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Description of *Leptopharynx bromeliophilus* nov. spec. and *Leptopharynx australiensis* nov. spec. (Ciliophora, Nassulida)

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Summary. Using standard morphological methods, we describe two new *Leptopharynx* species, each discovered in a specific biogeographic region and habitat. *Leptopharynx bromeliophilus* nov. spec., a minute species (25 × 20 µm) discovered in tanks of bromeliads from Jamaica, is small-mouthed and has a slightly concave preoral region, an average of 27 basal bodies in kinety 4, and a total of 142 basal bodies on average. *Leptopharynx australiensis* nov. spec., a comparatively large species (40 × 25 µm) discovered in jungle soil of Australia, is large-mouthed and has a distinctly oblique preoral region, widely spaced kinetids in kinety 1, a total of 184 basal bodies on average, and the oral primordium is inside of a cortical fold thus appearing right of the posterior end of kinety 1. Four new features are recognized for distinguishing *Leptopharynx* species: (1) to have a monomorphic (producing either small- or large-mouthed cells) or polymorphic (producing microstomes and macrostomes) life cycle; (2) the spacing of the kinetids in kinety 1 as either ordinary or wide; (3) the shape (flat or concave) and angle (≤ 15° slightly oblique, ≥ 40° distinctly oblique) of the preoral region; and (4) the total number of basal bodies, which has proven statistically.

Key words: Australia, α-taxonomy, bromeliad tanks, Jamaica, *Leptopharynx costatus*, soil ciliates.

INTRODUCTION

Species of the genus *Leptopharynx* Mermod, 1914 are commonly found in limnetic and terrestrial habitats. Most data available are from the cosmopolitan *Leptopharynx costatus* (Foissner *et al.* 2002). The identification and separation of *Leptopharynx* species is difficult, mainly due to the sparse data on the ciliary pattern as revealed by silver impregnation. To date, only *L. costatus*, *L. macrostoma*, and *L. bromelicola* have been investigated with modern methods (Foissner 1979, 1989; Foissner *et al.* 1994, 2011; Njiné 1979). Based on the data available, Foissner *et al.* (2011) recognized nine reliable species and proposed the following main features for distinguishing *Leptopharynx* species: distinct ridges present *vs.* absent along the right side ciliary rows; special features, like spines or wings on the body, and of the oral basket; dikinetids present *vs.* absent from somatic kinety 3; number of kinetids in kinety 6 as two for the *L. costatus* pattern or > five for the *L. bromelicola* pattern; beginning and structure of kinety 9 as either underneath or far underneath the adoral membranelles and with or without dikinetids; postoral complex present *vs.* absent; and preoral kinety 4 continuous *vs.* discontinuous.

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The value of the species features proposed by Foissner *et al.* (2011) is supported by the present study, in which we describe two new species from different habitats and geographic regions: *Leptopharynx bromeliophilus* from tanks of bromeliads in Jamaica and *L. australiensis* from jungle soil of Australia. Both have a remarkable shape of the preoral region, which is concave and moderately oblique in *L. bromeliophilus*, while flat and strongly oblique in *L. australiensis*. Further, *L. bromeliophilus* possibly produces only small-mouthed cells, while *L. australiensis* possibly produces only large-mouthed cells.

MATERIALS AND METHODS

For details on the samples and locations, see the individual species descriptions. *Leptopharynx bromeliophilus* occurred in considerable number in a tank bromeliad (*Vriesea* sp.) from Jamaica, while *L. australiensis* was reactivated from the resting cysts of an air-dried soil sample from Australia, using the non-flooded Petri dish method (NFPM). Briefly, the NFPM involves placing 50–500 g litter and soil in a Petri dish (13–18 cm wide, 2–3 cm high) and saturating, but not flooding it, with distilled water. Such a culture is analysed for ciliates by inspecting about 2 ml of the run-off on days 2, 7, 14, 21, and 28; for a detailed description of the NFPM, see Foissner *et al.* (2002).

Both species were observed *in vivo* and in protargol preparations (Foissner 1991); *Leptopharynx bromeliophilus* was investigated also with the Klein-Foissner silver nitrate method. Counts and measurements on silvered specimens were conducted at a magnification of × 1,000. The "total number of basal bodies" excludes those of the adoral membranelles, which are difficult to count. *In vivo* measurements were performed at magnifications of × 40–1,000. Drawings of live specimens were based on free-hand sketches and micrographs, while those of impregnated cells were made with a drawing device. Terminology is according to Corliss (1979) and Lynn (2008).

RESULTS

Leptopharynx bromeliophilus nov. spec. (Figs 1–13, 16–26; Table 1)

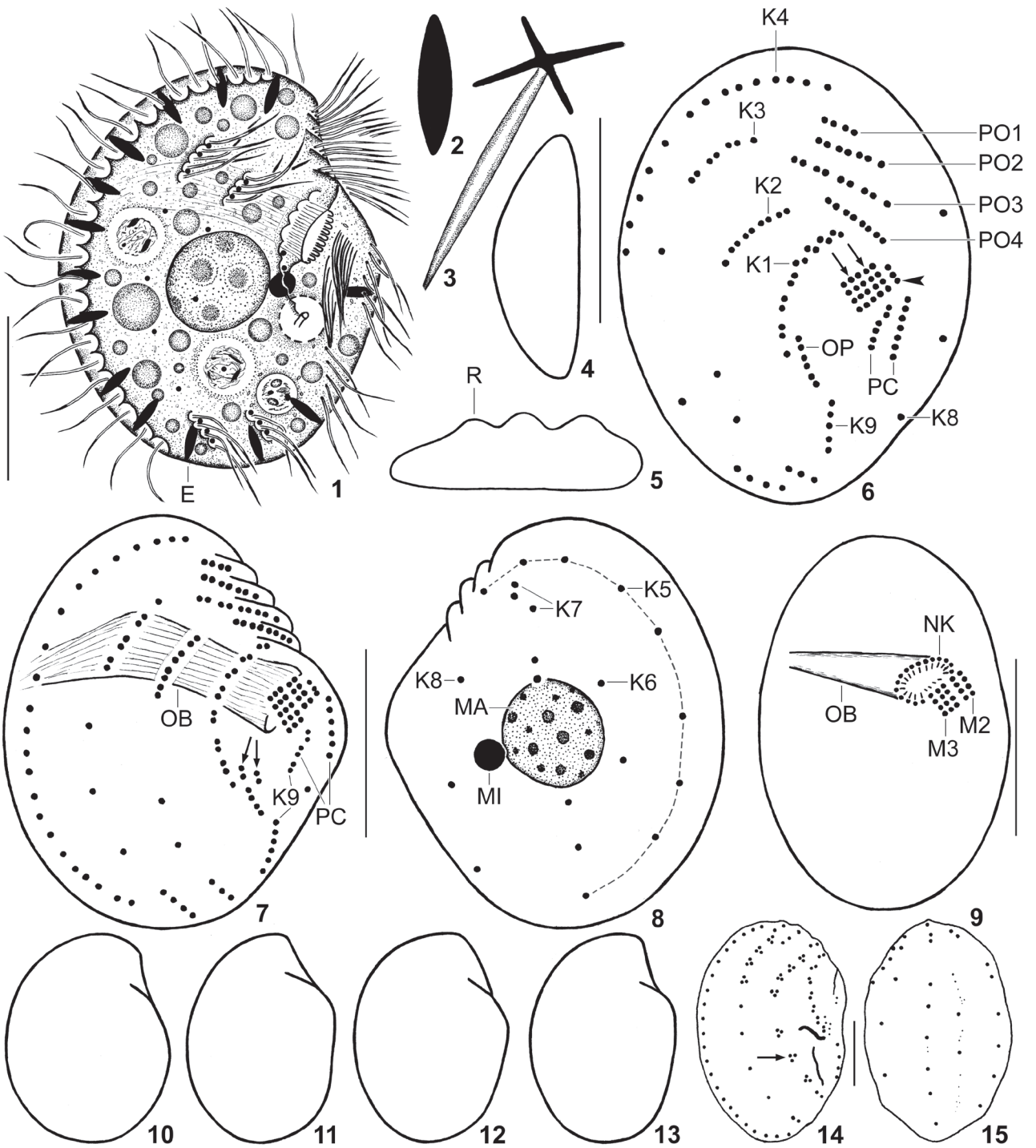
Diagnosis: Size about 25 × 20 µm *in vivo*; *Leptopharynx costatus*-shaped but preoral region usually slightly concave. Somatic ciliature of *costatus* type, *i.e.*, with postoral complex and 9 ciliary rows, of which kineties 1, 2 and 3 have dikinetids anteriorly and kinety 6 consists of two to three kinetids in mid-body. Kinety 4 with an average of 27 monokinetids; and a total of 142 basal bodies on average. Adoral membranelle 1 lacking, membranelles 2 and 3 composed of two and three rows of basal bodies, respectively. Possibly produces only small-mouthed cells with the oral basket about 4 µm wide.

Type locality: Tanks of *Vriesea* sp., a bromeliad on garden trees of a small farm near the village of Ecclesdown, Jamaica, N18°03′ W76°20′.

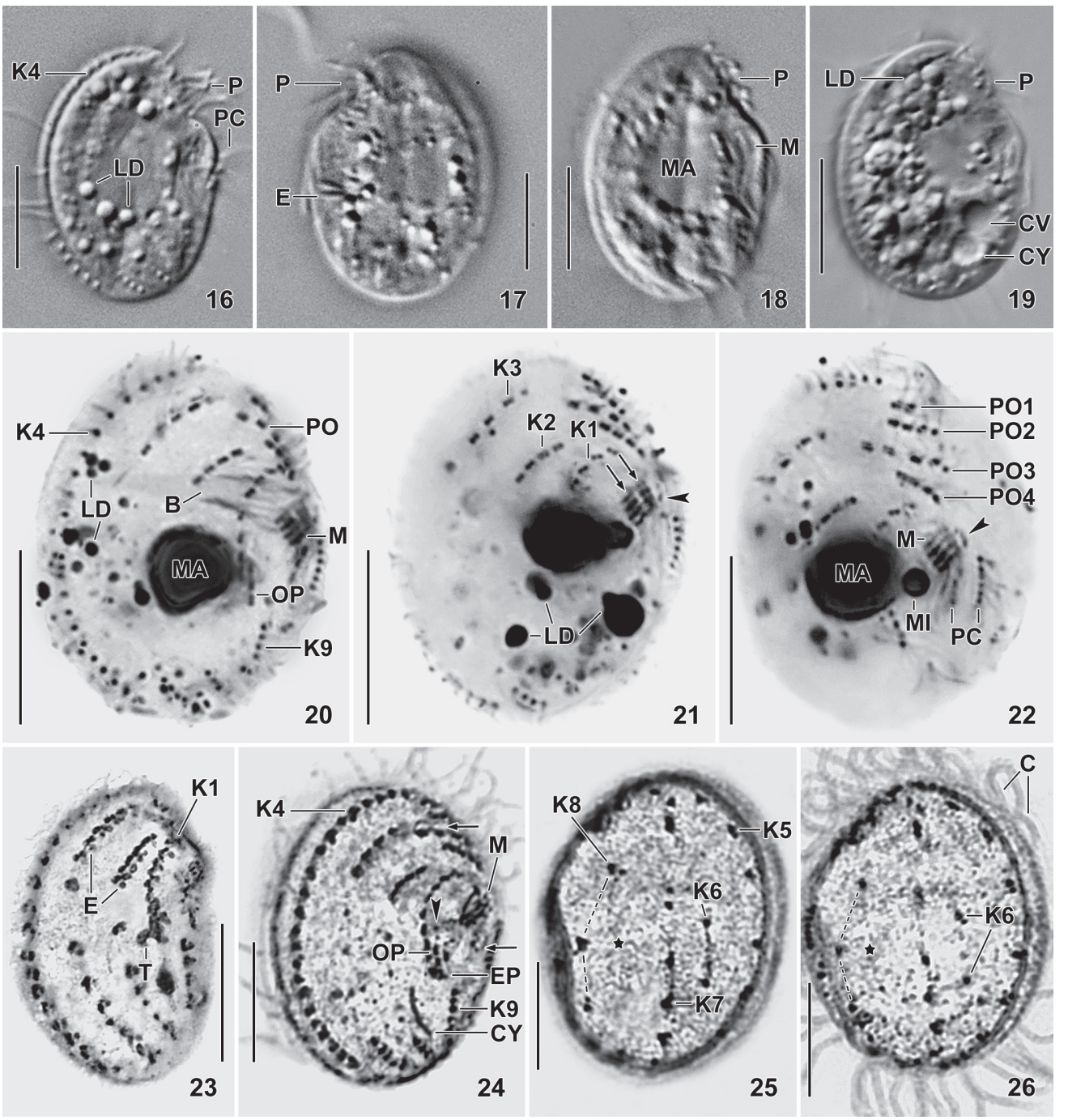
Type material: One holotype slide with protargol-impregnated specimens and 14 paratype slides with protargol-impregnated and Klein-Foissner silver nitrate-impregnated specimens have been deposited in the Biology Centre of the Museum of Upper Austria, Linz (LI). The holotype and important paratype specimens have been marked by black ink circles on the coverslip.

Etymology: Composite of *Bromeliaceae* (the plants in whose leaf-tanks it occurs) and the Greek adjective *phil* (to like), referring to its typical habitat.

Description: Size *in vivo* 15–30 × 15–25 µm, on average about 25 × 20 µm, as calculated from some measurements of live specimens and values shown in Table 1. Body shape broadly ellipsoidal with a length: width ratio of 1.1–1.4:1 and a median of 1.3:1. Dorsal side broadly convex; ventral side bulbous in mid-body, *i.e.*, in oral area, preorally moderately receding (≤ 35°) and more or less concave, postorally usually slightly receding, rarely straight, strongly receding or slightly convex, forming a sigmoidal ventral outline together with the preoral concavity usually lost in silver preparations. Laterally flattened up to 2.5:1, right side convex, left with three inconspicuous ridges, dorsal margin leaf-like flattened (Table 1 and Figs 1, 4, 5, 10–13, 16–19). Nuclear apparatus usually in middle third of cell underneath oral basket. Macronucleus occupies about 25% of body length, globular to very broadly ellipsoidal, with some pale nucleoli; micronucleus usually attached to ventral half of macronucleus, globular (Table 1 and Figs 1, 8, 18, 20–22). Contractile vacuole near posterior third of cell, in silver nitrate preparations with short tube extending to excretory pore on ventral side underneath oral primordium (Fig. 23). Cytopyge in silver nitrate preparations represented by a thick, short silverline right or underneath of the excretory pore, *i.e.*, underneath blister formed by contractile vacuole; rather close to posterior segment of somatic kinety 2 and right of posterior segment of kinety 9 (Table 1 and Figs 1, 19, 24). Extrusomes as usual, left of kineties, bluntly fusiform and compact, about 2.5–3 × 0.4 µm in size when resting, while about 10 µm long and with four rod-shaped arms when exploded (Figs 1, 2, 3, 17, 23). Cortex as in *Leptopharynx costatus*, *i.e.*, rigid and glossy. Silverline pattern as described by



Figs 1–15. *Leptopharynx bromeliophilus* (1–13) and *L. costatus* (14, 15) from life (1–5, 10–13), after protargol impregnation (6–9), and after silver nitrate impregnation (14, 15). **1** – right side view of a representative specimen, length 25 μm; **2**, **3** – a resting (~3 × 0.4 μm) and an exploded extrusome; **4** – dorsal view showing flattening of right side; **5** – ridge pattern of left side; **6** – ventral view of a paratype specimen. Oral basket not impregnated. Arrows mark adoral membranelles, arrowhead denotes a row of basal bodies left of membranelle 2; **7**, **8** – right and left side view of holotype specimen, length 21 μm. Arows mark oral primordium. The hatched line connects monokinetids of kinety 5 (but see text); **9** – ventrolateral view showing oral apparatus; **10–13** – shape variability; **14**, **15** – *Leptopharynx costatus* described by Prelle (1961). Arrow marks dikinetids in posterior region of kinety 2. E – extrusome, K1–9 – somatic kineties, M2, 3 – adoral membranelles, MA – macronucleus, MI – micronucleus, NK – nasse kinetosomes, OB – oral basket, OP – oral primordium, PC – postoral complex, PO1–4 – preoral kineties, R – cortical ridges. Scale bars: 10 μm (1, 6–9), 5 μm (14, 15).



Figs 16–26. *Leptopharynx bromeliophilus* from life (16–19), after protargol impregnation (20–22), and after Klein-Foissner silver nitrate impregnation (23–26). **16**, **17** – right and left side view showing the *costatus*-shaped body and the preoral concavity; **18** – right side view focused to the bases of the adoral membranelles. Note the slightly concave preoral region; **19** – right side view of a specimen packed with lipid droplets and food vacuoles; **20** – right side view of holotype specimen; **21**, **22** – ventrolateral and ventral view of paratype specimens showing the ciliary pattern. Arrows mark adoral membranelles 2 and 3, while arrowheads denote basal bodies left of membranelle 2 which consists of only two rows of basal bodies**; 23**, **24** – right side views showing ciliary pattern and extrusomes left of kineties. Arrows mark silverline meshes; arrowhead denotes the oral primordium; **25**, **26** – left side views showing kinety 6 composed of two kinetids. Note the dense cortical granulation and the trapezoid area (asterisks) between kineties 7 and 8; the hatched line connects kinetids of kinety 8. B – oral basket, C – cilia, CV – contractile vacuole, CY – cytopyge, E – extrusomes, EP – excretory pore, K1–9 – somatic kineties, LD – lipid droplets, M – adoral membranelles, MA – macronucleus, MI – micronucleus, OP – oral primordium, P – preoral concavity, PC – postoral complex, PO1–4 – preoral kineties, T – excretory tube. Scale bars: 10 µm.

Foissner *et al.* (2011) in *L. bromelicola*, that is, cortex studded with minute, argyrophilic granules, except left of preoral kineties and dikinetids of postoral complex, where small meshes occur (Figs 24–26). Cytoplasm rather hyaline, contains 3–4 µm-sized food vacuoles, in well-fed specimens studded with lipid droplets 1–3 µm across. Possibly feeds on bacteria. Lipid droplets and other inclusions often impregnate with protargol, making photographic documentation of ciliary pattern difficult (Figs 1, 16, 19, 20, 21). Glides rather rapidly and continuously on microscope slides; never swims.

Somatic cilia only about 5 µm long *in vivo*. Invariably nine somatic and four preoral ciliary rows (kineties) with a total of 142 basal bodies on average (Tables 1–3 and Figs 1, 6–8, 20–26). Kineties 2–5 and 7 bipolar, rows 1, 6, 8 and 9 shortened anteriorly and/or posteriorly. Kinety 1 extends at right margin of oral field, ends underneath mid-body, composed of narrowly spaced, ciliated dikinetids more or less obliquely arranged in anterior region; a monokinetid at posterior end. Kineties 2 and 3 on right body side, consist of narrowly spaced, ciliated dikinetids in anterior third, of widely spaced, barren monokinetids in middle third, and of some narrowly spaced, ciliated monokinetids in posterior region; kinety 3 invariably commences with a single monokinetid. Kineties 4 and 5 limit dorsal margin of right and left side, respectively; kinety 4 composed of narrowly spaced, ciliated monokinetids throughout; kinety 5 composed of widely and evenly spaced, ciliated monokinetids, origin uncertain because the anteriormost kinetid could belong to kinety 8 (Fig. 8). Kinety 6 on left body side, shortened anteriorly and posteriorly, usually consisting of two, rarely of three widely spaced, ciliated monokinetids in mid-body. Kinety 7 consists of widely spaced, ciliated monokinetids, forming more or less distinct pairs in anterior half; first pair sometimes out of line, *i.e.*, dislocated to the right. Kinety 8 begins in second body third (but see above), consists of three widely spaced, ciliated monokinetids. Kineties 7 and 8 produce a more or less trapezoid area because usually more narrowly spaced anteriorly than posteriorly (Figs 8, 25, 26). Kinety 9 on ventral side of body, commences underneath adoral membranelles with three likely barren dikinetids, interrupted as described below (postoral complex), and then extending to posterior body margin with an average of five ciliated monokinetids (Table 1 and Figs 6–8, 20–26).

Four oblique preoral kineties on ventral side, composed of ciliated dikinetids and some ciliated monokinetids at left end. Postoral complex as in *L. costatus*, *i.e.*, composed of the monokinetidal posterior portion of preoral kinety 4 and the dikinetidal anterior portion of somatic kinety 9; first dikinetid sometimes slightly dislocated to the left (Table 1 and Figs 1, 6, 7, 16, 20–22, 24).

Oral apparatus in mid-body within a fusiform more or less projecting area containing two distinct, narrowly spaced adoral membranelles obliquely arranged to main body axis at left anterior corner of oral basket; cilia about 7 µm long *in vivo* (Table 1 and Figs 1, 6, 7, 9, 16, 18, 20–22, 24). Adoral membranelle 1 lacking; membranelle 2 composed of two rows of basal bodies; membranelle 3 of three rows (Figs 9, 21); left of membranelle 2 a short row of basal bodies belonging to the postoral complex, as in *L. costatus* (Foissner *et al.* 2011) and *L. australiensis* (see below). Oral basket inconspicuous *in vivo* and protargol preparations, in frontal view elliptical and about 4µm in size, extends to dorsal side of cell narrowing gradually; does not curve posteriorly; nasse kinetosomes recognizable only in a single, darkly impregnated specimen (Fig. 9). Oral primordium similar to that of *L. costatus*, *i.e.*, underneath oral basket and consisting of some minute, barren granules (basal bodies?) impregnating only with silver nitrate (Fig. 24, arrowhead); and of two short rows of barren dikinetids impregnating with protargol and silver nitrate left of posterior end of somatic kinety 1; inner, left row frequently lacking, when present composed of only a single dikinetid or a dikinetid and a monokinetid (Table 1 and Figs 1, 6, 7, 9, 20–22, 24).

Occurrence and ecology: *Leptopharynx bromeliophilus* is very likely widely distributed in the Caribbean area because we found it not only in Jamaica but also in *Tillandsia heterophylla* from Mexico. Usually, it is sparse in the environmental samples, but it was fairly numerous at the type locality. The Mexican population became moderately abundant in a raw culture set up with wheat grains.

Leptopharynx australiensis nov. spec. (Figs 27–45, 47, 49, 51–55; Table 1)

Diagnosis: Size about 40 × 25 µm; body semidiscoidal with distinctly oblique preoral region confluent with distal end of oral basket. Somatic ciliature of *costatus* type, *i.e.*, with postoral complex and 9 ciliary rows, of which kineties 1, 2 and 3 have dikinetids anteriorly. Kinety 1 consisting of widely spaced, ciliated dikinetids; kinety 6 composed of two kinetids; and a total of 184 basal bodies on average. Adoral membranelle 1 consisting of four basal bodies, membranelles 2 and 3

Table 1. Morphometric data from *Leptopharynx bromeliophilus* (upper line) and *Leptopharynx australiensis* (lower line). Data from *L. bromeliophilus* based, if not mentioned otherwise, on protargol-impregnated, randomly selected specimens from environmental specimens. Data from *L. australiensis* based on protargol-impregnated, randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of specimens investigated, SD – standard deviation, SE – standard error of mean, x̄ – arithmetic mean.

Characteristics	x̄	M	SD	SE	CV	Min	Max	n
Body, length in protargol preparations	19.4	20.0	2.1	0.5	10.9	15.0	22.0	21
	33.6	34.0	3.6	0.8	10.6	28.0	42.0	21
Body, width in protargol preparations	15.1	15.0	1.5	0.3	9.6	13.0	18.0	21
	23.3	23.0	2.9	0.6	12.4	18.0	29.0	21
Body, length in dry silver nitrate preparations	24.8	25.0	2.2	0.5	9.0	21.0	30.0	21
	–	–	–	–	–	–	–	–
Body, width in dry silver nitrate preparations	20.0	20.0	1.5	0.3	7.4	17.0	23.0	21
	–	–	–	–	–	–	–	–
Body length: width, ratio in protargol preparations	1.3	1.3	0.1	0.1	4.7	1.2	1.4	21
	1.4	1.4	0.1	0.0	6.5	1.3	1.7	21
Body length: width, ratio in dry silver nitrate preparations	1.2	1.3	0.1	0.1	4.8	1.1	1.3	21
	–	–	–	–	–	–	–	–
Anterior body end to first adoral membranelle, distance[a]	6.5	7.0	1.0	0.2	15.8	4.0	9.0	21
	6.7	6.0	1.3	0.3	20.1	5.0	10.0	21
Body length: anterior body end to first adoral membranelle, ratio[a]	3.0	3.0	0.4	0.1	12.0	2.4	4.0	21
	5.1	5.2	0.8	0.2	14.8	3.4	6.7	21
Anterior body end to macronucleus, distance	7.6	8.0	1.1	0.2	14.2	6.0	10.0	21
	11.2	11.0	2.0	0.4	17.6	8.0	15.0	21
Anterior body end to excretory pore of contractile vacuole in protargol preparations, distance	–	–	–	–	–	–	–	–
	17.9	17.0	1.9	0.4	10.9	15.0	21.0	21
Anterior body end to excretory pore of contractile vacuole in dry silver nitrate preparations, distance	15.8	15.0	1.8	0.4	11.2	13.0	20.0	21
	–	–	–	–	–	–	–	–
Macronucleus, length	5.2	5.0	0.5	0.2	10.3	4.0	6.0	21
	6.9	7.0	0.6	0.1	8.4	6.0	8.0	21
Macronucleus, width	4.8	5.0	0.6	0.1	13.1	4.0	6.0	21
	6.4	6.0	0.6	0.1	9.3	5.0	7.0	21
Micronucleus, diameter	1.4	1.5	–	–	–	1.0	2.0	21
	1.9	2.0	–	–	–	1.5	2.0	21
Oral basket, width	2.8	3.0	–	–	–	2.0	3.0	21
	10.1	10.0	0.9	0.2	8.8	8.0	12.0	21
Somatic kineties, number	9.0	9.0	0.0	0.0	0.0	9.0	9.0	21
	9.0	9.0	0.0	0.0	0.0	9.0	9.0	21
Somatic kinety 1, number of dikinetids	6.5	7.0	0.6	0.1	9.3	5.0	7.0	21
	7.0	7.0	0.0	0.0	0.0	7.0	7.0	21
Somatic kinety 1, number of monokinetids	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
Somatic kinety 2, number of dikinetids	4.0	4.0	–	–	–	4.0	5.0	21
	4.9	5.0	0.7	0.2	15.0	4.0	7.0	21
Somatic kinety 2, number of monokinetids	5.4	5.0	0.7	0.2	13.7	4.0	7.0	21
	10.8	10.0	2.1	0.5	19.5	8.0	16.0	21
Somatic kinety 3, number of dikinetids	3.0	3.0	–	–	–	3.0	4.0	21
	4.6	4.0	1.0	0.2	22.5	3.0	6.0	21

Characteristics	x̄	M	SD	SE	CV	Min	Max	n
Somatic kinety 3, number of monokinetids	8.0	8.0	0.7	0.1	8.3	7.0	9.0	21
	19.0	19.0	2.4	0.5	12.6	15.0	25.0	21
Somatic kinety 4, number of monokinetids (does not have dikinetids)	27.0	27.0	2.1	0.5	7.8	23.0	30.0	21
	35.8	35.0	3.8	0.8	10.6	31.0	43.0	21
Somatic kinety 5, number of monokinetids (does not have dikinetids)	7.9	8.0	0.9	0.2	11.2	7.0	10.0	21
	16.5	16.0	2.5	0.5	15.3	12.0	22.0	21
Somatic kinety 6, number of monokinetids (does not have dikinetids)	2.3	2.0	–	–	–	2.0	3.0	21
	2.2	2.0	0.5	0.1	24.1	2.0	4.0	21
Somatic kinety 7, number of monokinetids (does not have dikinetids)	8.4	8.0	0.6	0.1	7.1	7.0	9.0	21
	9.2	9.0	0.8	0.2	8.3	8.0	11.0	21
Somatic kinety 8, number of monokinetids (does not have dikinetids)	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
Somatic kinety 9, number of monokinetids in posterior segment	5.0	5.0	–	–	–	5.0	6.0	21
	6.2	6.0	0.6	0.1	9.7	5.0	8.0	21
Preoral ciliary rows, number	4.0	4.0	0.0	0.0	0.0	4.0	4.0	21
	4.0	4.0	0.0	0.0	0.0	4.0	4.0	21
Preoral kinety 1, number of dikinetids (does not have monokinetids)	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
Preoral kinety 2, number of dikinetids	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
Preoral kinety 2, number of monokinetids	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
Preoral kinety 3, number of dikinetids	4.0	4.0	0.0	0.0	0.0	4.0	4.0	21
	4.0	4.0	0.0	0.0	0.0	4.0	4.0	21
Preoral kinety 3, number of monokinetids	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
Preoral kinety 4, number of dikinetids (for monokinetids, see postoral complex)	4.0	4.0	0.0	0.0	0.0	4.0	4.0	21
	4.0	4.0	0.0	0.0	0.0	4.0	4.0	21
Oral primordium, number of dikinetids[b], *i.e.*, without minute granules ahead	3.0	3.0	–	–	–	3.0	4.0	21
	3.7	4.0	0.0	0.0	0.0	3.0	4.0	21
Adoral membranelle 1, number of basal bodies	–	–	–	–	–	–	–	–
	3.6	4.0	0.7	0.2	18.5	2.0	4.0	21
Adoral membranelle 2, number of basal body rows	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
Adoral membranelle 2, number of basal bodies	8.2	8.0	0.6	0.1	7.3	8.0	10.0	21
	12.9	12.0	1.4	0.3	10.8	12.0	15.0	21
Adoral membranelle 3, number of basal body rows	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
Adoral membranelle 3, number of basal bodies	13.4	12.0	1.5	0.3	11.4	12.0	15.0	21
	12.9	12.0	1.4	0.3	10.8	12.0	15.0	21
Left row of postoral complex, number of monokinetids[c]	6.6	7.0	–	–	–	6.0	7.0	21
	6.1	6.0	–	–	–	6.0	7.0	21
Right row of postoral complex, number of dikinetids[d]	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
	2.9	3.0	–	–	–	2.0	3.0	21

[a] Membranelle 1 is the first membranelle in *Leptopharynx australiensis*, while membranelle 2 is the first in *L. bromeliophilus*.
[b] Without basal bodies of inner left row in *Leptopharynx bromeliophilus*.
[c] Without basal bodies left of adoral membranelle 2.
[d] This is the anterior segment of somatic kinety 9.

each composed of three rows of basal bodies. Possibly produces only large-mouthed cells with the oral basket about 12 µm wide.

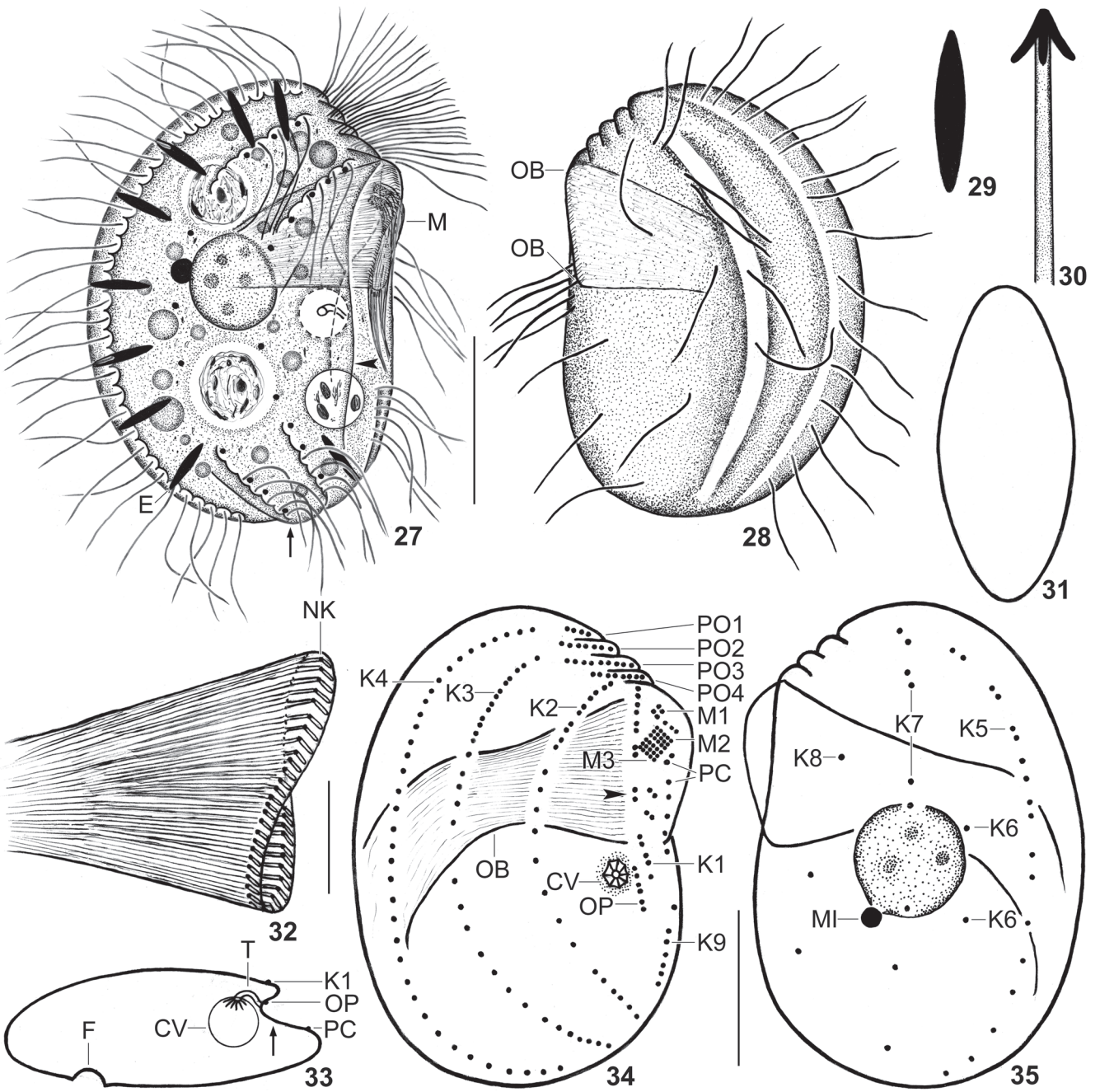
Type locality: Soil with litter and fine roots from a jungle in the Botanical Gardens of Cairns, Australia, S16°54′ E145°45′.

Type material: One holotype and six paratype slides with protargol-impregnated specimens have been deposited in the Biology Centre of the Museum of Upper Austria, Linz (LI). The holotype and important paratype specimens have been marked by black ink circles on the coverslip.

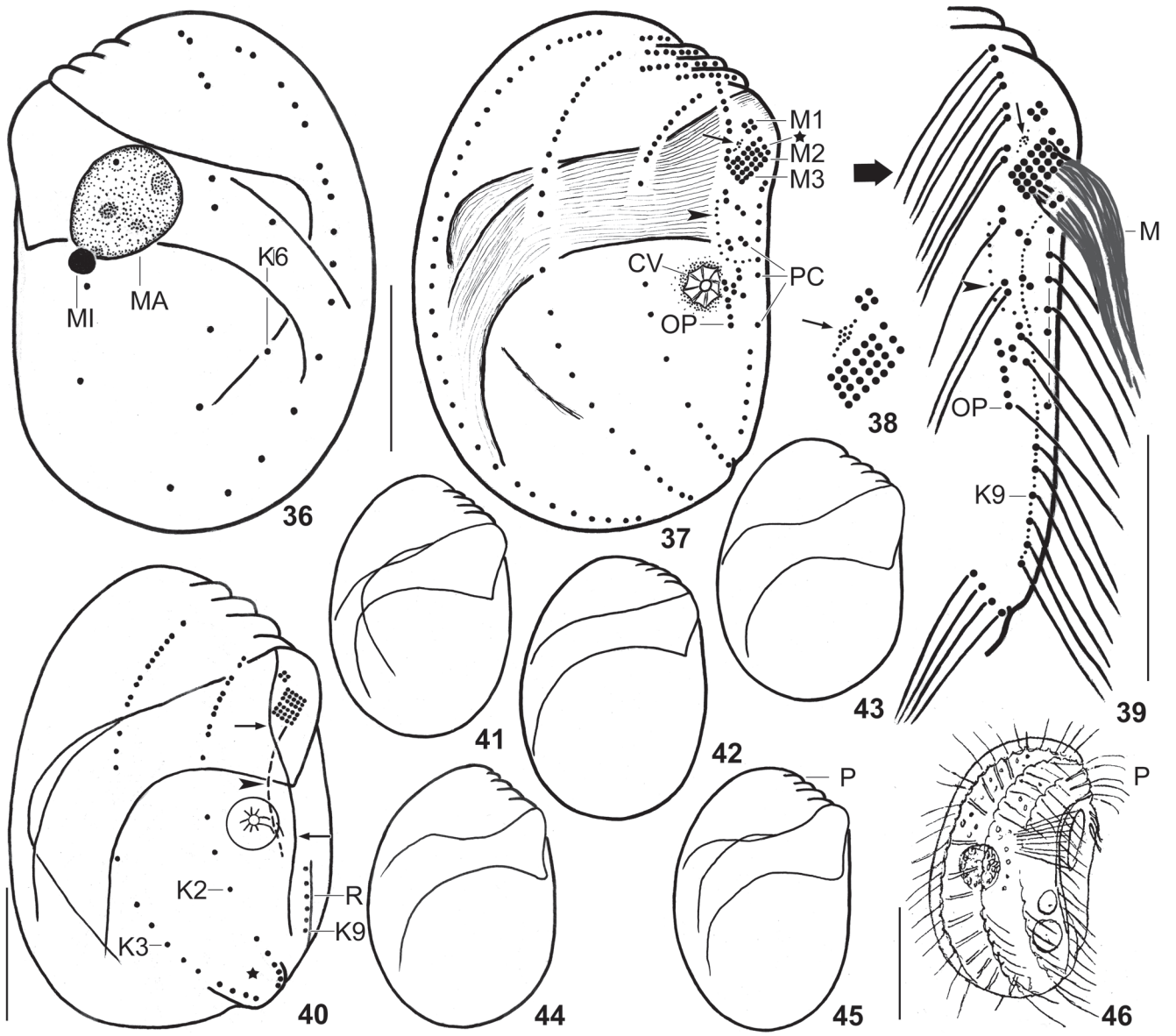
Etymology: Named after the country discovered.

Description: Size 30–50 × 20–30 µm, on average about 40 × 25 µm, as calculated from some measurements of live specimens and values shown in Table 1. Body semidiscoidal with an average length: width ratio of 1.4:1 and a conspicuous preoral truncation extending to body midline in an average angle of 40° (Figs 27, 28, 34–37, 40–45, 47, 49, 51–55). Dorsal margin distinctly convex, ventral side flat to slightly concave or convex, in micrographs usually rather distinctly concave (Figs 51, 54) when focused to the raised right side ciliary rows and the deeper lying ventral margin thus becomes invisible (Fig. 33). Laterally flattened up to 2:1 with both sides distinctly convex (Fig. 31). Nuclear apparatus usually in or near to body centre, rarely in anterior or posterior half of cell (Figs 36, 52) and right or left of body's midline, anterior third frequently covered by the oral basket. Macronucleus occupies about 21% of body length, globular to broadly ellipsoidal, with pale nucleoli about 2 µm across. Micronucleus attached to macronucleus at various positions, globular (Table 1 and Figs 27, 35, 36, 52, 55). Contractile vacuole in or near mid-body, right of anterior half of oral primordium, with distinct tube recognizable in protargol preparations; contains fibre bundles forming star-like pattern around tube base (Figs 34, 37). Cytopyge posterior and slightly left of contractile vacuole, usually forming a blister rarely containing food remnants (Table 1 and Figs 27, 33, 34, 37, 40, 47, 49, 54). Extrusomes as in congeners, *i.e.*, left of kineties, bluntly fusiform and compact, about 6 µm long when resting, while about 15 µm and with four rod-shaped arms when exploded (Figs 27, 29, 30, 47). Cortex as in *Leptopharynx costatus*, *i.e.*, rigid and glossy. Right side in most specimens slightly raised between posterior quarter of kineties 2 and 3, producing an inconspicuous, stout process and a minute indentation at posterior cell margin (Figs 27, 37, 39, 40, 52, 53). Left side with a rather distinct furrow, recognizable *in vivo* and in some protargol-impregnated specimens, containing kinety 6 (Fig. 28). Details of ventral side difficult to observe, possibly organized as follows (Figs 27, 33, 40): (i) conspicuous ridges or furrows along and between preoral kineties; (ii) a sharp line produced by the edge of the right side, extending left of kinety 1 and between posterior portion of kineties 2 and 9; (iii) a rather deep postoral furrow containing the oral primordium, commences left of oral basket and extends to near posterior third of cell; and (iv) a flat ridge left of posterior portion of kinety 9. Cytoplasm colourless, with few to many deeply impregnating lipid droplets 1–3 µm across, depending on nutrition state. Feeds on small flagellates and ciliates, possibly also on bacteria (Figs 27, 47, 49, 51). Glides continuously.

Somatic cilia about 10 µm long *in vivo*. Invariably nine somatic and four preoral ciliary rows with a total of 184 basal bodies on average (Tables 1–3 and Figs 27, 28, 34–37, 39, 40, 51–55). Kineties 2–5 and 7 bipolar, rows 1, 6, 8 and 9 shortened anteriorly and/ or posteriorly. Kinety 1 extends at right margin of ventral side and ends underneath mid-body, composed of conspicuously widely spaced dikinetids and one monokinetid at posterior end; usually fully ciliated, but anterior cilium of a few dikinetids shortened or lacking in some specimens (Fig. 39). Kineties 2 and 3 on right body side, consist of narrowly spaced, ciliated dikinetids in anterior third, of widely spaced, ciliated monokinetids in middle third, and of narrowly spaced, ciliated monokinetids in posterior region; kinety 3 usually commencing with a single monokinetid. Kineties 4 and 5 limit dorsal margin of right and left body side, respectively; kinety 4 composed of narrowly spaced, ciliated monokinetids throughout; kinety 5 composed of widely spaced, ciliated monokinetids forming more or less distinct pairs in anterior half. Kinety 6 on left body side, usually consisting of two, rarely of three or four widely spaced, ciliated monokinetids in middle third of body, forming pairs only when basal bodies number more than two. Kinety 7 composed of widely spaced, ciliated monokinetids, forming more or less distinct pairs in anterior half; first and second pair obliquely arranged, second pair sometimes dislocated to the left and then easily confused with kinety 6. Kinety 8 begins in second quarter of body, consists of three widely spaced, ciliated monokinetids. Kinety 9 on ventral side of body, commences underneath adoral membranelles with three likely barren dikinetids, interrupted in mid-body (see postoral complex), and then extending to posterior body margin



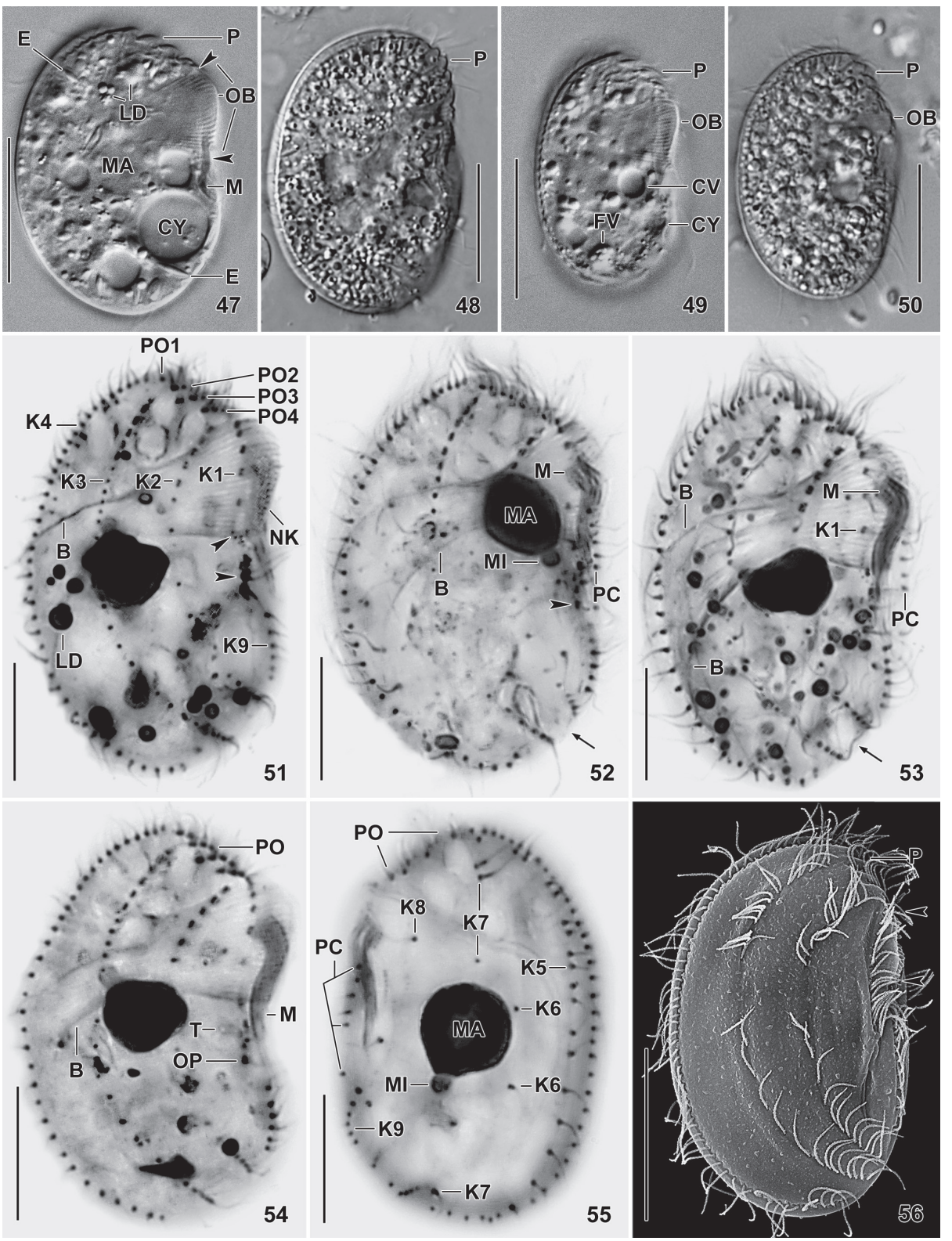
Figs 27–35. *Leptopharynx australiensis* from life (27–32) and after protargol impregnation (33–35). **27**, **28** – right and left side view of representative specimens. Note the raised area between posterior quarter of kineties 2 and 3 (arrow), the edge of the right side left of kinety 1 (arrowhead), a furrow in the ventral side (hatched line), the ciliation of the left side (28), the furrow extending on left side and containing kinety 6 (28), the distinctly oblique preoral region, and the large oral basket; **29**, **30** – a resting (~6 µm long) and an exploded extrusome; **31** – dorsal view showing the convex right and left side; **32** – side view of the oral basket. Note the 8-shaped opening, the angled distal end of the basket rods, and the nasse kinetosomes in the rod angles; **33** – transverse section in mid-body, showing the ridge and furrow pattern of the ventral and left side (scheme composed from several specimens). The arrow marks the furrow in the ventral side containing the oral primordium, while the furrow on left side contains kinety 6. The excretory tube opens ventrally; **34**, **35** – right and left side view of a paratype specimen, length 31 µm. Note the widely spaced dikinetids in kinety 1 (arrowhead). The kinetids of kineties 5 and 7 form pairs anteriorly. Kinety 6 consists of only two ciliated kinetids (cp. Fig. 28). CV – contractile vacuole, E – extrusome, F – furrow, K1–9 – somatic kineties, M1–3 – adoral membranelles, MI – micronucleus, NK – nasse kinetosomes, OB – oral basket, OP – oral primordium, PC – postoral complex, PO1–4 – preoral kineties, T – excretory tube. Scale bars: 15 µm (27, 28), 5 µm (32), 10 µm (34, 35).



Figs 36–46. *Leptopharynx australiensis* (36–45) and *L. eurystoma* (46) from life (46) and after protargol impregnation (36–45). **36–39** – left and right side view, adoral membranelles and ciliation of ventral side of holotype specimen, length 32 µm (additional labels, see Figs 34, 35). The asterisk marks a minute row of basal bodies left of membranelle 2. Arrowheads mark anterior part of oral primordium; arrows denote granules right of membranelles 2 and 3. Some dikinetids of kinety 1 lost the anterior cilium, and only the posteriormost kinetid of the oral primordium is ciliated. The postoral complex consists of the anterior, dikinetidal portion of kinety 9 (dotted line) and the posterior portion of preoral kinety 4 (hatched line). The right row of membranelles 2 and 3 is barren; **40** – semischematic view, showing the ridge pattern and the raised area between posterior portion of kineties 2 and 3 (asterisk). Arrows mark edge of right side left of kinety 1; arrowhead denotes a ventral furrow; **41–45** – right side views showing variability of shape and oral basket; **46** – *L. eurystoma* (from Kahl 1931). Scale bars: 10 µm (36, 37, 39, 40), 20 µm (46).

▶▶

Figs 47–56. *Leptopharynx australiensis* (47, 49, 51–55) and *L. costatus* (48, 50, 56) from life (47–50), after protargol impregnation (51–55), and in the SEM (56). **47**, **49** – right side views showing the distinctly oblique preoral region. Note the conspicuous oral basket (arrowheads); **48**, **50**, **56** – right side views of macrostomous (48, 56; arrowheads mark the oral basket) and microstomous (50) *L. costatus*; **51–55** – right and left side views of holotype (52) and paratype specimens (51, 53–55), showing the ciliary pattern and the distinctly oblique preoral region. Note the widely spaced kinetids of kinety 1, the oral primordium (arrowheads) right of kinety 1, and the raised area between posterior portion of kineties 2 and 3 (arrows). Scale bars: 25 µm (47, 48, 56), 20 µm (49, 50), 10 µm (51–55).



Abbreviations for Figs 36–56: B – oral basket, CV – contractile vacuole, CY – cytopyge, E – extrusomes, FV – food vacuole, K1–9 – somatic kineties, LD – lipid droplets, M1–3 – adoral membranelles, MA – macronucleus, MI – micronucleus, NK – nasse kinetosomes, OB – oral basket opening, OP – oral primordium, P – preoral region, PC – postoral complex, PO1–4 – preoral kineties, R – cortical ridge, T – excretory tube.

with an average of six ciliated monokinetids (Table 1 and Figs 34, 37, 39, 54, 55).

Four oblique preoral kineties on ventral side, composed of ciliated dikinetids and some ciliated monokinetids at left end (Table 1 and Figs 27, 34, 37, 39, 47, 49, 51–54). Postoral complex as in *L. costatus*, *i.e.*, composed of the monokinetidal posterior portion of preoral kinety 4 and the dikinetidal anterior portion of somatic kinety 9; dikinetids widely spaced and obliquely arranged, first dikinetid usually dislocated to the left (Figs 37, 39).

Oral apparatus conspicuous due to the large oral basket, in anterior half of body within a deepened, fusiform oral field. Three narrowly spaced adoral membranelles obliquely arranged to main body axis left of anterior half of oral basket (Table 1 and Figs 27, 34, 37–40, 47, 49, 51–55). Membranelle 1 (M1) anterior of membranelles 2 and 3, composed of two to four barren basal bodies. Membranelle 2 (M2) and membranelle 3 (M3) very close together, distinctly larger than M1 each composed of three rows of basal bodies; each row consists of an average of four basal bodies with cilia about 15 µm long *in vivo*, right row barren; right of membranelles 2 and 3 some faintly impregnated granules (basal bodies?) possibly belonging to the oral primordium or remnants of a paroral (Figs 37–39); left of M2 a short row of basal bodies, belonging to the postoral complex. Oral basket conspicuous because opening of long axis 10–15 µm wide *in vivo* and 8–12 µm in protargol preparations in both large and small-sized specimens occupying almost one third of body length (Table 1 and Figs 47, 49); laterally strongly flattened with 8-shaped entrance due to slightly different length of the basket rods (Figs 32, 49); extends to body midline, where it abruptly curves to dorsal posterior body end and nematodesmata become rather disordered (Figs 27, 34–37, 40–45, 47, 49, 51–54). Nasse kinetosomes faintly impregnated, not at distal end of basket rods but subapically at base of rod angles (Figs 32, 51). Oral primordium consisting of two parts (Table 1 and Figs 33, 34, 37, 39, 40, 51, 52, 54); upper part extending right and underneath of oral basket, forming an L-shaped row composed of faintly impregnated granules (basal bodies?); posterior part in a ventral cortical fold, thus appearing right of somatic kinety 1 when observed in laterally oriented specimens, composed of four dikinetids, of which three form a partially or completely ciliated row, while the fourth dikinetid, which is frequently absent, is left of the row.

Occurrence and ecology: As yet found only at type locality, that is, in a slightly acidic (pH 5.7), very wet soil with some litter and fine roots from a jungle in the Botanical Gardens of Cairns, Australia.

DISCUSSION

Comparison of *L. bromeliophilus* with similar species: Using the characters for distinguishing *Leptopharynx* species suggested by Foissner *et al.* (2011) and the present study (see below), *L. bromeliophilus* is most similar to the microstome of *L. costatus* Mermod, 1914, recently described by Foissner *et al.* (2011). However, it differs from that species by five reliable features (Tables 2 and 3): (i) body size *in vivo* on average distinctly smaller (about 25 × 20 µm *vs.* 30–40 × 20–25 µm; Foissner *et al.* 2011), (ii) preoral concavity present *vs.* absent, (iii) less basal bodies in kinety 4, even if body size is "normalized" (on average 27 *vs.* ≥ 37), (iv) adoral membranelle 2 consisting of two *vs.* three rows of basal bodies, and (v) the supposed lack of large-mouthed cells. As we did not have pure cultures, we cannot exclude the possibility that *L. bromeliophilus* is polymorphic producing microstomes and macrostomes. Of the about 100 protargol-impregnated cells observed, all were small-mouthed.

Leptopharynx minimus Alekperov, 1993, which is as small as *L. bromeliophilus*, differs in having three (*vs.* two) adoral membranelles and two unipolar kineties on the right body side. The small (15–20 × 10–13 µm) winter form of *L. costatus*, described by Prelle (1961) from a *Sphagnum* pond in France, is possibly identical with *L. bromeliophilus* but lacks the preoral concavity and has dikinetids in the posterior portion of kinety 2 (Figs 14, 15). *Leptopharynx stenostomatus* (Gellért, 1942) Foissner *et al.*, 2011, also a rather small species (28–35 µm), differs from *L. bromeliophilus* by the absence of the preoral concavity and the number of kinetids in kinety 6 (6 *vs.* 2–3), one of the most important features in the genus.

Comparison of *L. australiensis* with similar species: In their brief revision, Foissner *et al.* (2011) recognized nine species. Four of these are similar to *L. australiensis*, *viz.*, *L. costatus*, *L. eurystoma*, *L. macrostoma,* and *L. euglenivorus*.

We observed more than 200 protargol-impregnated specimens from the non-flooded Petri dish culture, all having a large oral basket, suggesting that *L. aus-*

traliensis is monomorphic, *i.e.,* lacks microstomes. *Leptopharynx costatus* Mermod, 1914, which makes microstomes and macrostomes (Foissner *et al.* 2011), differs from *L. australiensis* not only by this feature but also by the much narrower spaced kinetids in kinety 1. Another important difference is the shape of the preoral region: slightly oblique in the macrostomes of *L. costatus*, while distinctly oblique and confluent with the distal end of the oral basket in *L. australiensis* (cp. Figs 48, 50 and 56 with Figs 27, 28, 34–37, 40–45, 47, 51–54). In contrast, the preoral region of the microstomes of *L. costatus* is moderately oblique and thus similar to that of *L. australiensis* (cp. Fig. 50 with Figs 47, 49). Further, the oral primordium extends left of the posterior end of somatic kinety 1 in *L. costatus*, while inside a cortical fold and thus appearing right of the posterior end of kinety 1 in *L. australiensis* (Figs 34, 37, 39, 51, 52, 54). The total number of basal bodies is quite different: on average184 in *L. australiensis vs.* 248 and 265 in macrostomes from two populations of *L. costatus* (Table 3).

Leptopharynx australiensis is quite similar to *L. eurystoma* (Kahl, 1931) Foissner *et al.*, 2011, of which no recent data are available. According to the brief description and figure provided by Kahl (1931), they differ mainly in the shape of the preoral region, which is distinctly oblique and confluent with the distal end of the oral basket in *L. australiensis* (Figs 27, 28, 47, 49), while slightly oblique and not confluent in *L. eurystoma* (Fig. 46). Furthermore, *L. eurystoma* is possibly the macrostome of *L. costatus*, where the preoral region is as steep as in *L. eurystoma* (Figs 48, 56), while it is moderately oblique in the microstome (Fig. 50), as well known from various investigations (Kahl 1931; Foissner 1979, 1989; Foissner *et al.* 2011; Prelle 1961). This interpretation is supported in that *L. eurystoma* occurred among a moss population of *L. costatus* and only very few specimens were found (Kahl 1931), as is typical for macrostomous *L. costatus* in environmental samples (≤ 6%; Foissner *et al.* 2011 and unpubl. observ.).

Leptopharynx macrostoma Njiné, 1979 is possibly a macrostomous *L. costatus* because both were found at the same site and the morphological characteristics largely agree with those of macrostomous *L. costatus*, especially the only slightly oblique preoral region and the low number (1–2) of kinetids in kinety 6 (Figs 48, 56; Foissner *et al.* 2011). Accordingly, *L. macrostoma* differs from *L. australiensis* by the features discussed for *L. costatus* above (see also Table 2). *Leptopharynx euglenivorus* Kahl, 1926 differs from *L. australiensis* by the distinct cortical ridges on both sides of the body, while *L. australiensis* has only a single furrow on the left side;

Table 2. Distinguishing features of protargol-impregnated *Leptopharynx bromeliophilus*, *L. australiensis* and microstomous *L. costatus*.

Characteristics	*L. bromeliophilus*[a]	*L. costatus*			*L. australiensis*[a]
		Foissner (1989)[b]	Germany[c]	Mexico[c]	
Body, length (µm)	19	28	22	25	34
Body, width (µm)	15	19	15	17	23
Body length: width, ratio	1.3	1.5	1.5	1.4	1.4
Body length: anterior body end to adoral membranelles, ratio	3:1	3.1:1	3.5:1	3.6:1	5.1:1
Preoral concavity (*in vivo*)	present	absent	absent	absent	absent
Number of dikinetids in kinety 3	3–4	4	5	5	5
Number of basal bodies in kinety 4	27	37	43	44	36
Number of basal bodies in kinety 6	2–3	2	2	2	2
Total number of somatic basal bodies	142	181	171 (185)[d]	172 (185)[d]	184
Number of basal body rows in adoral membranelle 2	2	3	3	3	3

[a] For details, see text and Table 1.
[b] Average values from the 15 protargol-impregnated specimens investigated by Foissner (1989). Not selected for small specimens.
[c] German and Mexican specimens selected for a size similar to that of *L. bromeliophilus* to obtain comparable data. Values based on 11 specimens each. The number of basal bodies in the preoral kineties is difficult to count in these minute cells and was thus taken from ordinary specimens.
[d] Values in parentheses are based on five randomly selected microstomous cells with an average size of 27 × 19 µm for the German specimens and of 37 × 26 µm for the Mexican specimens.

moreover, the somatic ciliary rows of *L. euglenivorus* merge beak-like at the ventral anterior end of the cell, while those of *L. australiensis* are distributed over the broad preoral region (Figs 27, 28, 34–37, 51–55).

New species characteristics of *Leptopharynx*

Foissner *et al.* (2011) proposed seven main features for distinguishing *Leptopharynx* species (see introduction chapter). Our investigations add five characteristics discussed in the following paragraphs.

(1) Foissner *et al.* (2011) assumed that all *Leptopharynx* species are polymorphic and thus produce both macrostomes and microstomes. However, the present data and some studies mentioned in Foissner *et al.* (2011) suggest that certain species are monomorphic, producing only small-mouthed cells (*L. bromeliophilus*) or large-mouthed cells (*L. australiensis*).

(2) Usually, the dikinetids of kinety 1 are very narrowly spaced, forming a membranoid structure, *e.g.*, in *L. bromeliophilus* (Figs 6, 7, 20) and *L. costatus* (Fig. 56). In contrast, they are conspicuously widely spaced in *L. australiensis* and two further new species described in a forthcoming study.

(3) The shape and angle of the preoral region. As yet, only slightly and moderately oblique preoral regions were known in *Leptopharynx* (Kahl 1931; Prelle 1961; Njiné 1979; Foissner 1989; Foissner *et al.* 1994, 2011). Thus, the slightly concave and the distinctly oblique preoral region of *L. bromeliophilus* and *L. australiensis,* respectively, is highly distinctive (Figs 1, 10–13, 16–19, 27, 28, 34–37, 40–45, 47, 49, 51–55). We fix the following limits: ≤ 15° slightly oblique, ≤ 35° moderately oblique, ≥ 40° distinctly oblique.

(4) As suggested by Foissner *et al.* (2011), the total number of basal bodies seems to be a valuable feature. However, they did not include it in the main characteristics because of the scarce data. Now, we have much more data and could perform a statistical analysis, showing that the variability coefficients are low, *i.e.,* 2.5–9.7%, on average ~6% (Table 3). Such value is highly informative, as explained by Foissner (1984, 1993): it is high enough to show variability but sufficiently low to be not too variable. Further, the microstomes of four populations of *L. costatus* have a highly similar average total number of basal bodies: 181–186! Likewise, it is quite similar in the macrostomes: 248 and 265 (Tables 2 and 3).

(5) The oral primordium is usually left of the posterior end of kinety 1, when specimens are observed laterally. *Leptopharynx australiensis* is unique in that the oral primordium is in a deep ventral fold thus appearing right of the posterior end of somatic kinety 1 (Figs 34, 37, 39, 51, 52, 54).

Table 3. Comparison of the total number of basal bodies, except of the adoral membranelles, in 12 populations from six *Leptopharynx* species. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of specimens investigated, SD – standard deviation, SE – standard error of mean, $\bar{x}$ – arithmetic mean.

Species	$\bar{x}$	M	SD	SE	CV	Min	Max	n
L. bromeliophilus	142.0	141.0	3.5	0.8	2.5	134.0	149.0	21
L. australiensis	183.8	183.0	9.6	2.1	5.2	164.0	204.0	21
L. costatus (microstome) Germany	185.0	187.0	5.4	2.4	2.9	177.0	191.0	5
L. costatus (macrostome) Germany	265.0	266.0	25.7	11.5	9.7	241.0	304.0	5
L. costatus (microstome) Mexico	185.0	192.0	13.3	5.9	7.2	165.0	197.0	5
L. costatus (macrostome) Mexico	247.8	252.0	13.1	5.9	5.3	230.0	264.0	5
L. costatus (microstome) Brazil	186.1	183.0	8.8	1.9	4.7	174.0	201.0	21
L. costatus (microstome) Foissner (1989)	181.3	185.0	15.9	4.1	8.8	152.0	200.0	15
L. bromelicola (macrostome)	344.9	344.0	17.8	4.0	5.2	375.0	297.0	20
L. bromelicola (microstome)	205.7	201.0	16.5	3.6	8.0	186.0	240.0	21
Leptopharynx n. sp. 1[a]	293.8	294.0	9.2	2.0	3.1	275.0	314.0	21
Leptopharynx n. sp. 2[b]	256.2	255.0	20.3	4.4	7.9	231.0	302.0	21

[a] From floodplain soil of Brazil. Will be described later.
[b] From soil of the USA. Will be described later.

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