Urotricha psenneri n. sp. and Amphileptus piger (Vuxanovici, 1962) n. comb., Two Planktonic Ciliates (Protozoa, Ciliophora) from an **Oligotrophic Lake in Austria**

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ABSTRACT. Two euplanktonic ciliates, Urotricha psenneri n. sp. (Prostomatida) and Amphileptus piger (Vuxanovici, 1962) n. comb. (Pleurostomatida), were discovered in the surface plankton of the oligotrophic Lake Traunsee in Austria. Their morphology and infraciliature were studied in live cells as well as in specimens impregnated with protargol and silver nitrate. Urotricha psenneri is a small urotrichid, less than 50 µm length and with a single caudal cilium. It is unique in having (i) a massive oral basket projecting as a conspicuous bulge with cylindrical microfibrillar annulus and (ii) a curved brosse row 1 in the broad, barren circumoral area. Amphileptus piger (Vuxanovici, 1962) is about 55 \times 13 μ m in vivo, has two macronuclear nodules with a single micronucleus in between in the posterior body half, has a single contractile vacuole with a terminal excretory pore, and few, but thick and thus highly conspicuous extrusomes. The amphileptid ciliary pattern (spica) is difficult to recognise due to the widely spaced basal bodies.

Key Words. Amphileptidae, fresh water, planktonic ciliate, Pleurostomatida, Prostomatida, taxonomy, Urotrichidae.

PLANKTONIC ciliates are considered among the most important phagotrophic protozoa both in terms of biomass and production (Weisse and Müller 1998; for a compendium see Foissner, Berger, and Schaumburg 1999). Except for the oligotrichs, prostomatids are the most typical and numerous freshwater planktonic ciliates (e.g. Müller 1989; Sonntag et al. 2002). Small prostome ciliates (< 30 μ m) of the genera Urotricha Claparède & Lachmann, 1859 and Balanion Wulff, 1916 are among the most common ciliates in pond and lake plankton (Macek et al. 1996; Müller 1989, 1991; Salbrechter and Arndt 1994; Schönberger 1994; Šimek et al. 1995; Sommaruga and Psenner 1993; Sonntag et al. 2002). Urotrichs are easily recognised by their fast, jumping movement but rather difficult to identify without silver impregnation. However, reliable keys are available for most species (Foissner and Pfister 1997; Foissner, Berger, and Schaumburg 1999).

The second species described here, belongs to the haptorid pleurostomes, which are flattened laterally and therefore excellently adapted to a surface-associated life in biofilms (Foissner et al. 1995). However, pleurostome ciliates have also been frequently recorded from lake plankton (for a review, see Foissner, Berger, and Schaumburg 1999), although only three species were originally described from such habitats. Pleurostomatids can be easily recognised as a group, but it is difficult to identify genera and species because differences are small and not easily recognised (e.g. the spica of the amphileptids).

MATERIALS AND METHODS

Urotricha psenneri and Amphileptus piger were found in autumn 2000 in the surface plankton of the oligotrophic lake Traunsee (47° 51' N, 13° 47' E); both were very rare. Holomictic Traunsee is about 191 m deep and situated in the Austrian limestone Alps. For further morphometric and abiotic characteristics on the lake and its planktonic ciliate community, see Jagsch, Gassner, and Dokulil (2002), Pechlaner and Sossau (1982), and Sonntag et al. (2002).

Cells were studied in vivo using a high-power oil immersion objective and differential interference contrast. Characteristics subject to change under coverglass pressure, like cell shape and movement, were studied in uncovered, swimming specimens using magnifications between $100 \times -250 \times$. The infraciliature (ciliary pattern) and various other cytological details were revealed with protargol (Foissner's technique) and Chatton-Lwoff silver nitrate-impregnation. See Foissner, Berger, and Schaumburg (1999) for a detailed description of all methods used. Unfortunately, the protargol slides were poorly fixed and thus bleached almost completely within two years. In spite of this, we deposit them because many details can be recognised with interference contrast optics.

Counts and measurements on silvered specimens were performed at a magnification of 1,000×. In vivo measurements were conducted at magnifications of $100 \times -1,000 \times$. 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.

RESULTS AND DISCUSSION

Urotricha psenneri n. sp. (Table 1 and Fig. 1-22)

Diagnosis. Size about 40 \times 25 μ m in vivo; ellipsoidal. Extrusomes about 1.5 µm long. One caudal cilium and an average of 37 ciliary rows. Oral basket projecting from body proper as conspicuous bulge and with compact basket rods anteriorly connected by a broad microfibrillar annulus. Circumoral kinety composed of about 22 dikinetids. Three minute brosse rows, upper row convex and in barren circumoral area.

Type location. Plankton of Lake Traunsee, Austria (47° 51' N, 13° 47' E).

Type material. Seven slides (one holotype, six paratypes) with Chatton-Lwoff silver nitrate-impregnated specimens and eleven protargol-impregnated paratype slides with some strongly bleached cells have been deposited in the Oberösterreichische Landesmuseum at Linz (LI), Austria. Relevant specimens are marked by black ink circles on the cover glass.

Dedication. The junior author dedicates this new species to Univ.-Prof. Dr. Roland Psenner (Innsbruck University), acknowledging the excellent supervision of the doctoral thesis.

Description. Size $30-50 \times 15-30 \ \mu\text{m}$ in vivo, usually about $40 \times 25 \ \mu\text{m}$; distinctly shrunken in protargol preparations (Table 1). Length: width ratio on average 1.5:1 in silver preparations. Narrowly to broadly ellipsoidal with unciliated posterior portion occupying, as is typical for genus, approximately 20% of body length separated from body proper by only slight constriction at its boundary (Fig. 1, 2, 9, 15-18). Macronucleus usually in or near mid-body; invariably displaced to near anterior end in specimens with a large food item; reniform to indistinctly fusiform with globular to ellipsoidal chromatin ag-

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Characteristics ¹	Method	Mean	Μ	SD	SE	CV	Min	Max	n
Body, length	Р	28.0	28	2.5	0.6	2.0	23	35	21
	CHL	36.3	36	3.7	1.4	3.9	31	43	7
Body, maximum width	Р	19.3	19	2.2	0.5	2.5	16	26	21
	CHL	23.4	23	3.7	1.4	6.0	20	31	7
Somatic ciliary rows, length	Р	22.7	22	2.4	0.5	2.3	18	29	21
Macronucleus, length	Р	8.6	8.5	1.5	0.3	3.9	6	11	21
Macronucleus, width	Р	5.3	5	0.6	0.1	2.3	4	6	21
Anterior end to macronucleus,									
distance	Р	11.0	11	3.1	0.7	6.1	5	16.5	21
Oral basket, maximum diameter	Р	8.6	9	1.1	0.2	2.7	7	11	21
Oral basket, length	Р	10.0	10	1.0	0.2	2.1	8	11	21
Oral basket width: body width,	Р	45.0	44	5.6	1.2	2.7	37	56	21
ratio in %	CHL	42.1	43	7.2	2.7	6.5	29	52	7
Excretory pore, diameter	Р	1.3	1.5			_	1	1.5	21
Somatic ciliary rows, number	P, CHL	37.1	37	1.6	0.3	0.8	35	41	27
Cilia in a somatic row, number	Р	27.4	27	3.0	0.7	2.4	23	33	21
Caudal cilia, number	Р	1.0	1	0.0	0.0	0.0	1	1	21
Circumoral dikinetids, number	Р	22.0	22	2.1	0.5	2.1	19	26	21

Table 1. Morphometric data on Urotricha psenneri.

¹ Field specimens from the same sample after protargol (P) or Chatton-Lwoff silver nitrate impregnation (CHL). Measurements in μ m. CV = coefficient of variation in %, M = median, Max = maximum, Mean = arithmetic mean, Min = minimum, n = number of specimens investigated, SD = standard deviation, SE = standard error of arithmetic mean.

gregates (Fig. 1, 2, 15–18). Micronucleus not recognised. Contractile vacuole subterminal and slightly eccentric, that is, with single excretory pore near end of kineties abutting the brosse (Fig. 1, 2, 6). Cortex longitudinally striated in vivo by ciliary rows (Fig. 1, 10). Somatic extrusomes, although rather numerous, recognisable only in some protargol preparations as minute $(1-1.5 \times < 0.4 \,\mu\text{m})$ rods attached mainly to ciliated body portion (Fig. 2, 3, 15, 16); in vivo not recognisable, not even under optimal conditions (oil-immersion, interference contrast). Cytoplasm colourless, contains some strongly refractive lipid droplets and, in some specimens, a large food vacuole with a pollen grain about 15 μ m across (Fig. 1, 9, 18). Movement as conspicuous as in most congeners, that is, by sudden, fast jumps transiting into wide spirals under gradual slowdown.

Somatic cilia about 6-7 µm long in vivo and protargol preparations, arranged in an average of 37 slightly spiralling, equidistant rows commencing subapically and terminating at about 80% of body length, leaving blank bowl-shaped posterior body portion (Fig. 1, 2, 5, 6). Ciliary rows widely separate from circumoral kinety, form indistinct spiral in frontal view because those right of brosse commence slightly more subapically than those at left (Fig. 5, 19, 21, 22). All ciliary rows with the exception of two abutting to posterior brosse margin commence with a dikinetid likely having only the posterior basal body ciliated because the anterior is smaller in silver preparations (Fig. 5, 12, 21, 22). Caudal cilium in deep pit on posterior pole centre, about half as long as body, accompanied by a second granule in silver nitrate preparations; this granule is bare because we observed only one caudal cilium in several live and 21 protargol-impregnated specimens (Table 1 and Fig. 1, 2, 6, 9, 17).

General organisation of oral apparatus and brosse (adoral organelles) as in congeners (Foissner and Pfister 1997). Details are conspicuously different, clearly distinguishing *U. psenneri* from all described species as follows: (i) oral basket more massive and conspicuous than in similar-sized congeners because comparatively wide (30-45% of body width) and highly refractive due to the compact teeth at the ends of the rods (Fig. 1, 3, 4, 8, 9–11, 13, 15–18); (ii) oral basket more distinctly dome-like protruding than in congeners, forms conspicuous, crown-like structure in slightly squeezed cells (Fig. 9–11), a

curious property never seen so clearly in any other species (Foissner, Berger, and Schaumburg 1999; Foissner and Pfister 1997); (iii) oral flaps unusually long, viz. about 4 μ m, while only 2–3 μ m in even 100- μ m-sized congeners (Foissner, Berger, and Schaumburg 1999; and WF., unpubl. data); (iv) the fibrous ring surrounding the urotrichid oral opening (Foissner and Pfister 1997) is modified to a conspicuous, cylindrical annulus (Fig. 3, 4, 15–18), and a second, less distinct annulus or thickening of the basket rods is found in the posterior half of the basket; (v) brosse kineties as minute as in most small congeners, but upper kinety uniquely convex and in the barren circumoral area (Fig. 2, 5, 7, 12, 14, 19, 21, 22), a rare feature as yet found in only three congeners (see below).

Occurrence and ecology. As yet only found at type location, where it was very rare and occurred in the surface layer (0-2/3 m), but not at 40 m depth. Interestingly, this species feeds on pollen grains, like several large urotrichs (Foissner and Pfister 1997), indicating that it might be more abundant in spring.

Comparison with related species. Urotricha psenneri belongs to a group of urotrichs having a size of less than 50 μ m and a single or two caudal cilia. For urotrichs with more than two caudal cilia, see the recent revision by Foissner and Pfister (1997). Unfortunately, no revision is available for the species with a single or two caudal cilia.

Within the single-caudal cilia-urotrichs, there are two groups: one has the brosse rows within the somatic ciliature, while the other has at least the upper brosse row in the barren circumoral area. Urotricha psenneri belongs to the second group, which includes Urotricha synuraphaga Kahl, 1927 (ovate, 9 circumoral dikinetids, oral basket about one-fourth of body width, upper brosse row straight; see redescription by Foissner 1997); Urotricha ristoi Krainer, 1995 (15–25 μ m, globular, 6 circumoral dikinetids, oral basket very narrow); and Urotricha dragescoi Foissner, 1984a (60–67 ciliary rows, 4–6 adoral organelles, extrusomes conspicuously fusiform). Furthermore, the massive, protruding oral basket with the broad annulus seems to be a unique feature of U. psenneri.

Although U. psenneri is a very distinct species, it is difficult to distinguish from other urotrichs with single caudal cilium in vivo. Thus, reliable identification requires both, live observation



Fig. 1-8. Urotricha psenneri from life (1, 7, 8), after protargol impregnation (2-4), and after Chatton-Lwoff silver nitrate impregnation (5, 6). 1. Left lateral view of a representative specimen containing an ingested pollen grain and many lipid droplets. 2. Ventral view showing ciliary pattern, macronucleus, oral apparatus, and adoral organelles. Note fringe of minute extrusomes recognisable only after protargol impregnation. 3, 4. Details of oral apparatus. Optical section (3) and side face view (4) of oral basket. Note the broad microfibrillar annulus, a unique feature of U. psenneri. 5, 6. Anterior and posterior polar views of ciliary pattern. Arrows denote adoral organelles (5) and excretory pore (6). 7. The brosse consists of three dikinetidal adoral organelles, of which the anterior organelle is conspicuously convex, a specific feature of U. psenneri (cp. Fig. 14). 8. Lateral view of pharyngeal rods with highly refractive rod teeth (black) and unusually long oral flaps (4 μ m). A, microfibrillar annulus; AO, adoral organelles; CC, caudal cilium; CK, circumoral kinety (basal body pairs from which the oral flaps originate); E, extrusomes; EP, excretory pore of contractile vacuole; OB, oral basket; OF, oral flaps (paired cilia forming digitate processes); PG, pollen grain; PI, pit; RT, rod teeth. Bar divisions = 5 μ m (1-6) and 3 μ m (7, 8).

(to see the conspicuous oral basket and the inconspicuous extrusomes) and silver impregnation (to see details of the infraciliature). However, the easiest way to distinguish *U. psenneri* from similar urotrichs probably is to squeeze it slightly with the cover slip to reveal the oral basket which is more conspicuous than in any other small *Urotricha* species (Fig. 9–11). Furthermore, all small urotrichs have shorter oral flaps (4 μ m vs. 2 μ m) and fewer circumoral dikinetids (19–26 vs. 9–16).

Amphileptus piger (Vuxanovici, 1962) n. comb. (Table 2 and Fig. 23-44)

Emended diagnosis. Size about 55 \times 13 µm in vivo; lanceolate with indistinct neck. Nuclear apparatus in posterior half of cell, consists of two macronuclear nodules and a single micronucleus in between. Extrusomes ellipsoidal to ovate, sparse but conspicuous because glossy and about 3 \times 1.3 µm in size. Cilia arranged in 9–11 right lateral rows gradually shortened in

midline (spica), four left lateral, and two perioral rows. Contractile vacuole with terminal excretory pore.

Type material. No type material of *A. piger* Vuxanovici, 1962 has been mentioned in the literature. We have deposited 25 slides with strongly bleached protargol-impregnated (Foissner's technique) specimens in the Oberösterreichische Landesmuseum at Linz (LI), Austria. Relevant specimens are marked by black ink circles on the cover glass.

Redescription. Size $40-80 \times 10-20 \ \mu m$ in vivo; usually about 55 \times 13 μm ; length:width ratio on average 4.5:1 in protargol preparations, while near 3.5:1 in vivo, likely because specimens are fragile and soon become inflated during observation. Shape as in most small congeners, that is, slenderly to broadly lanceolate with indistinct neck slightly curved dorsally, anterior end more narrowly rounded than posterior, widest below mid-body; laterally flattened up 2:1; non-contractile but very flexible. Two (rarely only one) almost abutting macronu-



Fig. 9–18. Urotricha psenneri in vivo (9–14) and after protargol impregnation (15–18). 9, 10. Slightly squashed specimen showing overall organisation and the conspicuous oral apparatus. Arrows denote posterior end of ciliary rows. Note the long oral flaps (4 μ m) and the conspicuous, strongly refractive rod teeth of the oral basket. 11, 13. Details of oral apparatus. 12. Anterior half of body of a heavily compressed specimen showing circumoral kinety composed of oral flaps, location of brosse in barren area, and somatic ciliary pattern. 14. The adoral organelles (brosse) consist of three rows of paired basal bodies (dikinetids), and the upper row is uniquely convex. 15–17. Main cell organelles. Note the prominent oral basket with two microfibrillar annuli clearly recognisable after protargol impregnation. 18. Specimen with macronucleus displaced to near anterior end due to a large food inclusion (pollen grain). A, microfibrillar annuli; B, brosse (adoral organelles); BA, barren area; CC, caudal cilium; CR, ciliary rows; CV, contractile vacuole; DK, dikinetids (paired basal bodies) at anterior end of ciliary rows; E, extrusomes; LD, lipid droplets; MA, macronucleus; OB, oral basket; OF, oral flaps; PG, pollen grain; PI, pit of caudal cilium; PR, pharyngeal rods; RT, rod teeth. Scale bars 5 μ m (11–14) and 10 μ m (10, 15–18).

clear nodules below mid-body on average, individual nodules slightly, rarely distinctly ellipsoidal; chromatin aggregates numerous and about 1 μ m across in protargol preparations. Micronucleus usually in between, rarely beside macronuclear nodules, globular, surface conspicuously granulated (Fig. 23, 26,

29, 30, 43). Contractile vacuole in posterior body end slightly neighboured ventral side, with single excretory pore at rear end (Fig. 23, 29, 38, 40). Extrusomes remarkable in location, number, shape, and strong light refraction: number varies from two to six, usually three, two in anterior half and one in posterior;

Fig. 19–22. Urotricha psenneri, ciliary pattern after Chatton-Lwoff silver nitrate impregnation. 19, 20. Oblique ventrolateral views of same ecimen. Note convex anterior adoral organelle (19; arrow). 21. Oblique anterior polar view showing oral opening (asterisk) encircled by reumoral kinety. Note location of adoral organelles within broad barren circumoral area and indistinct spiral course of ciliary rows (arrows). 22.

Fig. 19-22. Urotricha psenneri, chiary pattern after Chatton-Lwoff silver nitrate impregnation. 19, 20. Oblique ventrolateral views of same specimen. Note convex anterior adoral organelle (19; arrow). 21. Oblique anterior polar view showing oral opening (asterisk) encircled by circumoral kinety. Note location of adoral organelles within broad barren circumoral area and indistinct spiral course of ciliary rows (arrows). 22. Right side view showing dikinetids at anterior end of ciliary rows. B, brosse (adoral organelles); BA, barren area; CK, circumoral kinety (basal body pairs from which the oral flaps originate); DG, paired (double) granules at anterior end of ciliary rows; OB, oral basket; P, ring of pores. Scale bars 10 μ m (19-21) and 5 μ m (22).

individual extrusomes ellipsoidal to ovate with a minute constriction anteriorly, conspicuous and recognisable as bright dots at even low magnification (100×) because 2–4.5 × 1–2 μ m in size, compact and glossy; become claviform when ejected; frequently impregnate strongly with protargol (Fig. 23, 24, 29, 38, 39, 41, 43). Cytoplasm colourless contains numerous bright lipid droplets up to 4 μ m across. Swims slowly while rotating about main body axis.

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Somatic and oral ciliary pattern similar as in congeners (for a brief review, see Foissner et al. 1995); thus, it will be described only briefly. Somatic cilia on right side of cell about 8 μ m long in vivo, widely spaced, arranged in an average of ten straight rows, those in midline gradually shortened producing a suture, the so-called spica and main generic feature; marginal kinetics gradually extend over ventral to dorsal side in posterior half of cell. On left side four rows each composed of about 1

CK

RA

Table 2.	Morphometric	data on	Amphileptus	piger.
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Characteristics'	Mean	M	SD	SE	CV	Min	Max	n
Body, length (in vivo) ²	56.0					50.0	60.0	10
Body, width (in vivo) ²	16.0		_		_	15.0	20.0	10
Body, length	51.3	51	6.7	1.5	13.1	41.0	64.0	21
Body, maximum width	11.7	12	2.4	0.5	20.3	9.0	17.0	21
Body length : width, ratio	4.5	5	0.8	0.2	17.7	3.2	5.8	21
Anterior end to end of dorsal brush								
row 2, distance	25.8	26	3.6	0.8	14.0	20	32	21
Anterior end to nuclear apparatus,								
distance	27.0	28	4.5	1.0	16.6	19	34	21
Distance between macronuclear								
nodules	0.3	0	0.7	0.1	197.5	0	2	21
Nuclear figure, length	13.6	13	2.2	0.5	16.4	10	18	21
Macronuclear nodules, length	6.7	7	1.1	0.3	17.1	5	9	21
Macronuclear nodules, width	5.4	5	0.8	0.2	15.0	4	7	21
Micronucleus, length	2.4	2.5	0.4	0.1	16.3	2	3	21
Micronucleus, width	2.0	2	0.2	0.0	11.2	1.5	2.5	21
Extrusomes, length (in vivo) ²	3.5	_	_		_	3.0	4.5	10
Extrusomes, width (in vivo) ²	1.3	—				1.0	2.0	10
Extrusomes, length	2.5	2.5			_	2	3.5	21
Extrusomes, width	1.2	1				1	1.5	21
Somatic kineties on right side, number	10.1	10	_		_	9	11	21
Somatic kineties on left side, number	4.0	4	0.0	0.0	0.0	4	4	21
Basal bodies in a continuous kinety								
on right side, number	22.2	22	2.5	0.5	11.3	17	27	21
Dikinetids in brush row 1, number	4.3	4	1.1	0.2	25.7	2	6	21
Dikinetids in brush row 2, number	16.8	17	2.8	0.6	16.4	12	21	21
Dikinetids in brush row 3, number	5.4	6	1.1	0.2	19.9	4	7	21
Perioral kineties, number	2.0	2	0.0	0.0	0.0	2	2	21
Macronuclear nodules, number	2.0	2	0.0	0.0	0.0	2	2	21
Micronucleus, number	1.0	1	0.0	0.0	0.0	1	1	21
Extrusomes, number	3.3	3	1.1	0.3	34.9	2	6	21

¹ Data, if not stated otherwise, from field specimens of two sampling occasions after protargol impregnation. Measurements in μ m. CV = coefficient of variation in %, M = median, Max = maximum, Mean = arithmetic mean, Min = minimum, n = number of specimens investigated, SD = standard deviation, SE = standard error of arithmetic mean.

² Measured at low magnification (\times 100) and thus rough.



Fig. 23-37. Amphileptus piger (23-34) and Amphileptus punctatus (35-37) in vivo (23-25; 31-34 from Vuxanovici (1962); 35 from Kahl (1926); 36, 37 from Foissner (1984b)) and after protargol impregnation (26-30). 23, 25. Left and right side view of a representative specimen. 24, 34. Extrusomes are $3 \times 1.3 \mu m$ in size, compact and glossy, and have a minute constriction anteriorly. 26-28. Left and right side view of oral and somatic ciliary pattern of a representative specimen. The spica becomes distinct only if the basal bodies are connected by lines (28). 29, 30. Left lateral views showing nuclear apparatus in posterior body half, conspicuous extrusomes in anterior and posterior half, ciliary pattern, oral apparatus, nematodesmata originating from perioral kineties, and the slightly subterminal contractile vacuole. 31-33. Left lateral (31), ventral (32), and transverse (33) view of a Romanian specimen. 35-37. Right and left lateral views, 100 μm , 125 μm , 125 μm . B1, 2, 3, brush rows; CV, contractile vacuole; E, extrusomes; MA, macronuclear nodule; MI, micronucleus; N, nematodesmata; OS, oral slit; P1, 2, perioral kineties; SK, anteriorly shortened kinety between brush rows 1 and 2. Bar divisions = 10 μm .

 μ m long, widely spaced bristles, except at anterior region, where three rows are modified to a dorsal brush composed of narrowly spaced pairs of slightly inflated, up to 2.5- μ m long bristles; between brush rows 1 and 2 an anteriorly shortened kinety without dikinetids. Brush row 1 in body midline, consists of an average of four bristle pairs. Brush row 2 near dorsal margin of cell, distinctly longer than rows 1 and 3, consists of an average of 17 bristle pairs, distance between last and penultimate pair invariably slightly enlarged. Brush row 3 at dorsal margin of cell, consists of an average of six bristle pairs (Fig. 23, 25, 26–30, 39, 44).

Oral slit in anterior third of ventral side, marked by rather distinct furrow in live and some protargol-impregnated specimens, supported by nematodesmata originating from perioral kineties. Left (first) perioral kinety composed of oblique dikinetids with basal bodies unusually widely spaced. Right (sec-



Fig. 38-44. Amphileptus piger in vivo (38-41) and after protargol impregnation (42-44). 38. Left side view of a squashed specimen to show the conspicuous extrusomes in side and transverse (arrowheads) view. 39. Left anterior end showing dorsal brush composed of narrowly spaced pairs of slightly inflated bristles. 40. Right side view of a freely motile, but slightly inflated specimen. 41. Partially exploded extrusome. 42-44. Right (42) and left (43, 44) side views. Arrow denotes micronucleus between macronuclear nodules (43). Note the heavily impregnated extrusomes. B, dorsal brush; CV, contractile vacuole; E, extrusomes; MA, macronuclear nodule; N, nematodesmata; OB, oral bulge; P1, 2, perioral kineties. Scale bars 10 μ m (38, 39), 30 μ m (40), 3 μ m (41) and 20 μ m (42-44).

ond) perioral kinety composed of narrowly spaced dikinetids with about 9- μ m long cilia curved anteriorly to form rather conspicuous mane. Both perioral kineties extend to about midbody, continuing posteriorly as ordinary ciliary rows with rather widely and irregularly spaced monokinetids.

Occurrence and ecology. Vuxanovici (1962) found numerous specimens in a clean sample from Lake Fundeni near Bucarest, Romania. We rediscovered *A. piger* in two adjacent subalpine, oligotrophic Austrian lakes, viz. in the autumn surface plankton (0–2/3 m) of Lake Traunsee (47° 51' N, 13° 47' E) and in integrated samples (0–20 m) from Lake Mondsee (47° 50' N, 13° 23' E). These findings indicate that *A. piger* is a euplanktonic species, which is emphasised by its behaviour in the laboratory: in contrast to many other pleurostomatids, it never glides on the microscope slide, but swims continuously and slowly rotating about main body axis.

Generic assignment. The right side ciliary rows of our specimens form a spica and the oral ciliature is composed of only two perioral kineties. Thus, they belong to the genus *Amphileptus* Ehrenberg, 1830, as defined by Foissner (1984b) and Foissner and Leipe (1995). Accordingly, *Litonotus piger* is transferred to the genus *Amphileptus*: *Amphileptus piger* (Vuxanovici, 1962) n. comb. (basionym: *Lionotus piger* Vuxanovici, 1962; note that *Lionotus* is a secondary wrong spelling of *Litonotus*).

Comparison with original description and related species. Pleurostomatid ciliates have been frequently recorded from lake plankton (for a review, see Foissner, Berger, and Schaumburg 1999), but only three species were originally described from such habitats, viz. *Litonotus vesiculosus* Stokes, 1885 (600 μ m); *Litonotus gandolfii* André, 1914 (rod-shaped extrusomes, a contractile vacuole each in anterior and posterior body half); and *L. piger* Vuxanovici, 1962 (see below). None of these species has been redescribed.

Species identification is difficult in the genera *Litonotus* and *Amphileptus* because most were described superficially and reliable redescriptions are rare (Foissner et al. 1995, Song and Wilbert 1989). Both genera are in urgent need of revision. Thus, we shall not discuss in detail synonymy, but concentrate on a meaningful identification with one of the many species (> 100!) available in the literature.

Our population belongs to a group of pleurostomatids having a size of less or near 100 µm, two macronuclear nodules with a single micronucleus in between, a single contractile vacuole, and, especially, thick and highly refractive extrusomes. Within that group, our specimens are most similar to Litonotus punctatus Kahl, 1926 (Fig. 35-37) and L. piger Vuxanovici, 1962 (Fig. 31-34). Litonotus punctatus and L. piger differ in only one feature, viz. contractility, which is high in the former and lacking in the latter. Although Vuxanovici's (1962) and Kahl's (1926) descriptions are entirely based on live observations, most features mentioned and/or illustrated match our specimens (Fig. 31-35). Specifically, the Austrian specimens match L. piger in body length (40-80 µm, respectively 40-60 µm; noncontractile); body shape (flattened and lanceolate, about 3.5:1, compared to 2.8:1); nuclear apparatus (two macronuclear nodules in posterior half); extrusomes (thick); number of right side ciliary rows (9-11, respectively, 10-12); movement (slow); distinct mane; lake habitat. Two differences must be discussed. First, the postero-lateral contractile vacuole described by Vuxanovici (1962) is slightly subterminal according to the figure (Fig. 31), while it is terminal in our specimens, as shown by the excretory pore. Second, Vuxanovici (1962) described and figured "ventral trichocysts 1.5-2 µm long" plus some cylindroidal structures in the neck region. While the latter are obviously identical with our extrusomes, we could not find the former. Indeed, the occurrence of two toxicyst-like structures would be unusual in pleurostomatids (for a brief review, see

Foissner et al. 1995). Thus, we interpret these minute trichocysts as perioral kinetids and/or the anterior end of the oral basket rods. Neither Kahl's (1926) nor Vuxanovici's (1962) figures show details of the ciliary pattern, and thus it is impossible to know whether their specimens belong to *Litonotus* or *Amphileptus*. Kahl (1931) later classified his species in *Hemiophrys*, which is now considered as a junior synonym of *Amphileptus* (Foissner and Leipe 1995). Indeed, the amphileptid ciliary pattern of our population is also difficult to recognise, even in silver preparations, because the basal bodies are widely spaced in the kineties (Fig. 27, 28). Taking together all observations and considerations, it is likely that the Romanian and the Austrian population belong to the same species, that is, *Amphileptus piger*. There is, at least, no definite feature arguing against.

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LITERATURE CITED

- André, E. 1914. Recherches sur la faune pélagique du Léman et description de nouveaux genres d' infusores. Rev. Suisse de Zool., 22: 179-193.
- Claparède, É. & Lachmann, J. 1859. Études sur les infusoires et les rhizopodes. *Mém. Inst. natn. génev.*, 6(year 1858):261-482.
- Ehrenberg, C. G. 1830. Beiträge zur Kenntnis der Organisation der Infusorien und ihrer geographischen Verbreitung, besonders in Sibirien. *Abh. Akad. Wiss. Berlin,* year 1832:1–88.
- Foissner, W. 1984a. Morphologie und Infraciliatur einiger limnischer Ciliaten (Protozoa: Ciliophora). Schweiz. Z. Hydrol., 46:210–223.
- Foissner, W. 1984b. Taxonomie und Ökologie einiger Ciliaten (Protozoa, Ciliophora) des Saprobiensystems. I: Genera Litonotus, Amphileptus, Opisthodon. Hydrobiologia, 119:193-208.
- Foissner, W. 1997. Faunistic and taxonomic studies on ciliates (Protozoa, Ciliophora) from clean rivers in Bavaria (Germany), with descriptions of new species and ecological notes. *Limnologica*, 27:179– 238.
- Foissner, W. & Leipe, D. 1995. Morphology and ecology of Siroloxophyllum utriculariae (Penard, 1922) n. g., n. comb. (Ciliophora, Pleurostomatida) and an improved classification of pleurostomatid ciliates. J. Eukaryot. Microbiol., 42:476–490.
- Foissner, W. & Pfister, G. 1997. Taxonomic and ecologic revision of urotrichs (Ciliophora, Prostomatida) with three or more caudal cilia, including a user-friendly key. *Limnologica*, 27:311–347.
- Foissner, W., Berger, H. & Schaumburg, J. 1999. Identification and ecology of limnetic plankton ciliates. *Informationsberichte des Bayer*. *Landesamtes für Wasserwirtschaft*, **3/99**:1–793.
- Foissner, W., Berger, H., Blatterer, H. & Kohmann, F. 1995. Taxonomische und ökologische Revision der Ciliaten des Saprobiensystems.—Band IV: Gymnostomatea, Loxodes, Suctoria. Informationsberichte des Bayer. Landesamtes für Wasserwirtschaft, 1/95:1-540.

- Jagsch, A., Gassner, H. & Dokulil, M. T. 2002: Long-term changes in environmental variables of Traunsee, an oligotrophic Austrian lake impacted by the salt industry, and two reference sites, Hallstättersee and Attersee. Water, Air, and Soil Pollut., Focus, 2:9–20.
- Kahl, A. 1926. Neue und wenig bekannte Formen der holotrichen und heterotrichen Ciliaten. Arch. Protistenk., 55:197-438.
- Kahl, A. 1927. Neue und ergänzende Beobachtungen holotricher Ciliaten I. Arch. Protistenk., 60:34–129.
- Kahl, A. 1931. Urtiere oder Protozoa I: Wimpertiere oder Ciliata (Infusoria) 2. Holotricha außer den im 1. Teil behandelten Prostomata. *Tierwelt Dtl.*, 21:181–398.
- Krainer, K.-H. 1995. Taxonomische Untersuchungen an neuen und wenig bekannten planktischen Ciliaten (Protozoa, Ciliophora) aus Baggerseen in Österreich. *Lauterbornia*, 21:39–68.
- Macek, M., Šimek, K., Pernthaler, J., Vyhnálek, V. & Psenner, R. 1996. Growth rates of dominant planktonic ciliates in two freshwater bodies of different trophic degree. J. Plankton Res., 18:463–481.
- Müller, H. 1989. The relative importance of different ciliate taxa in the pelagic food web of Lake Constance. *Microb. Ecol.*, 18:261–273.
- Müller, H. 1991. Pseudobalanion planctonicum (Ciliophora, Prostomatida): ecological significance of an algivorous nanociliate in a deep meso-eutrophic lake. J. Plankton Res., 13:247-262.
- Pechlaner, R. & Sossau, C. 1982. Die Ergebnisse der fünfjährigen Studie,Limnologische Untersuchung Traunsee-Traun'. Amt OÖ Landesregierung, Bericht 13:1-100.
- Salbrechter, M. & Arndt, H. 1994. The annual cycle of protozooplankton in the alpine, mesotrophic Lake Mondsee (Austria). *Mar. Microb. Food Webs*, 8:217–234.
- Schönberger, M. 1994. Planktonic ciliated protozoa of Neusiedler See (Austria/Hungary)—a comparison between the turbid open lake and a reedless brown-water pond. *Mar. Microb. Food Webs*, 8:251–263.
- Šimek, K., Bobková, J., Macek, M., Nedoma, J. & Psenner, R. 1995. Ciliate grazing on picoplankton in a eutrophic reservoir during the summer phytoplankton maximum: a study at the species and community level. *Limnol. Oceanogr.*, 40:1077-1090.
- Sommaruga, R. & Psenner, R. 1993. Nanociliates of the order Prostomatida: their relevance in the microbial food web of a mesotrophic lake. Aquat. Sci., 55:179–187.
- Song, W. & Wilbert, N. 1989. Taxonomische Untersuchungen an Aufwuchsciliaten (Protozoa, Ciliophora) im Poppelsdorfer Weiher, Bonn. Lauterbornia, 3:1–221.
- Sonntag, B., Posch, T., Klammer, S., Griebler, C. & Psenner, R. 2002. Protozooplankton in the deep oligotrophic Traunsee (Austria) influenced by discharges of soda and salt industries. *Water, Air, and Soil Pollut., Focus*, 2:211-226.
- Stokes, A. C. 1885. Notes on some apparently undescribed forms of freshwater infusoria No. 2. Am. J. Sci., 29:313-328.
- Vuxanovici, A. 1962. Contributii la sistematica ciliatelor (Nota II). Studii Cerc. (Biol. Anim.), 14:331-349.
- Weisse, T. & Müller, H. 1998. Planktonic protozoa and the microbial food web in Lake Constance. Arch. Hydrobiol., Spec. Issues Advanc. Limnol., 53:223-254.
- Wulff, A. 1916. Ueber das Kleinplankton der Barentssee. Wiss. Meeresunters. Helgoland (N. F.), 13:95-125.

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