guide to the literature. 2nd ed. Oxford/New York/Toronto/Sydney/Paris/Frankfurt: Pergamon Press 1979.

- , and J. LOM: An annotated glossary of protozoological terms. In: LEE, J. J., S. H. HUTNER and E. C. BOVEE (eds.): An illustrated guide to the protozoa. Lawrence, Soc. Protozool. 1985, 576—602.
- DIESING, K. M.: Revision der Prothelminthen. Abt.: Amastigen. II. Amastigen ohne Peristom. Sitzungsber. kaiserlichen Akad. Wiss. Math.-Naturwiss. Classe, Wien **52** (1866) 505—579.
- DRAGESCO, J.: Ciliés libres du Cameroun. Ann. Fac. Sci. Yaoundé, Yaoundé Numéro hors série (1970) 1—141.
- et A., DRAGESCO-KERNEIS: Ciliés libres de l'Afrique intertropicale. Introduction à la connaissance et à l'étude des ciliés. Faune tropicale **26** (1986) 1—559.
- et T. NJINE: Compléments à la connaissance des ciliés libres du Cameroun. Ann. Fac. Sci. Cameroun n° **7—8** (1971) 97—140.
- ENGELMANN, T. W.: Zur Naturgeschichte der Infusionsthier. Z. wiss. Zool. **11** (1862) 347—393.
- FOISSNER, W.: Methylgrün-Pyronin: Seine Eignung zur supravitalen Übersichtsfärbung von Protozoen, besonders ihrer Protrichocysten. Mikroskopie **35** (1979) 108—115.
- : Ökologie und Taxonomie der Hypotrichida (Protozoa: Ciliophora) einiger österreichischer Böden. Arch. Protistenkd. **126** (1982) 19—143.
- : Infraciliatur, Silberliniensystem und Biometrie einiger neuer und enig bekannter terrestrischer, limnischer und mariner Ciliaten (Protozoa: Ciliophora) aus den Klassen Kinefragminophora, Colpodea und Polyhymenophora. Stapfia **12** (1984) 1—165.
- : Soil protozoa: fundamental problems, ecological significance, adaptations in ciliates and testaceans, bioindicators and guide to the literature. Progr. Protistol. **2** (1987a) (in press).
- : Neue und wenig bekannte hypotriche und colpodide Ciliaten (Protozoa, Ciliophora) aus Böden und Moosen. Zool. Beitr. N.F. **31** (1987b) 187—282.
- , und T. PEER: Protozoologische Untersuchungen an Almböden im Gasteinertal (Zentralalpen, Österreich). I. Charakteristik der Taxotope, Faunistik und Autökologie der Testacea und Ciliophora. Veröff. Österr. MaB-Programms **9** (1985) 27—50.
- , M. SCHLEGEL and D. M. PRESCOTT: Morphology and morphogenesis of *Onychodromus quadricornutus* n. sp. (Ciliophora, Hypotrichida), an extraordinarily large ciliate with dorsal horns. J. Protozool. **34** (1987) 150—159.
- HEMBERGER, H.: Revision der Ordnung Hypotrichida Stein (Ciliophora, Protozoa) an Hand von Protargolpräparaten und Morphogenesedarstellungen. Diss. Mathem.-Naturw. Fak. Univ. Bonn, Bonn 1982.
- : Neue Gattungen und Arten hypotricher Ciliaten. Arch. Protistenkd. **130** (1985) 397—417.
- JERKA-DZIADOSZ, M.: Cortical development in *Urostyla*. I. Comparative study on morphogenesis in *U. cristata* and *U. grandis*. Acta Protozool. **10** (1972) 74—100.
- KAHL, A.: Urtiere oder Protozoa I. Wimpertiere oder Ciliata (Infusoria), 3. Spirotricha. In: DAHL, F. (ed.): Die Tierwelt Deutschlands. **25**, 1932, 399—650.
- LÜFTENEGGER, G., W. FOISSNER und H. ADAM: Der Einfluß organischer und mineralischer Dünger auf die Bodenfauna einer planierten, begrüneten Schipiste oberhalb der Waldgrenze. Z. Vegetationst. **9** (1986) 149—153.
- MARTIN, J., C. FEDRIANI and J. PEREZ-SILVA: Morphogenetic pattern in *Laurentiella acuminata* (Ciliophora, Hypotrichida): its significance for the comprehension of ontogeny and phylogeny of hypotrichous ciliates. J. Protozool. **30** (1983) 519—529.
- RIOU, G.: Les sols de la savane de Lamto. Bull. de liaison des chercheurs de Lamto num. spéc. (1974) 3—44.
- SMALL, E. B., and D. H. LYNN: Phylum Ciliophora Doflein, 1901. In: LEE, J. J., S. H. HUTNER and E. C. BOVEE (eds.): An illustrated guide to the protozoa. Lawrence, Soc. Protozool. 1985, 393—575.
- SOKAL, R. R., and F. J. ROHLF: Biometry. 2nd ed. San Francisco: W. H. Freeman and Company 1981.
- STERKI, V.: Beiträge zur Morphologie der Oxytrichinen. Z. wiss. Zool. **31** (1878) 29—58.

- STOKES, A. C.: Some new hypotrichous infusoria from American fresh waters. *Ann. Mag. nat. Hist.* (5) **20** (1887) 104—114.
- TUFFRAU, M.: Proposition d'une classification nouvelle de l'ordre Hypotrichida (Protozoa, Ciliophora), fondée sur quelques données récentes. *Ann. Sci. nat. (Zool.)* (13) **8** (1986—1987) 111—117.
- WALLENGREN, H.: Zur Kenntnis der vergleichenden Morphologie der hypotrichen Infusorien. *Bih. Svenska Vetensk. Akad. Handl.* **26** (1900) 1—31.
- WIACKOWSKI, K.: The morphology and morphogenesis of *Keronella gracilis* n. gen., n. spec. (Hypotrichida, Ciliophora). *Protistologica* **21** (1985) 81—91.
- WIENSBERGER, E.: Division and reorganization in the genus *Pseudokeronopsis* and relationships between urostylids and oxytrichids (Ciliophora, Hypotrichida). *Arch. Protistenkd.* **134** (1987) 149—160.
- , W. FOISSNER and H. ADAM: Biometric and morphogenetic comparison of the sibling species *Stylonychia mytilus* and *S. lemnae*, including a phylogenetic system for the oxytrichids (Ciliophora, Hypotrichida). *Arch. Protistenkd.* **132** (1986) 167—185.
- WRZESNIOWSKI, A.: Beobachtungen über Infusorien aus der Umgebung von Warschau. *Z. wiss. Zool.* **20** (1877) 467—511.

Dr. HELMUT BERGER, Hydrologische Untersuchungsstelle Salzburg, Lindhofstraße 5, A-5020 Salzburg (Austria)

Univ.-Prof. Dr. WILHELM FOISSNER, Institut für Zoologie der Universität Salzburg, Hellbrunnerstraße 34, A-5020 Salzburg (Austria)