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Neotypification and Ontogenesis of *Leptopharynx costatus costatus* Mermod, 1914

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ABSTRACT. Using standard methods, we studied the morphology and ontogenesis of a German *Leptopharynx costatus costatus*. This population makes two morphs: microstomes with a size of 40 × 25 μm, about 190 basal bodies, and 5 μm wide oral basket; and macrostomes with a size of 55 × 40 μm, about 264 basal bodies, and 15 μm wide oral basket. Because the identity is threatened, this population is designated as the neotype of *L. costatus costatus*. Ontogenesis is complex due to the preoral kineties and the postoral complex produced by kineties 9 and 10. Stomatogenesis is mixokinetal: the opisthe membranelles 1 and 2 are formed by the oral primordium, whereas membranelle 3 is produced by the posterior portion of somatic kinety 1. The nasse kinetosomes are generated by the anterior portion of the oral primordium. Preoral kineties 1 and 3 develop de novo, while kinety 2 originates by intrakinetal proliferation of kinety 8; preoral kinety 4 is produced by the postoral complex, thus being a somatic kinety. Kinety 6 has two anterior kinetids in line with kinety 7. These observations require changes in the descriptive morphology, support the classification of *Leptopharynx* into the Microthoracidae, and sustain the nonmonophyly of the Nassophorea.

Key Words. Germany, Leptopharyngidae, Microthoracidae, Nassophorea, phylogeny, stomatogenesis.

WHEN we began to investigate leptopharyngids, we recognized that these tiny ciliates are difficult to investigate and much more complex than suggested by the literature. *Leptopharynx costatus* is possibly the most complex species in the genus, making four morphs and two subspecies: *Leptopharynx costatus costatus* Mermod, 1914 and *Leptopharynx costatus gonohymen* Foissner & Omar, 2012. Of the four morphs listed in Table 2, only the small and large morph of *L. costatus gonohymen* have been fully described by Omar and Foissner (2012). *Leptopharynx costatus costatus* makes three morphs; the small morph is similar to the small morph of *L. costatus gonohymen* and has been described from two populations by Omar and Foissner (2012); the two large morphs are very similar to each other, differing mainly in the presence vs. absence of adoral membranelle 1. Njiné (1979) investigated ontogenesis in *Leptopharynx macrostoma*, but he did not describe the origin of the postoral complex and of the preoral kineties, two main features of the leptopharyngids and microthoracids in general.

This brief review shows our ignorance on this common ciliate, casting doubts on previous identifications. Thus, we reinvestigated in detail a German population, which has been referred to in previous studies (Foissner et al. 2011; Omar and Foissner 2011, 2012), showing its morphology, life cycle, and ontogenesis, using live observation, silver impregnation, and scanning electron microscopy. Based on this improved knowledge, we neotypify *L. costatus* with the German population, suggest some changes in the descriptive morphology of leptopharyngids, support the classification of *Leptopharynx* into the Microthoracidae, and sustain the nonmonophyly of the class Nassophorea.

MATERIAL AND METHODS, TERMINOLOGY

Leptopharynx costatus costatus occurred in a *Paramecium* culture used for feeding fish larvae. The source of this culture is likely the Max-Plank Institute in Freiburg, Germany (Foissner et al. 2011). The sample was treated in the following way: the water was sieved through a 60-μm plankton net to remove *Paramecium*. A portion of the cleaned sample, spring water, and some squashed wheat grains were used to establish a pure nonclonal culture at room temperature. *Leptopharynx costatus costatus* grew well under these conditions, feeding on bacteria and heterotrophic flagellates. Dividers occurred mainly during exponential growth, while macrostome specimens became rather numerous in declining and, especially, old cultures. We can rule out the possibility that this morph represents a distinct genotype or subspecies because it is connected via many intermediate specimens to the microstome morph.

Cells were studied in vivo using a high-power oil immersion objective and differential interference contrast optics. The infraciliature and various cytological structures were revealed by SEM and silver impregnation, as described by Foissner and Xu (2007). For protargol impregnation, the specimens were fixed in 70% (w/v) ethanol, which resulted in excellent impregnations, mainly because food vacuoles and other cytoplasmic inclusions impregnated lightly or not at all. However, the cells became rather strongly inflated, especially the oral basket. Thus, body and basket size were measured also in specimens fixed with a small drop of osmium tetroxide, which preserves these features without distortion.

Counts and measurements on prepared specimens were performed at a magnification of 1,000X. In vivo measurements were conducted at magnifications of 100–1,000X. Although these are only rough estimates, it is worth giving such data as specimens may change in preparations. Illustrations of live specimens were based on free-hand sketches and micrographs, while those of prepared cells were made with a drawing device.

Terminology is according to Corliss (1979), Foissner et al. (2011), Lynn (2008), and Omar and Foissner (2012). We use the term "morph" for the four organization types of *L. costatus*. The most common and distinct morphs are microstome and macrostome specimens as well as small-sized and large-sized morphs (Omar and Foissner 2011, 2012). The term "nasse kinetosomes" refers to a circular row of basal bodies subapically connected to the rods of the oral basket. This row, which we call "nasse row," is probably homologous to the paroral of other ciliates and unwinds in dividers, proliferating laterally to form the nasse kinetosomes and oral anlagen of both the proter and opisthe (Peck 1974). The term "group C basal bodies" refers to a very short kinety left of adoral membranelle 2; it belongs to the postoral complex and somatic kinety 10 (Omar and Foissner 2012).

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RESULTS

Description of the neotype of *Leptopharynx costatus costatus* Mermod, 1914. The neotype produces a small (microstome, MI) and a large (macrostome, MA) morph (Table 1, Fig. 1–44). For the sake of clarity, both are described together because they are very similar morphologically. They differ mainly by morphometric features, which are higher/larger in the MA than in the MI (Table 1).

After osmium fixation (in vivo), the MI of *L. costatus costatus* have a size of 35–50 × 20–35 μm, usually it is 40 × 25 μm, whereas the MA are 40–70 × 30–50 μm, frequently about 55 × 40 μm (Table 1). Likewise, the size of the oral basket is very different: 4–7 μm in MI and 9–20 μm in MA. In the protargol preparations, some features are highly distorted by the alcohol fixation, namely the length: width ratio of the body, the oral basket width, as well as body shape in general (Fig. 7, 38, 41). The measurements suggest classifying protargol-impregnated specimens $\leq$ 30 μm as MI and those $\geq$ 30 μm as MA. This limit was increased to 36 μm for the Klein–Foissner silver nitrate preparations. Specimens with a size of 30–32 μm in the protargol preparations were classified according to the oral basket width: 4–5 μm in the MI and 7–13 μm in the MA.

In vivo, the body shape of the MI is ellipsoidal to broadly ellipsoidal with a range of 1.6–2.0:1 and an average of 1.7:1; the ventral side is more flattened than the convex dorsal side, and the preoral region is moderately oblique (Table 1, Fig. 1–3, 5, 6, 8–10, 15–17, 19, 20, 22, 23, 29). The MA are broadly ellipsoidal to semidiscoidal with a length: width ratio of 1.3–1.5:1, on average 1.4:1; the dorsal side is distinctly convex, the ventral side is flat to slightly convex, and the preoral region is slightly oblique (Table 1, Fig. 11, 13–15, 18, 21, 30, 33–35, 39, 40, 42, 43). Both MI and MA are laterally flattened up to 4:1 and are very narrowly elliptical in ventral and dorsal view with slightly convex sides in ordinary specimens, while the left side is more convex than the right in well-fed cells (Fig. 7, 25, 28, 38, 41).

The nuclear apparatus is in or near the body center and slightly posterior to the oral basket; rarely, it is in the anterior half or the posterior third in MA specimens. The macronucleus, which is comparatively small (i.e. ~ 21% of body length in the MI and ~ 16% in the MA), globular to very broadly ellipsoidal and contains globular, argyrophilic masses, probably nucleoli, up to 2 μm across. The globular micronucleus is usually attached to the ventral side of the macronucleus, rarely to its dorsal side (Table 1, Fig. 1, 6, 10, 16, 17, 30, 33, 35, 39–41). The contractile vacuole is in the third quarter of the ventral side, right of the posterior part of the oral primordium, and has a distinct tube recognizable in protargol and in silver nitrate preparations; it contains fiber bundles forming a star-like pattern around the tube base (Table 1, Fig. 5, 8, 13, 16, 18, 33, 34, 38, 39). The cytopyge is slightly posterior to the contractile vacuole, usually forming a blister with food remnants; in silver nitrate preparations, the cytopyge is represented by a thick, short silverline extending between the posterior portion of somatic kineties 2 and 10; in SEM micrographs, it appears as a short cleft posterior to kinety 1 (Fig. 8, 13, 18, 22, 42). The extrusomes, which are left of the somatic and posterior to the preoral kineties, are bluntly fusiform and compact. In vivo and when resting, they have a size of about 5 × 1 μm; when exploded, they are up to 20 μm long and show four distal rod-shaped arms 4–5 μm long in scanning micrographs (Fig. 1, 10, 12, 13, 29–31). The colorless cytoplasm contains few to many lipid droplets 1–3 μm across, depending on nutritional state, and a few food vacuoles, up to 10 μm across in the MA (Fig. 1, 2, 8–11, 13–15, 30).

The cortex is rigid and glossy; the ciliary rows extend in shallow furrows on both sides of the cell. The ventral edge of the right side is marked by a sharp line produced by kinety 1 and the cytopyge cleft; a flat ridge extends right of the anterior portion of kinety 1; a crenellation occurs along somatic kineties 1–4 and the anterior portion of kinety 5. The furrows accompanying kineties 6 and 7 merge anteriorly, forming a single furrow containing the anteriormost, pair-like monokinetids of kinety 6. The posterior portion of kinety 10 extends in a slight furrow. The rather flat oral field has a shallow concavity left and posterior to the oral basket, containing the adoral membranelles and the oral primordium (Fig. 1–3, 8, 9, 13, 14, 22, 23, 26, 27, 29, 42–44).

The silverline pattern is as described by Foissner et al. (2011) in *Leptopharynx bromelicola*: the cortex is studded with minute, argyrophilic granules, except in the preoral area, where distinct, small meshes occur. The silverline meshes of the individual preoral kineties are not connected with each other (Fig. 18–21).

All somatic cilia of *L. costatus costatus* are 8–10 μm long in vivo and 5–9 μm in SEM micrographs. There are 10 somatic kineties in the MI, while 10 or 11 in the MA, each kinety showing a specific kinetid number and pattern. The latter is almost identical in MI and MA, while the total average of kinetids is 190 and 264 basal bodies in the MI and MA, respectively (Table 1). Kineties 2–5 and 7 are bipolar, while kineties 1, 6, and 8–10 are shortened anteriorly and/or posteriorly. Kineties 1–4 are on the right side, kineties 5–8 are on the left, and kineties 9 and 10 are located ventrally (Table 1, Fig. 1–9, 13, 16–20, 22, 23, 28–30, 33–35, 38–41).

Kinety 1 extends at the right margin of the oral field and ends slightly posterior to mid-body. It is composed of dikinetids spaced so narrowly that the cilia form a membrane-like structure. The kinetids in the anterior region are usually obliquely arranged, and an average of 1 and 2 monokinetids are at the posterior end in the MI and MA, respectively; usually, kinety 1 is fully ciliated, but the cilia of a few kinetids are shortened or lacking in some specimens (Fig. 21, 26, 27, 33). The posterior portion is slightly dislocated to the left in some MA specimens (Fig. 34). Kineties 2 and 3 are composed of narrowly spaced, ciliated dikinetids in the anterior third, followed by a more or less wide break and widely spaced, usually barren monokinetids in the posterior half; the posterior portion is made of narrowly spaced, ciliated monokinetids in both kineties; and kinety 3 usually commences with a monokinetid. The extra kinety, which is on the right side of some MA specimens, is between kineties 2 and 3 and is very similar to these kineties, sometimes even commencing with a single monokinetid, as kinety 3 (Table 1, Fig. 33). Kineties 4 and 5 limit the dorsal margin of the right and left body side: they are composed of narrowly and widely spaced, ciliated monokinetids throughout, respectively. Kinety 6 consists of two widely spaced, ciliated monokinetids in the middle body third and, according to the ontogenesis, of two narrowly spaced, oblique, nonciliated monokinetids near the anterior end of the cell; in SEM micrographs, these kinetids are in an oblong pit (Fig. 2, 23, 24, 43). Kinety 7 consists of widely spaced, usually ciliated monokinetids, forming more or less distinct pairs in the anterior half (Fig. 2, 6, 17, 23). Kinety 8 begins in the second quarter of the body and consists of three widely spaced, ciliated monokinetids. Kinety 9 consists, according to the ontogenetic data, of two portions (Fig. 53, 54, 58, 60): the anterior portion, which is composed of four ciliated dikinetids, is posterior and very similar to the preoral kineties; the posterior

Table **1.** Morphometric data on the macrostome (MA) and the microstome (MI) morph of the neotype population of *Leptopharynx costatus costatus*.

Characteristics[a]	Morph	Method	Mean	M	SD	SE	CV	Min	Max	*n*	% change[b]
Body, length (μm)	MA	OS	56.4	57.0	7.3	1.7	12.9	41.0	68.0	19	35.5
	MI	OS	41.6	40.0	3.4	0.7	8.2	36.0	48.0	21	
Body, width (μm)	MA	OS	39.7	40.0	5.7	1.3	14.3	28.0	48.0	19	61.4
	MI	OS	24.6	24.0	3.5	0.8	14.1	20.0	35.0	21	
Body length: width, ratio (from micrographs)	MA	IV	1.4	1.4	0.1	0.1	4.5	1.3	1.5	21	−17.6
	MI	IV	1.7	1.7	0.1	0.1	5.9	1.6	2.0	21	
Body, length (μm)	MA	PR	38.8	40.0	3.7	0.8	9.4	30.0	45.0	21	41.0
	MI	PR	27.5	27.0	2.3	0.5	8.2	23.0	32.0	21	
Body, width (μm)	MA	PR	26.7	27.0	2.8	0.6	10.5	19.0	31.0	21	49.2
	MI	PR	17.9	18.0	1.7	0.4	9.3	14.0	21.0	21	
Body length: width, ratio	MA	PR	1.5	1.5	0.1	0.1	5.8	1.3	1.6	21	0.0
	MI	PR	1.5	1.5	0.1	0.1	8.0	1.3	1.8	21	
Body, length (μm)	MA	DS	45.2	45.0	5.2	1.1	11.6	36.0	60.0	21	48.2
	MI	DS	30.5	31.0	3.4	0.8	11.3	25.0	36.0	21	
Body, width (μm)	MA	DS	32.3	32.0	4.3	0.9	13.2	24.0	43.0	21	57.6
	MI	DS	20.5	21.0	2.7	0.6	13.3	16.0	27.0	21	
Body length: width, ratio	MA	DS	1.4	1.4	0.1	0.1	6.1	1.3	1.7	21	−6.6
	MI	DS	1.5	1.5	0.1	0.1	5.2	1.3	1.6	21	
Body, length (μm)	MI	SEM	36.3	37.0	2.4	0.5	6.7	30.0	39.0	21	–
Body, width (μm)	MI	SEM	22.1	23.0	2.0	0.4	8.9	18.0	25.0	21	–
Body length: width, ratio	MI	SEM	1.7	1.7	0.1	0.1	5.4	1.5	1.8	21	–
Anterior body end to first adoral membranelle, distance (μm)[c]	MA	PR	11.2	11.0	2.3	0.5	20.7	6.0	15.0	21	38.3
	MI	PR	8.1	8.0	1.0	0.2	13.5	6.0	10.0	21	
Body length: anterior body end to first adoral membranelle, ratio[c]	MA	PR	3.6	3.4	0.8	0.2	21.8	2.6	5.7	21	5.9
	MI	PR	3.4	3.4	0.4	0.1	10.9	2.8	4.3	21	
Anterior body end to macronucleus, distance (μm)	MA	PR	18.3	19.0	2.6	0.6	14.1	13.0	24.0	21	61.9
	MI	PR	11.3	11.0	1.0	0.2	8.5	10.0	13.0	21	
Anterior body end to excretory pore of contractile vacuole, distance (μm)	MA	PR	22.9	24.0	3.1	0.7	13.7	16.0	27.0	21	48.7
	MI	PR	15.4	15.0	1.2	0.3	8.0	13.0	17.0	21	
Anterior body end to excretory pore of contractile vacuole, distance (μm)	MA	DS	25.0	25.0	2.6	0.6	10.4	20.0	30.0	21	36.6
	MI	DS	18.3	18.0	1.9	0.4	10.1	15.0	21.0	21	
Macronucleus, length (μm)	MA	PR	6.4	6.0	0.6	0.1	9.3	5.0	7.0	21	8.5
	MI	PR	5.9	6.0	0.5	0.1	8.2	5.0	7.0	21	
Macronucleus, width (μm)	MA	PR	6.3	6.0	0.7	0.2	11.4	5.0	7.0	21	21.2
	MI	PR	5.2	5.0	0.5	0.1	9.9	4.0	6.0	21	
Micronucleus, diameter (μm)	MA	PR	2.0	2.0	–	–	–	2.0	2.5	21	0.0
	MI	PR	2.0	2.0	–	–	–	1.5	2.0	21	
Oral basket, width (μm)	MA	PR	10.3	10.0	1.4	0.3	13.8	7.0	13.0	21	151.2
	MI	PR	4.1	4.0	–	–	–	4.0	5.0	21	
Oral basket, width (μm)	MA	OS	15.4	15.0	2.9	0.7	18.7	9.0	20.0	19	201.9
	MI	OS	5.1	5.0	0.7	0.2	14.0	4.0	7.0	19	
Body length: oral basket width, ratio	MA	PR	3.8	3.8	0.4	0.1	10.5	3.0	4.8	21	−43.3
	MI	PR	6.7	6.5	0.6	0.1	9.7	5.4	8.0	21	
Somatic kineties, number	MA	PR	10.3	10.0	–	–	–	10.0	11.0	21	3.3
	MI	PR	10.0	10.0	0.0	0.0	0.0	10.0	10.0	21	
Somatic kinety 1, number of dikinetids	MA	PR	13.4	13.0	1.2	0.3	9.3	11.0	15.0	21	69.6
	MI	PR	7.9	8.0	0.7	0.1	8.3	7.0	9.0	21	
Somatic kinety 1, number of monokinetids	MA	PR	1.6	2.0	–	–	–	0.0	2.0	21	33.3
	MI	PR	1.2	1.0	–	–	–	0.0	3.0	21	
Somatic kinety 2, number of dikinetids	MA	PR	7.7	8.0	1.5	0.3	19.5	5.0	10.0	21	48.0
	MI	PR	5.2	5.0	0.5	0.1	10.3	4.0	6.0	21	
Somatic kinety 2, number of monokinetids	MA	PR	14.0	14.0	2.6	0.6	18.6	10.0	18.0	21	38.6
	MI	PR	10.1	10.0	1.1	0.2	10.5	9.0	13.0	21	
Extra kinety, number of dikinetids[d]	MA	PR	6.3	6.0	–	–	–	6.0	7.0	6	–
	MI	PR	Not present								
Extra kinety, number of monokinetids[d]	MA	PR	15.3	15.0	1.1	0.4	6.7	14.0	17.0	6	–
	MI	PR	Not present								
Somatic kinety 3, number of dikinetids	MA	PR	8.3	9.0	1.9	0.4	22.3	4.0	11.0	21	53.7
	MI	PR	5.4	5.0	1.2	0.3	22.4	3.0	8.0	21	
Somatic kinety 3, number of monokinetids	MA	PR	21.6	23.0	4.2	0.9	19.5	14.0	28.0	21	45.9
	MI	PR	14.8	15.0	2.3	0.5	15.6	11.0	19.0	21	
Somatic kinety 4, number of monokinetids (does not have DI)	MA	PR	69.4	69.0	5.3	1.2	7.7	59.0	81.0	21	51.5
	MI	PR	45.8	46.0	2.4	0.5	5.2	41.0	50.0	21	
Somatic kinety 5, number of monokinetids (does not have DI)	MA	PR	14.7	15.0	1.7	0.4	11.3	11.0	17.0	21	28.9
	MI	PR	11.4	12.0	1.0	0.2	8.6	9.0	13.0	21	

(continued)

Table **1.** (continued)

Characteristics[a]	Morph	Method	Mean	M	SD	SE	CV	Min	Max	*n*	% change[b]
Somatic kinety 6, number of monokinetids (does not have DI)	MA	PR	4.0	4.0	0.0	0.0	0.0	4.0	4.0	21	0.0
	MI	PR	4.0	4.0	0.0	0.0	0.0	4.0	4.0	21	
Somatic kinety 7, number of monokinetids (does not have DI)	MA	PR	7.7	8.0	0.7	0.1	8.6	7.0	9.0	21	0.0
	MI	PR	7.7	8.0	–	–	–	7.0	8.0	21	
Somatic kinety 8, number of monokinetids (does not have DI)	MA	PR	3.1	3.0	–	–	–	3.0	4.0	21	3.3
	MI	PR	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21	
Somatic kinety 9, number of DI (for monokinetids, see PC)	MA	PR	4.0	4.0	0.0	0.0	0.0	4.0	4.0	21	0.0
	MI	PR	4.0	4.0	0.0	0.0	0.0	4.0	4.0	21	
Somatic kinety 10, number of monokinetids (for DI, see PC)	MA	PR	10.2	10.0	1.6	0.4	16.0	8.0	13.0	21	50.0
	MI	PR	6.8	7.0	0.8	0.2	12.3	5.0	8.0	21	
Preoral ciliary rows, number	MA	PR	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21	0.0
	MI	PR	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21	
Preoral kinety 1, number of dikinetids (does not have monokinetids)	MA	PR	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21	0.0
	MI	PR	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21	
Preoral kinety 2, number of dikinetids	MA	PR	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21	0.0
	MI	PR	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21	
Preoral kinety 2, number of monokinetids	MA	PR	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21	0.0
	MI	PR	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21	
Preoral kinety 3, number of dikinetids	MA	PR	4.0	4.0	0.0	0.0	0.0	4.0	4.0	21	0.0
	MI	PR	4.0	4.0	0.0	0.0	0.0	4.0	4.0	21	
Preoral kinety 3, number of monokinetids	MA	PR	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21	0.0
	MI	PR	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21	
Oral primordium, number of dikinetids in posterior part	MA	PR	4.7	5.0	0.7	0.1	14.1	4.0	6.0	21	17.5
	MI	PR	4.0	4.0	0.5	0.1	11.2	3.0	5.0	21	
Oral primordium, number of monokinetids in posterior portion	MA	PR	0.1	0.0	–	–	–	0.0	1.0	21	0.0
	MI	PR	0.1	0.0	–	–	–	0.0	1.0	21	
Oral primordium, number of granules (basal bodies?) in anterior portion	MA	PR	6.4	6.0	1.4	0.3	21.3	5.0	9.0	16	48.8
	MI	PR	4.3	4.0	–	–	–	4.0	5.0	6	
Adoral membranelle 1, number of basal bodies	MA	PR	4.0	4.0	0.0	0.0	0.0	4.0	4.0	21	–
	MI	PR				Not present					
Adoral membranelle 2, number of basal body rows	MA	PR	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21	0.0
	MI	PR	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21	
Adoral membranelle 2, number of basal bodies	MA	PR	13.7	15.0	1.8	0.4	13.1	12.0	18.0	21	10.5
	MI	PR	12.4	12.0	1.4	0.3	11.5	9.0	15.0	21	
Adoral membranelle 3, number of basal body rows	MA	PR	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21	0.0
	MI	PR	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21	
Adoral membranelle 3, number of basal bodies	MA	PR	13.7	15.0	1.8	0.4	13.1	12.0	18.0	21	8.7
	MI	PR	12.6	12.0	1.2	0.3	9.6	12.0	15.0	21	
Left row of postoral complex, number of monokinetids[e]	MA	PR	7.0	7.0	0.9	0.2	12.8	5.0	8.0	21	16.7
	MI	PR	6.0	6.0	0.0	0.0	0.0	6.0	6.0	21	
Right row of postoral complex, number of dikinetids[f]	MA	PR	3.3	3.0	–	–	–	3.0	4.0	21	10.0
	MI	PR	3.0	3.0	–	–	–	2.0	3.0	21	
Right row of postoral complex, number of monokinetids[f]	MA	PR	0.2	0.0	–	–	–	0.0	1.0	21	–
	MI	PR	0.0	0.0	0.0	0.0	0.0	0.0	0.0	21	
Basal bodies, total number (except of adoral membranelles)	MA	PR	264.0	265.0	18.8	4.1	7.1	234.0	301.0	21	39.1
	MI	PR	189.8	191.0	5.4	1.2	2.8	180.0	199.0	21	

CV, coefficient of variation in %; DI, dikinetids; Mean, arithmetic mean; M, median; Max, maximum; Min, minimum; *n*, number of specimens investigated; PC, postoral complex; SD, standard deviation; SE, standard error of mean; DS, dry silver nitrate impregnation; OS, fixation with 2% osmium tetroxide; PR, protargol impregnation; SEM, scanning electron microscopy; IV, in vivo.

[a]Data based on randomly selected specimens from pure cultures.

[b]% The increase/decrease in the mean value for the macrostomes relative to the microstomes.

[c]Membranelle 1 is the first membranelle in the macrostomes, whereas membranelle 2 is the first in the microstomes.

[d]Between somatic kineties 2 and 3 in 6 of 21 macrostome specimens, while absent in the microstomes.

[e]Including a single monokinetid, which possibly belongs to preoral kinety 3, posterior of the row.

[f]This is the anterior segment of somatic kinety 10, without group C basal bodies.

portion is posterior to the adoral membranelles and composed of a short row of ciliated monokinetids (see postoral complex). Kinety 10 consists, according to the ontogenetic data, of three portions: (i) the group C basal bodies left of the adoral membranelles, (ii) some barren, oblique dikinetids posterior to the adoral membranelles, and (iii) a rear portion consisting of 7 and 10 ciliated monokinetids in the MI and MA, respectively (Fig. 3, 4, 7, 33, 34, 36).

There are three preoral kineties composed of ciliated dikinetids and a few monokinetids posteriorly (Table 1, Fig. 1, 3, 5, 7–9, 13, 14, 16–18, 20–23, 27, 30, 33, 34, 38, 39, 41). These kineties occupy the preoral ventral side and extend more obliquely in the MI (55°) than in the MA (45°).

The postoral complex is composed, according to the ontogenetic data, of the posterior portion of the interrupted kinety 9 and the anterior portion of the interrupted kinety 10 (Fig. 5, 7, 36, 38). The monokinetidal posterior portion of kinety 9 is ciliated, while the dikinetids of the anterior portion of kinety 10 are barren and obliquely arranged (Table 1, Fig. 3, 5, 7, 18, 33, 34, 36, 38). Far posteriorly to the rear portion of

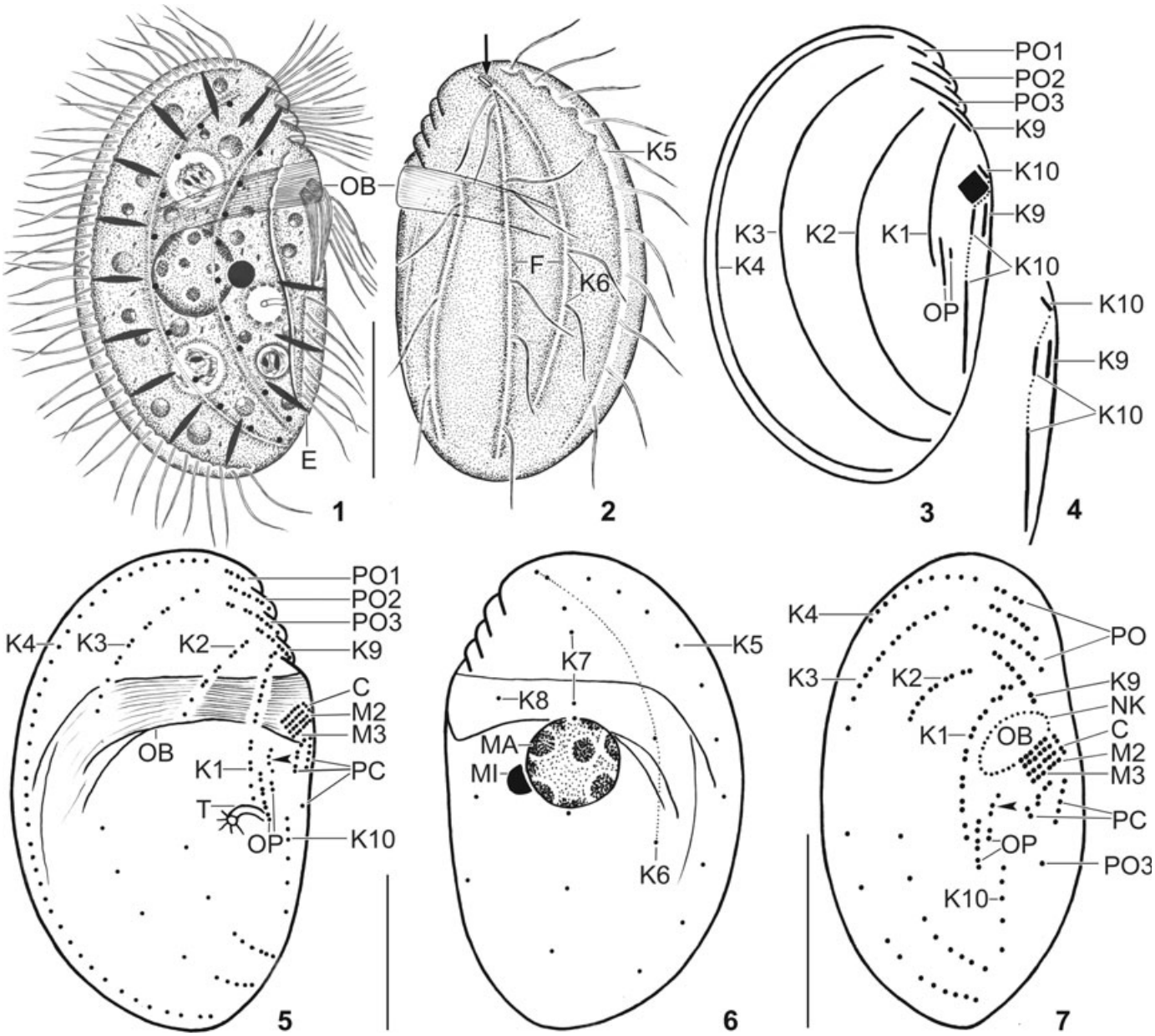

Fig. **1–7.** *Leptopharynx costatus costatus*, microstome specimens from life (1–2) and after protargol impregnation (3–7). **1, 2.** Right- and left-side view of a representative specimen, length 40 μm, showing the ellipsoidal body shape, the narrow oral basket, and the shallow furrows the somatic ciliary rows extend. Arrow marks pit produced by the anteriormost pair-like kinetids of kinety 6. **3, 4.** Kinety designation and numbering, according to the ontogenetic data; for the left side, see Fig. 6. **5, 6.** Right- and left-side view of hapantotype specimen, length 31 μm, showing the ciliary pattern and the nuclear apparatus. Arrowhead marks anterior portion of oral primordium. Dotted line connects kinetids of kinety 6. **7.** Ventral view showing the ciliary pattern and the elliptical oral basket opening marked by the nasse kinetosomes. Arrowhead marks anterior portion of oral primordium. C, group C basal bodies; E, extrusome; F, furrows; K1–10, somatic kineties; M2, 3, adoral membranelles; MA, macronucleus; MI, micronucleus; NK, nasse kinetosomes; OB, oral basket; OP, oral primordium; PC, postoral complex; PO(1–3), preoral kineties; T, excretory tube. Scale bars = 15 μm (Fig. 1, 2) and 10 μm (Fig. 5–7).

kinety 9 is a single monokinetid possibly belonging to preoral kinety 3, as indicated by the silver nitrate preparations (Fig. 20) and the ontogenetic data (Fig. 51, 53, 58, 61).

The oral apparatus is in the anterior half of the cell within a bluntly fusiform area, the left half of which contains the adoral membranelles in a bowl-shaped concavity. It is composed of a distinct basket made of nematodesmata; two and three adoral membranelles in the MI and MA, respectively; and a paroral consisting of a single row of basal bodies (nasse kinetosomes) subapically connected with the basket rods (Fig. 32). The up to 4-μm-long bases of the adoral membranelles insert obliquely left of the posterior half of the oral basket. The membranellar cilia form two obconical, posteriorly directed bundles up to 10 μm long in protargol and SEM preparations. The membranellar cilia are almost motionless, as evident from live and SEM observations, where the ciliary

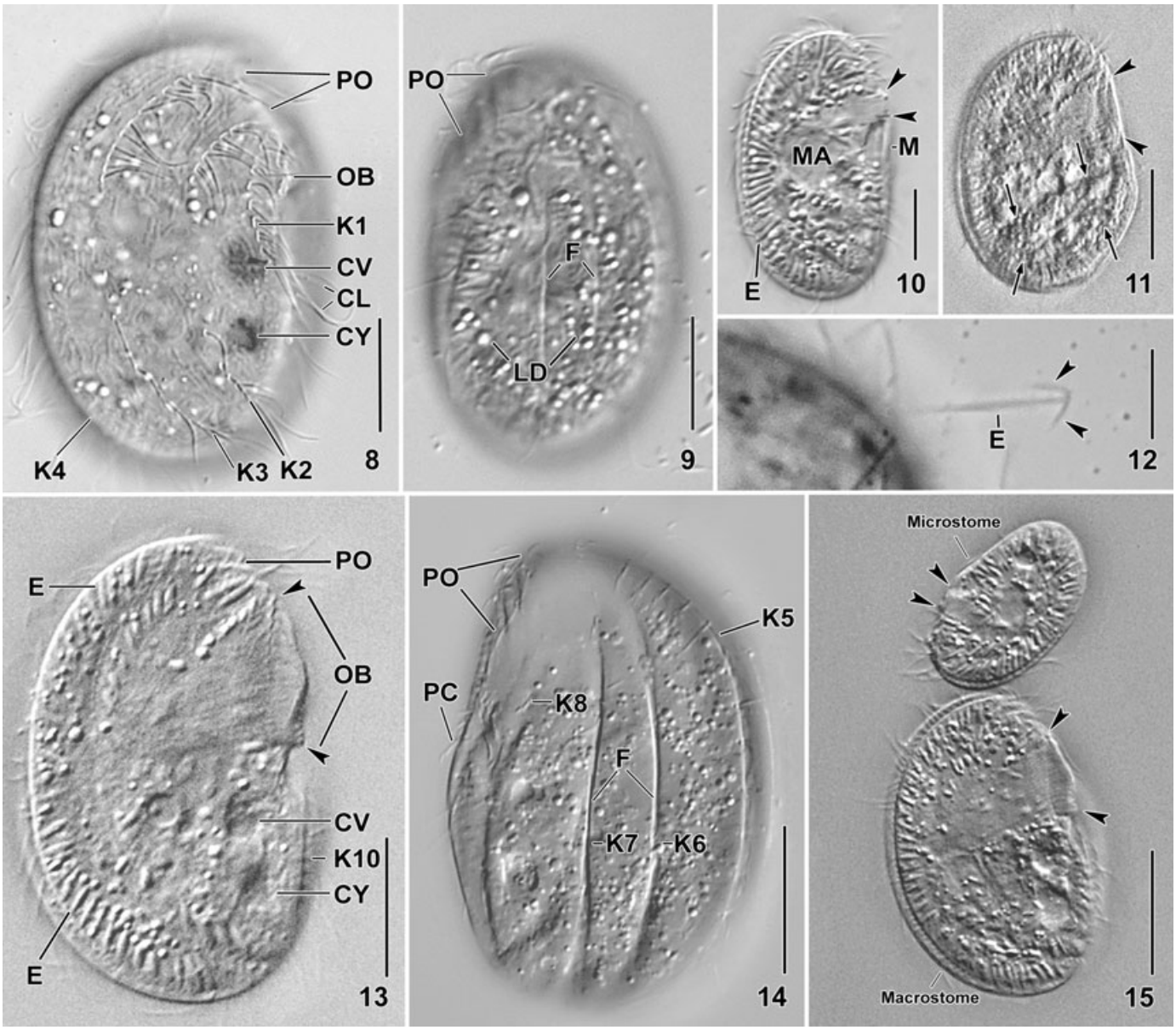

Fig. **8–15.** *Leptopharynx costatus costatus*, microstome (8–10, 12, 15) and macrostome (11, 13–15) specimens from life. **8, 9.** Right- and left-side overview of microstome specimens. Note the moderately oblique preoral region, the crenellation right of the kineties of the right side, and the shallow kinety furrows on the left side (9). **10.** Right-side view of an ellipsoidal specimen. Note the narrow oral basket (arrowheads) and numerous extrusomes along kinety 4. **11.** Right-side view of a macrostome specimen, which ingested a microstome (arrows). Arrowheads denote the wide oral basket opening. **12.** An exploded extrusome, showing the rod-shaped arms (arrowheads). **13, 14.** Right- and left-side view of a macrostome, showing the enormous oral basket (arrowheads) and the deep furrows of kineties 6–8 (14). **15.** Right-side view of a microstome and a macrostome specimen, showing the pronounced difference in body size and oral basket width (arrowheads). CL, cilia; CV, contractile vacuole; CY, cytopyge; E, extrusomes; F, furrows; K1–10, somatic kineties; LD, lipid droplets; M, adoral membranelles; MA, macronucleus; OB, oral basket; PC, postoral complex; PO, preoral kineties. Scale bars = 10 μm (Fig. 8–10, 12), 15 μm (Fig. 11, 13, 14), and 20 μm (Fig. 15).

bundles invariably have the same shape and location, i.e. in the concavity between oral basket and left margin of cell (Fig. 1, 10, 22, 26, 27, 30).

Adoral membranelle 1 (M1), which is present only in the MA, is anterior of membranelles 2 and 3 and composed of four basal bodies. This membranelle, which is quite distinct in protargol preparations (Fig. 33, 34, 37–40), is not recognizable in the SEM, showing that the basal bodies are barren. Membranelle 2 (M2) and membranelle 3 (M3) are very close together, forming a flat ciliary field composed of 6 basal body rows, each composed of an average of four and five basal bodies in the MI and MA, respectively; the right row of both is possibly barren (Table 1, Fig. 1, 5, 7, 16, 17, 30, 33, 34, 37, 38, 41). Left of M2 is a very short row of basal bodies (group C), belonging to the postoral complex and kinety 10 (Fig. 36, 37).

The opening of the oral basket is moderately oblique with respect to the main body axis (Fig. 7, 26, 27, 37, 41). When seen frontally, the basket opening is very slenderly elliptical in the SEM micrographs, while it is broadly elliptical in the

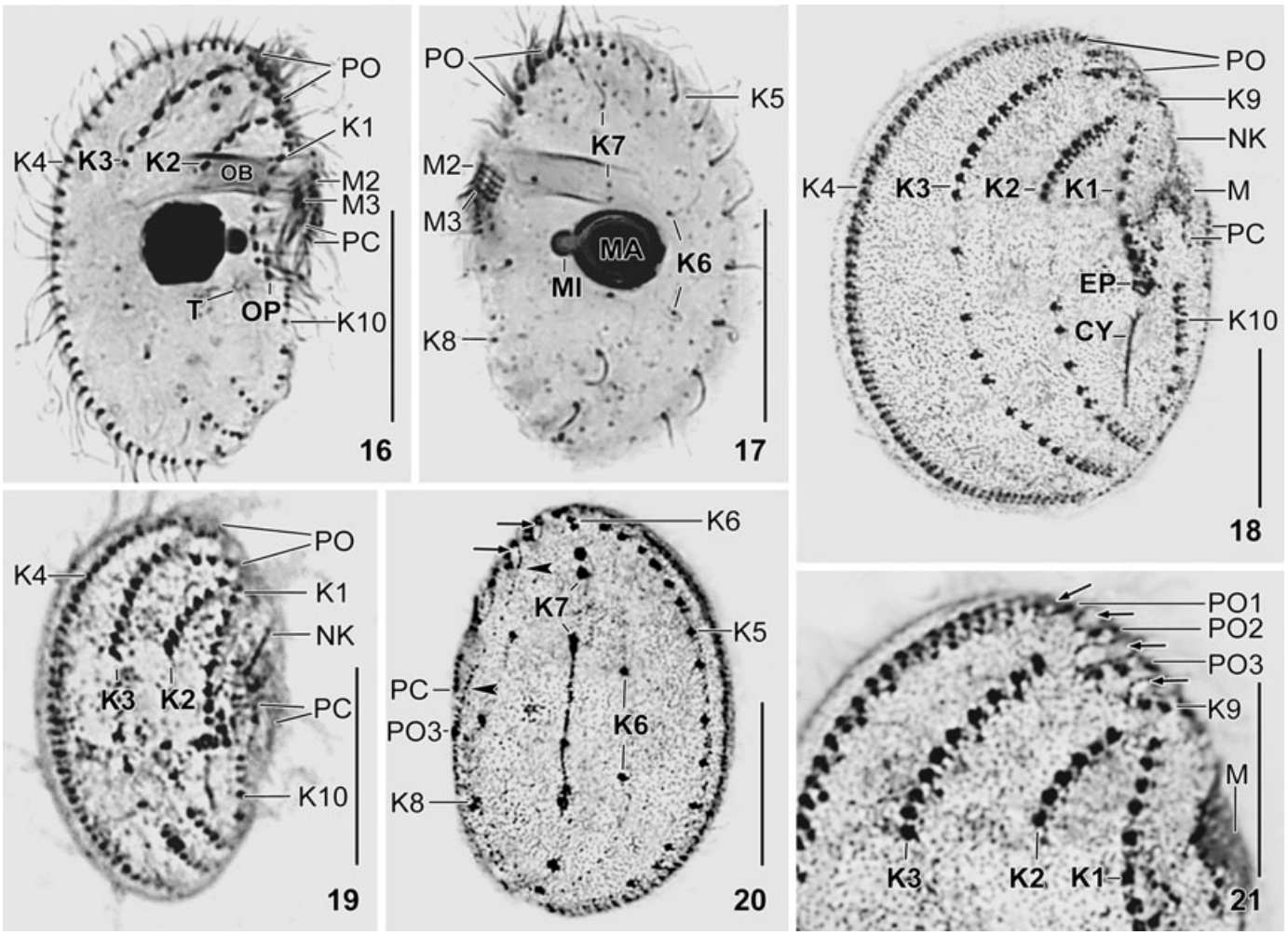

Fig. **16–21.** *Leptopharynx costatus costatus*, somatic and oral ciliary pattern of microstome (16, 17, 19, 20) and macrostome (18, 21) specimens after protargol (16, 17) and Klein–Foissner silver nitrate (18–21) impregnation. **16, 17.** Right- and left-side view, showing the ciliary and nuclear pattern. Note the narrow oral basket and the obliquely arranged adoral membranelles. **18, 21.** Right-side views showing the dense cortical granulation and the silverline meshes (21, arrows) accompanying the preoral kineties. **19, 20.** Right- and left-side view showing the ciliary pattern and the silverline meshes associated with the preoral kineties (arrows). Arrowheads mark a granular line connecting preoral kinety 3 with a monokinetid belonging to the postoral complex. CY, cytopyge; EP, excretory pore; K1–10, somatic kineties; M(2, 3), adoral membranelles; MA, macronucleus; MI, micronucleus; NK, nasse kinetosomes; OB, oral basket; OP, oral primordium; PC, postoral complex; PO(1–3), preoral kineties; T, excretory tube. Scale bars = 15 μm.

protargol preparations due to distortion by alcohol fixation. Thus, the basket rods form a distinctly flattened tube extending to the body midline, where they abruptly curve to the dorsal posterior body end and the nematodesmata become rather disordered. The long axis of the oral basket opening is highly different in MI and MA: about 5 and 15 μm on average in vivo, respectively (Table 1, Fig. 1, 2, 5–7, 10, 11, 13, 15–17, 30, 33–35, 38–41, 44). The nasse kinetosomes, which are faintly impregnated, are barren and possibly produce the basket rods (Peck 1974). They are not at the distal end of the rods but subapical at the base of the rod angles (Fig. 32). In SEM micrographs, the cortex of the right body side extends over the distal end of the right half of the oral basket (Fig. 26, 27).

The oral primordium consists of two groups of basal bodies: the anterior group, which is slightly posterior to the oral basket, is barren and usually so faintly impregnated that it is difficult to recognize. It is composed of three to four basal bodies forming a short, convex row in the MI; and an average of six basal bodies forming a long, convex to L-shaped row in the MA. The posterior group of basal bodies of the oral primordium consists of two rows of ciliated dikinetids left of the posterior region of somatic kinety 1. Rarely, there is a ciliated monokinetid at the posterior end of the longer right row, the left row usually consists of only a single dikinetid (Table 1, Fig. 5, 7, 16, 22, 33, 34, 41).

Ontogenesis of *Leptopharynx costatus costatus*. Rather many dividers were observed in blooming cultures. Thus, each stage could be studied in at least five specimens. The study was performed on microstome specimens because only one out of the about 200 protargol-impregnated dividers was a macrostome (Fig. 45–70).

Division mode. Fission is homothetogenic, occurring in freely motile cells. Stomatogenesis is mixokinetal. The parental oral apparatus is reorganized, except for the adoral membranelles. The first sign of division is the elongation of the micronucleus (Fig. 45).

Development of oral apparatus and somatic kinety 1. The first kinetosomal activities to be recognized are the sudden

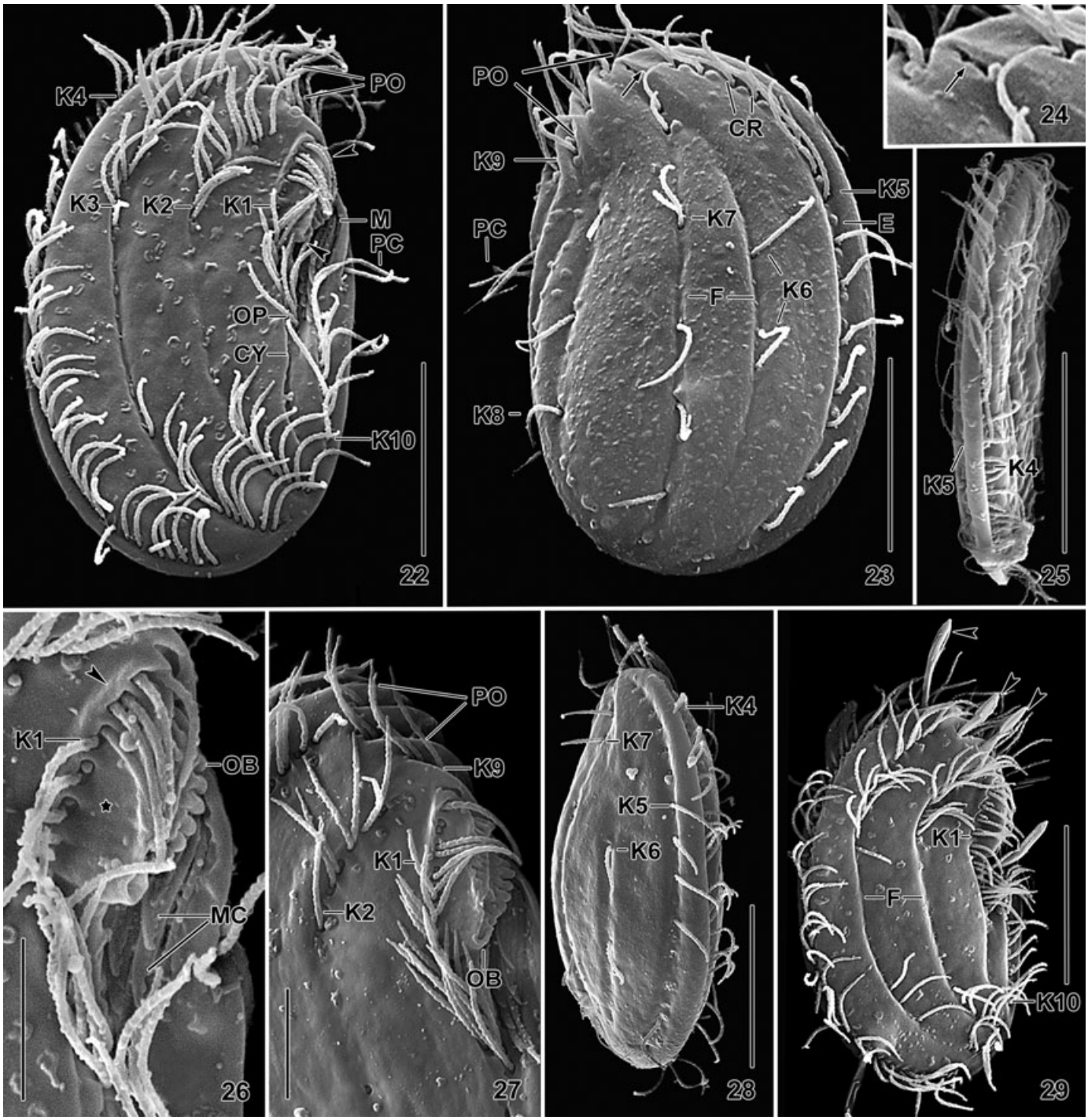

Fig. **22–29.** *Leptopharynx costatus costatus*, microstome specimens in the scanning electron microscope. **22–24.** Right- and left-side view showing the shallow kinety furrows; the comparatively narrow oral basket (arrowheads); the lack of cilia in the center of the right side; and the pit (23, arrow) formed by the anteriormost, nonciliated monokinetids of kinety 6, shown at higher magnification in Fig. 24. Note the ridge right of the anterior portion of kinety 1 and the cleft formed by the cytopyge. **25, 28.** Dorsal views showing the distinct lateral flattening of the body. The discoidal specimen shown in Fig. 28 has a convex left side, possibly due to a good nutrition state. **26, 27.** Right-side views showing the oral cortex and ciliary pattern, the oral basket, and the ridges and furrows accompanying the preoral kineties. The arrowhead marks the inconspicuous ridge right of the anterior portion of kinety 1. The cortex of the right body side extends over the distal end of the right half of the oral basket (asterisk). **29.** Right-side view showing the cortical furrows and some exploding extrusomes between the preoral kineties (arrowheads). CR, crenellation of somatic kinety 9 furrow; CY, cytopyge; E, extrusomes; F, furrows; K1–10, somatic kineties; M, adoral membranelles; MC, membranellar cilia; OB, oral basket; OP, oral primordium; PC, postoral complex; PO, preoral kineties; R, ridge. Scale bars = 15 μm (Fig. 22, 23, 25, 28, 29) and 5 μm (Fig. 26, 27).

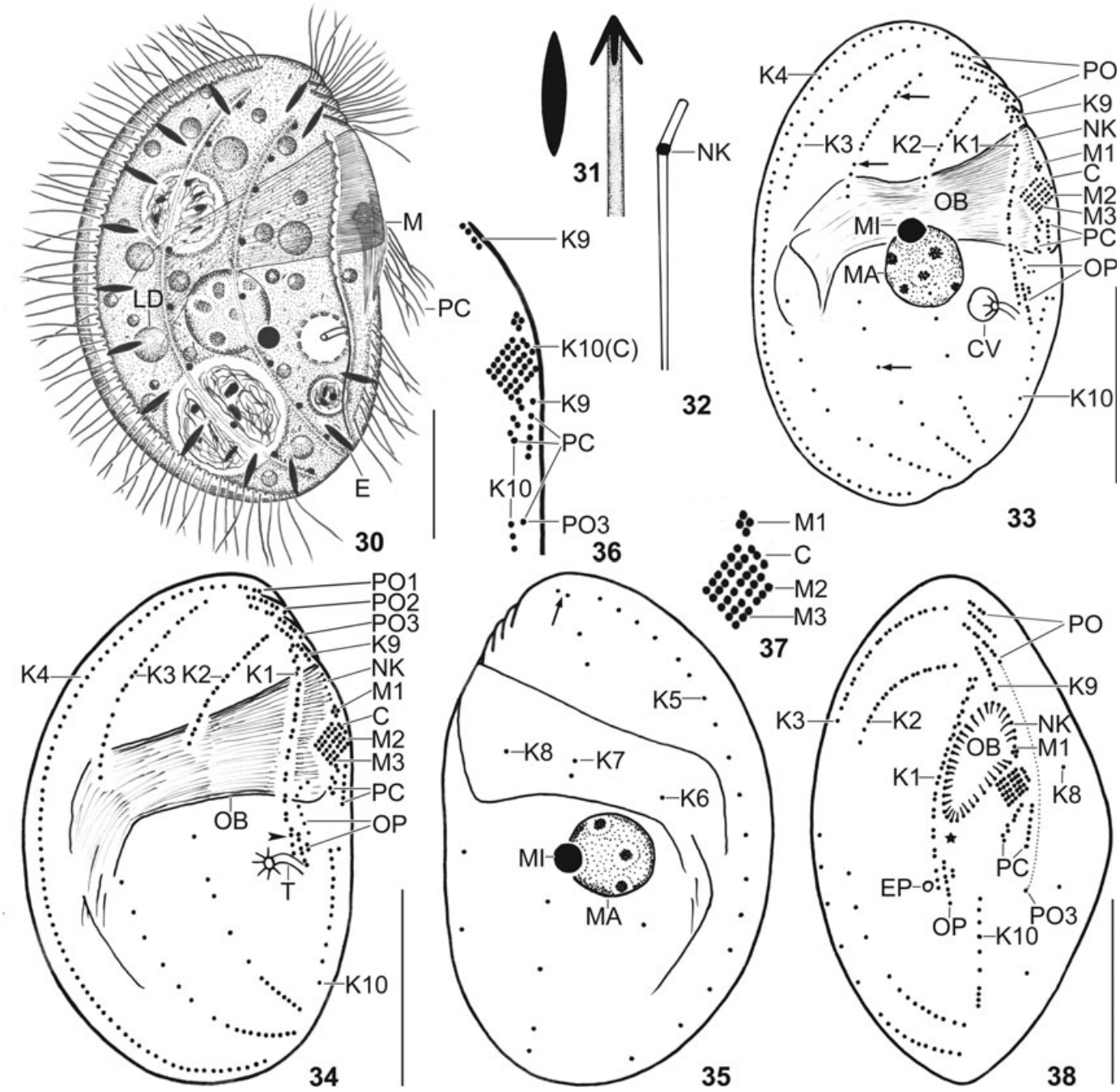

Fig. **30–38.** *Leptopharynx costatus costatus*, macrostome specimens from life (30–32) and after protargol impregnation (33–38). **30.** Right-side view of a representative specimen, length 50 μm. Note the enormous oral basket and the semidiscoidal body. **31.** A resting (~ 5 μm) and an exploded extrusome with anchor-like arms at distal end. **32.** An oral basket rod. The nasse kinetosome is located subapically at the base of the rod angle. **33.** Right-side view of a paratype specimen with an extra kinety (arrows) between kineties 2 and 3. The extra kinety is similar to kinety 3 and begins with a monokinetid. **34–37.** Right and left side ciliary pattern (34, 35), oral basket (34, 35), arrangement of basal bodies on ventral side (36), and adoral membranelles (37) of a hapantotype specimen. The arrowhead in Fig. 34 marks the slightly dislocated posterior end of kinety 1. The arrow in Fig. 35 denotes the anterior monokinetids of kinety 6 previously considered to belong to kinety 7. The left monokinetidal row of the postoral complex belongs to somatic kinety 9. Both the right dikinetidal row and the group C basal bodies belong to kinety 10, and the single monokinetid underneath the left row possibly belongs to preoral kinety 3 (36). **38.** Ventral view of a paratype specimen. Note the flat adoral membranelles and the elliptical oral basket opening, arranged obliquely to main body axis**.** The anterior portion of the oral primordium is not impregnated (asterisk). The dotted line connects preoral kinety 3 (see also Fig. 20). C, group C basal bodies; CV, contractile vacuole; E, extrusome; EP, excretory pore of contractile vacuole; K1–10, somatic kineties; LD, lipid droplets; M(1–3), adoral membranelles; MA, macronucleus; MI, micronucleus; NK, nasse kinetosomes; OB, oral basket; OP, oral primordium; PC, postoral complex; PO(1–3), preoral kineties; T, excretory tube. Scale bars = 20 μm (Fig. 30) and 15 μm (Fig. 33–35, 38).

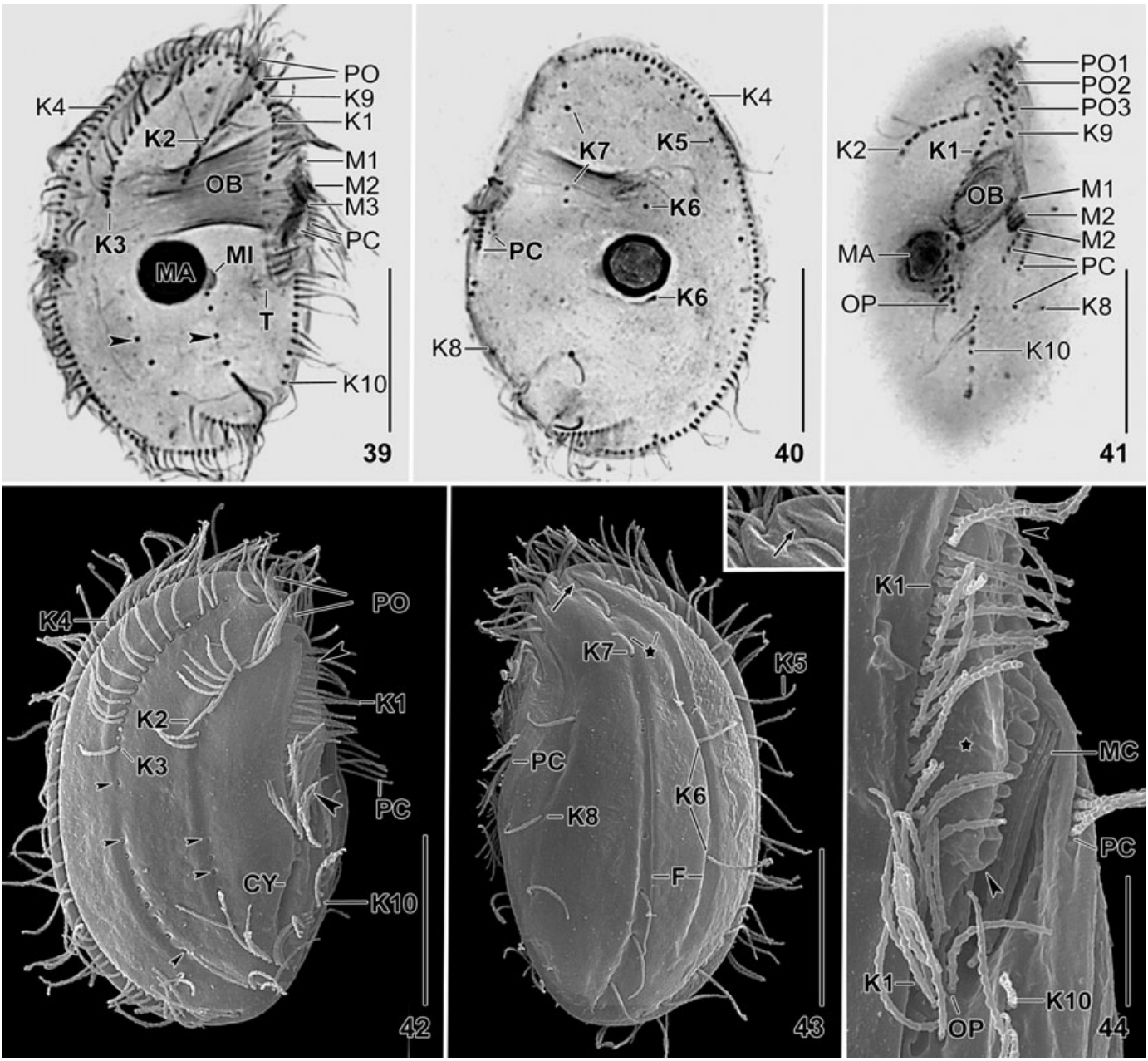

Fig. **39–44.** *Leptopharynx costatus costatus*, macrostome specimens after protargol impregnation (39–41) and in the SEM (42–44). The specimens are only $\leq$ 40 μm long due to strong shrinkage. **39, 40.** Right- and left-side overview. The arrowheads mark nonciliated monokinetids in kineties 2 and 3 (cp. Fig. 42). **41.** Ventral view showing the oblique, elliptical oral basket opening and the anterior portion of kinety 9. **42, 43.** Right- and left-side overview showing the shallow kinety furrows and the pits produced by the nonciliated kinetids in kineties 2 and 3 (small arrowheads). The furrows of kineties 6 and 7 merge anteriorly (asterisk), where the nonciliated monokinetids of kinety 6 reside in a minute pit (arrow and inset). Large arrowheads delimit the wide oral basket. **44.** Ventrolateral view showing the cortex and ciliary pattern as well as the enormous oral basket (arrowheads). The cortex of the right body side extends over the distal end of the right half of the oral basket (asterisk). CY, cytopyge; K1–10, somatic kineties; M1–3, adoral membranelles; MA, macronucleus; MC, membranellar cilia; MI, micronucleus; OB, oral basket; OP, oral primordium; PC, postoral complex; PO (1–3), preoral kineties; T, excretory tube. Scale bars = 15 μm (Fig. 39–43) and 5 μm (Fig. 44).

appearance of adoral membranelle 1 in the proter and the proliferation of basal bodies in the oral primordium (Fig. 45, 46, 65): the anterior portion of the oral primordium becomes the opisthe's nasse row, while the posterior portion differentiates into membranelles 1 and 2 (Fig. 47). In late early dividers, the posterior portion of kinety 1 proliferates and becomes membranelle 3 of the opisthe, while the number of kinetids increases in the anterior portion of kinety 1 by intrakinetal proliferation of basal bodies; the parental oral basket is resorbed (Fig. 48, 66). In early mid-dividers, the kinetids of kinety 1 become more widely spaced elongating the kinety posteriorly, where it touches the right end of the opisthe's nasse row, forming a highly characteristic V-like pattern (Fig. 50, 67, 68). Next, the new adoral membranelles and the

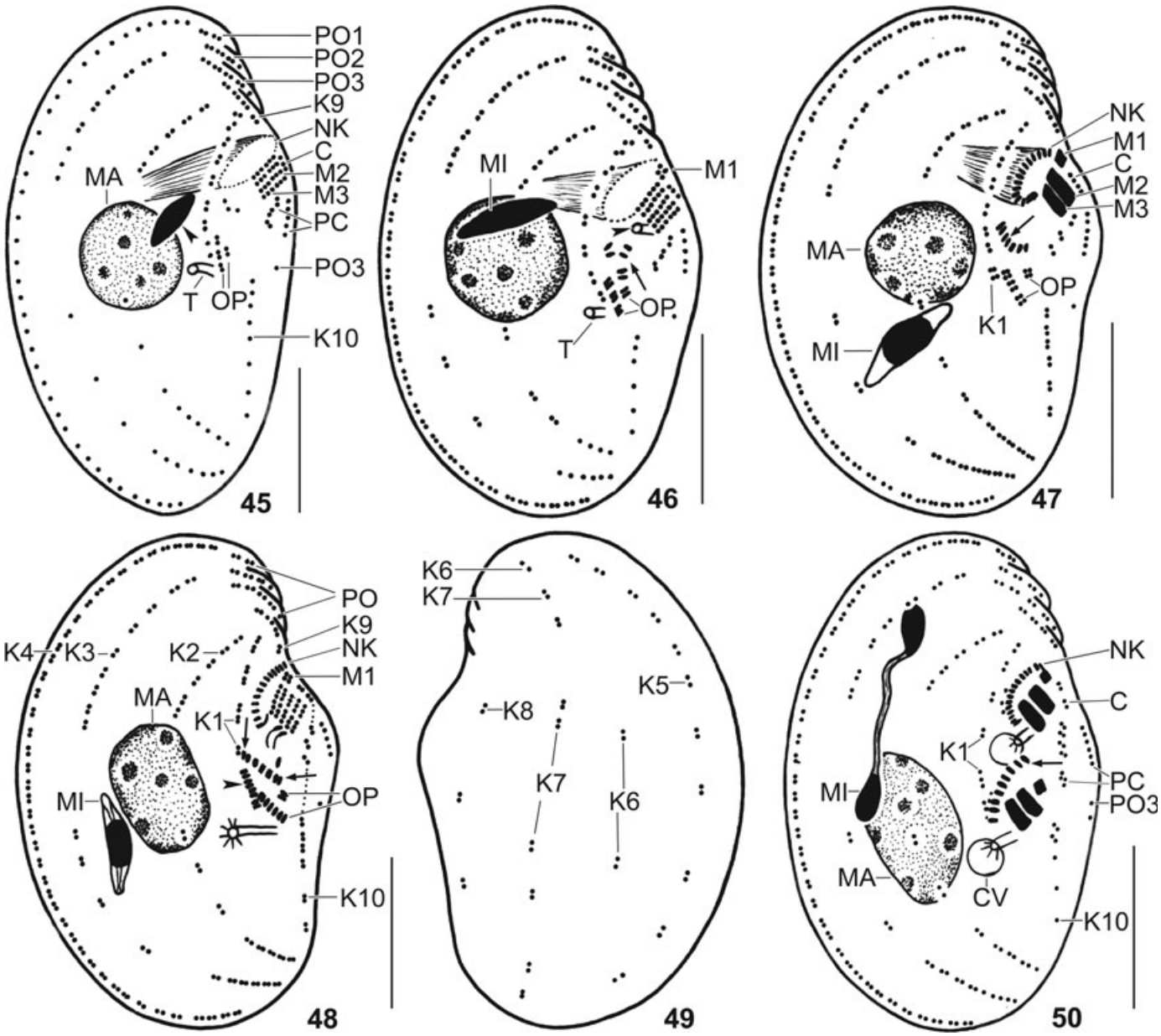

Fig. **45–50.** *Leptopharynx costatus costatus*, protargol preparations of early dividers (45–49) and of an early mid-divider (50). **45.** Right-side view of a very early divider, showing the fusiform micronucleus (arrowhead). **46, 47.** Right side view of early dividers, showing membranelle 1, which is absent in the morphostatic microstomes. The oral primordium begins to proliferate and the anterior portion (arrows) becomes curved (47). A new excretory tube is formed (arrowhead). Note unwinding of the circle of nasse kinetosomes, which are now oblong, and the proliferation of kinetids in the somatic kineties and the posterior portion of somatic kinety 1 (47). **48, 49.** Right- and left-side view of a late early divider, showing the proliferation of kinetids in the somatic kineties and the disappearance of the oral basket. Note the tripartite structure of kinety 10. The arrows delimit the straight anterior portion of the oral primordium, which will become the nasse kinetosomes of the opisthe. The arrowhead denotes the proliferating posterior portion of kinety 1, which produces membranelle 3. The posterior portion of the oral primordium (OP) forms adoral membranelles 1 and 2. **50.** Right-side view of an early mid-divider, showing the anterior portion of the oral primordium, i.e. the new nasse kinetosomes, forming a V-like pattern with the posterior portion of kinety 1 (arrow). Three new adoral membranelles assembled in the opisthe and look like those of the proter. C, group C basal bodies; CV, contractile vacuole; K1–10, somatic kineties; M1–3, adoral membranelles; MA, macronucleus; MI, micronucleus; NK, nasse kinetosomes; OP, oral primordium; PC, postoral complex; PO(1–3), preoral kineties; T, excretory tube. Scale bars = 10 μm.

nasse row, which is composed of two rows of basal bodies, possibly dikinetids, arrange in the species-specific pattern, i.e. as in the proter. Further, a wide break is formed in the middle of kinety 1 (Fig. 50, 51, 67, 68). In mid-dividers, new oral basket rods appear in proter and opisthe, likely produced by the nasse kinetids. Further, the dikinetids of kinety 1 separate and become monokinetids in proter and opisthe (Fig. 52), and the dikinetidal nasse row commences to split laterally (Fig. 53, 54). In late mid-dividers, the nasse row has split (Fig. 57, 58): the left row becomes nasse kinetosomes, while the right row forms the oral anlagen in both proter and opisthe. In late and very late dividers, the kinetids of kinety 1 become dikinetidal

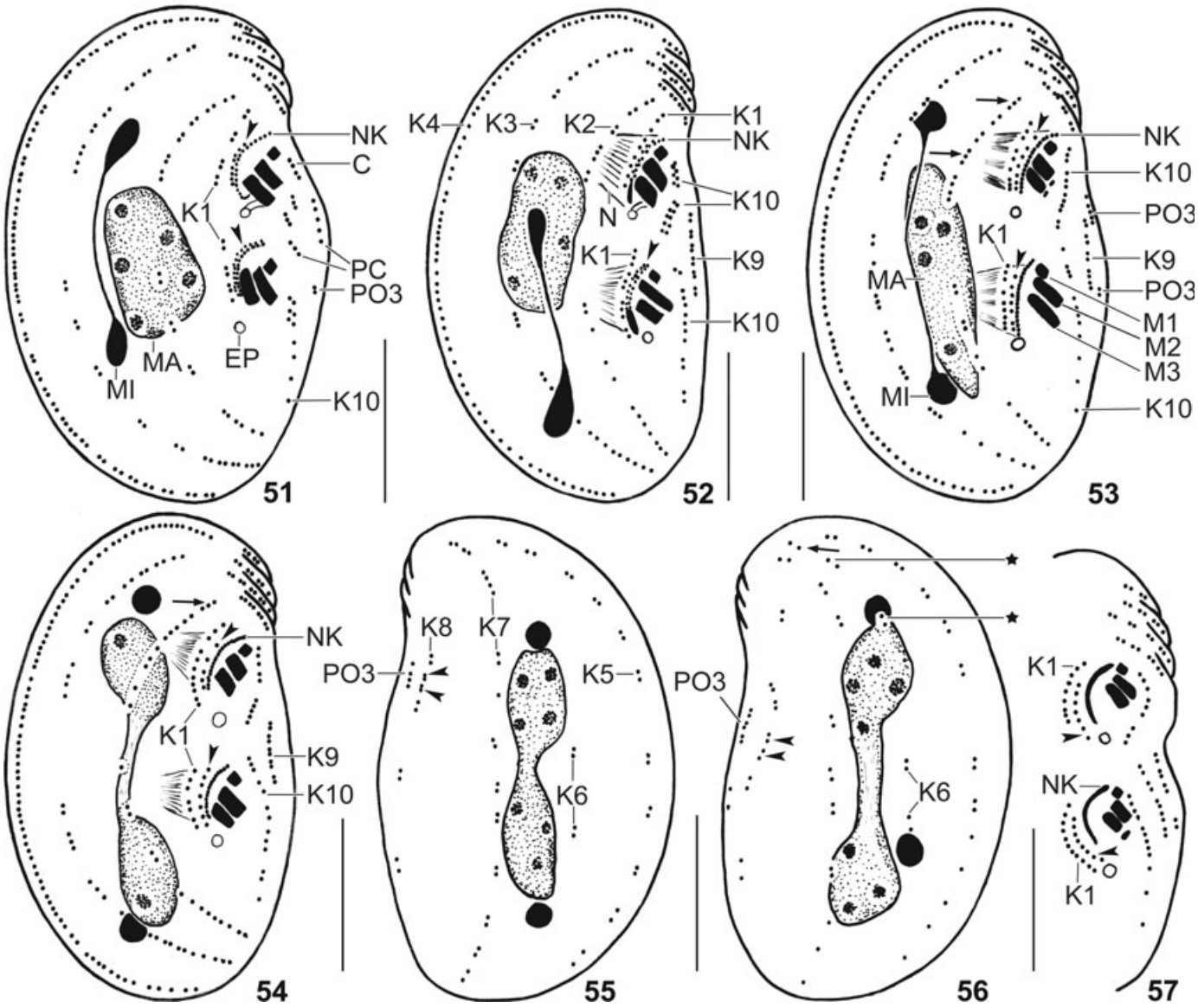

Fig. **51–57.** *Leptopharynx costatus costatus*, protargol preparations of early to late mid-dividers. **51, 52.** Right-side view of early mid-dividers, showing the dumbbell-shaped micronucleus, the elongated macronucleus, and the growing oral basket. The arrowheads mark the dikinetidal nasse kinetosomes of proter and opisthe. Note the group C basal bodies and the right row of the postoral complex which arrange one after the other to form kinety 10 of the proter (see also Fig. 50). Kinety 1 splits in the middle and becomes monokinetidal (52). **53, 54.** Right-side view of mid-dividers, showing proter's kinety 10 consisting of monokinetids. The row of nasse kinetosomes split laterally: the right row becomes the oral primordium (arrowheads), the left nasse kinetosomes. The arrows mark trikinetids in kinety 2. **55, 56.** Left-side view of mid-dividers, showing the interkinetal origin of preoral kinety 3 right of kinety 8. The arrowheads mark the intrakinetal origin of preoral kinety 2. The arrow denotes the anterior kinetids of kinety 6, while the asterisks mark de novo generated kinetids later forming proter's kinety 6. **57.** Ventrolateral view of a late mid-divider, showing the monokinetidal kinety 1 and the right row of nasse kinetosomes (arrowheads), which will form the oral primordium in both proter and opisthe. C, group C basal bodies; EP, excretory pore; K1–10, somatic kineties; M1–3, adoral membranelles; MA, macronucleus; MI, micronucleus; N, nematodesmata; NK, nasse kinetosomes; PC, postoral complex; PO3, preoral kinety. Scale bars = 10 μm.

again (Fig. 60) and the row of nasse kinetosomes becomes C-shaped with the adoral membranelles in between its ends (Fig. 62).

Development of preoral kineties. The parental preoral kineties do not visibly reorganize during cell division and those of the opisthe develop in mid- and very late-dividers. They are difficult to distinguish from each other because they are close together. Very likely, preoral kineties 1 and 3 originate de novo, while kinety 2 originates within kinety 8. First kinety 3 develops, followed by kineties 2 and 1. In mid-dividers, preoral kinety 3 originates between somatic kineties 8 and 9 as a few kinetosomes rather far posterior to preoral kinety 3 of the proter (Fig. 53, 55). These kinetosomes migrate to mid-body left of the dividing postoral complex, i.e. opisthe's kinety 9 (Fig. 56); the single monokinetid posterior to the postoral complex of the morphostatic stage becomes part of this kinety. Preoral kinety 2 originates as faintly impregnated granules within kinety 8 (Fig. 55), very likely by proliferation

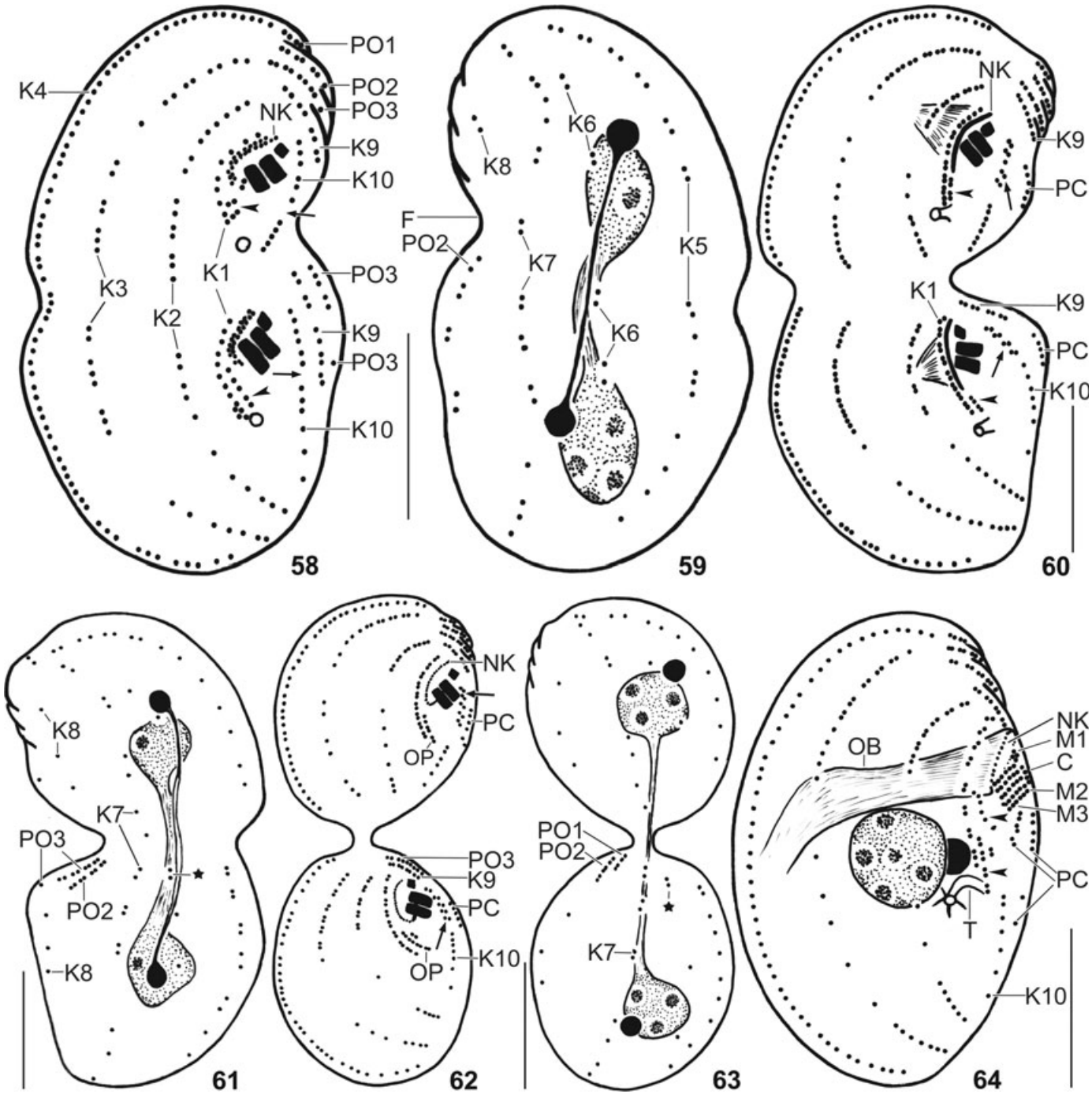

Fig. **58–64.** *Leptopharynx costatus costatus*, protargol preparations of a late mid-divider (58, 59), late and very late dividers (60–63), and of a postdivider (64). **58, 59.** Right- and left-side view showing the onset of cell division, the new oral primordia (arrowheads), the break in mid of kinety 10 of proter and opisthe (arrows), and the proliferation of kinetids in kineties 5–8. **60, 61.** Right- and left-side view of a late divider, showing the new oral primordia (arrowheads), the separation of the posterior half of kinety 9 to form the left row of the postoral complex, and the assemblage of opisthe's preoral kineties. The anterior half of kinety 10 becomes dikinetidal (arrows). The asterisk denotes the anterior kinetosomes of kinety 6 of the opisthe; they will disappear in a cleft (Fig. 23, 24). **62, 63.** Right- and left-side view of a very late divider. Preoral kinety 1 originates between preoral kinety 2 and somatic kinety 7. The arrows mark the anterior dikinetidal portion of kinety 10; later, these dikinetids form the group C basal bodies and the right row of the postoral complex (Fig. 64). The asterisk denotes the anterior kinetosomes of kinety 6. **64.** Right-side view of a postdivider. It differs from the morphostatic microstomes only by the presence of adoral membranelle 1 (cp. Fig. 5). The arrowheads mark the anterior and posterior portion of the oral primordium. C, group C basal bodies; F, division furrow; K1–10, somatic kineties; M1–3, adoral membranelles; NK, nasse kinetosomes; OB, oral basket; OP, oral primordium; PC, postoral complex; PO1–3, preoral kineties; T, excretory tube. Scale bars = 10 μm.

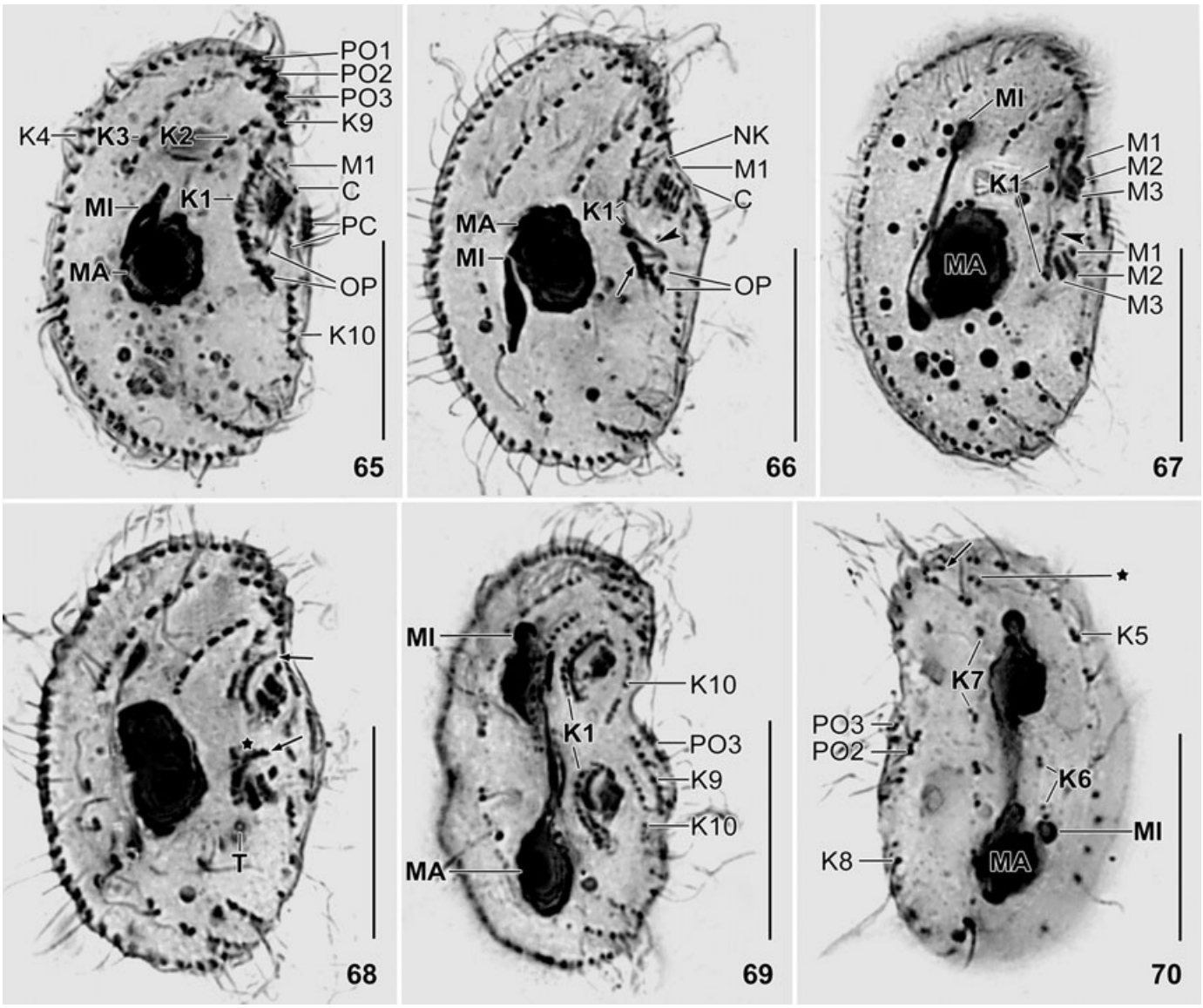

Fig. **65–70.** *Leptopharynx costatus costatus*, protargol preparations of microstome dividers. **65.** Right-side view of an early divider, showing the fusiform micronucleus, the inconspicuous adoral membranelle 1, and proliferation of kinetids in the somatic kineties and the oral primordium. **66.** Right-side view of a late early divider. The arrowhead marks the straight anterior portion of the oral primordium. The arrow denotes the proliferating posterior portion of kinety 1, which will become membranelle 3 of the opisthe. **67, 68.** Right-side view of early mid-dividers, showing the adoral membranelles similarly arranged in proter and opisthe. The arrowhead marks the nasse kinetosomes, which were formed by the anterior portion of the oral primordium. Arrows denote the dikinetidal nasse kinetosomes of proter and opisthe (68). The asterisk marks the V-shaped figure formed by kinety 1 and the opisthe row of nasse kinetosomes. Note the dumbbell-shaped micronucleus and the elongated macronucleus. **69.** Right-side view of a late mid-divider, showing the dumbbell-shaped macronucleus and micronucleus, and somatic kinety 9, which originated from the postoral complex. **70.** Left-side view of a mid-divider, showing the de novo originated opisthe preoral kineties 2 and 3. The arrow denotes parental basal bodies of kinety 6, while the asterisk marks de novo produced kinetids. C, group C basal bodies; K1–10, somatic kineties; M1–3, adoral membranelles; MA, macronucleus; MI, micronucleus; NK, nasse kinetosomes; OP, oral primordium; PC, postoral complex; PO1–3, preoral kineties; T, excretory tube base. Scale bars = 15 μm.

of parental kinetids. In very late dividers, just before the separation of proter and opisthe, preoral kinety 1 originates between preoral kinety 2 and somatic kinety 7 (Fig. 63).

Development of somatic kineties 2–8. The proliferation of somatic kinetids commences concomitantly in these kineties during the early stages of division (Fig. 46–49). They separate in late dividers when the division furrow becomes recognizable (Fig. 58, 59, 69).

The proliferation in the monokinetidal parts of the ciliary rows produces new kinetosomes anteriorly; this is indicated by the presence of cilia in the posterior kinetosomes of the newly formed pairs. In this stage, *Leptopharynx* becomes a "dikinetidal ciliate" except for the left row of the postoral complex (Fig. 47–49). In the dikinetidal part of kineties 2 and 3 the kinetids separate, each producing a new kinetosome anteriorly, as suggested by the occurrence of trikinetids (Fig. 52–54). In the opisthe, kinety 6 proliferates ordinarily by producing a new kinetosome anterior to each monokinetid to form two dikinetids (Fig. 49). During the late division stages and postdivisional cell shaping, the anterior dikinetid migrates

anterior to kinety 7, while the posterior dikinetid separates and forms two monokinetids (Fig. 61, 63). The proter kinety 6 develops as follows: three dikinetids appear in the anterior quarter of the cell, possibly produced de novo or, in the anterior pair, by activation of existing basal bodies (Fig. 56, 59, 70; see also Fig. 23, 24); the anterior pair remains and migrates anteriorly of kinety 7 while one kinetosome each is resorbed in the two other pairs.

Development of somatic kinety 9. This kinety consists of a dikinetidal anterior portion (preoral kinety 4) and a monokinetidal posterior portion, which is part of the postoral complex (Fig. 51). In mid-dividers, the monokinetidal portion begins to proliferate, forming a dikinetidal row in the opisthe (Fig. 52). This condition remains unchanged for a while (Fig. 53, 54, 57). In late mid-dividers and late dividers, this row divides in the middle, and then the posterior half becomes monokinetidal and part of the opisthe's postoral complex (Fig. 58, 60), while the anterior portion becomes the anterior dikinetidal portion of opisthe's kinety 9 (preoral kinety 4). In the proter, the anterior portion of kinety 9 begins to elongate posteriorly (Fig. 58) and becomes interrupted in the middle (Fig. 60, 62): the anterior portion forms "preoral kinety 4," while the posterior portion forms the left row of the postoral complex.

Development of somatic kinety 10. This kinety consists of three portions (Fig. 45): the two group C dikinetids; the three dikinetids of the postoral complex; and the long, monokinetidal posterior portion. The genesis of kinety 10 is very complex and thus will be described in detail.

The genesis commences in the posterior portion, which becomes dikinetidal in early dividers (Fig. 47). In late early dividers, kinety 10 consists of dikinetids throughout (Fig. 48). Then, the three portions of the kinety align, producing a straight kinety, in which the dikinetids of the two rear thirds of the posterior portion become monokinetidal (Fig. 50, 51). In mid-dividers, all dikinetids become monokinetidal and the kinetids proliferate new basal bodies (Fig. 53, 54). In late mid-dividers, kinety 10 is monokinetidal and splits in the middle (Fig. 54, 57, 58, 69): the anterior portion becomes kinety 10 of the proter, the posterior portion becomes kinety 10 of the opisthe. In late dividers, five dikinetids are formed in the anterior portion of both proter's and opisthe's kinety 10 (Fig. 60, 62): three of these dikinetids migrate posteriorly becoming the right, dikinetidal row of the postoral complex, while two dikinetids migrate to the left of adoral membranelle 2, forming the group C basal bodies, i.e. the anterior portion of kinety 10 (Fig. 64).

Development of the postoral complex. It is composed of two rows of basal bodies: the posterior, ciliated monokinetidal portion of somatic kinety 9 and the anterior, nonciliated dikinetidal portion of somatic kinety 10 (Fig. 36). The monokinetidal row originates as follows: in the opisthe, the parental postoral complex proliferates in mid-dividers, forming a dikinetidal row (Fig. 36, 52–54); in late mid-dividers and late dividers, this row divides in the middle, the anterior, dikinetidal half forms opisthe's kinety 9, while the posterior half becomes monokinetidal and part of the opisthe's postoral complex (Fig. 58, 60, 62). In the proter, the dikinetidal anterior portion of kinety 9 elongates posteriorly and divides in the middle in late mid-dividers (Fig. 58): the anterior portion forms the dikinetidal "preoral kinety 4," while the posterior portion becomes monokinetidal generating the left row of the postoral complex (Fig. 60, 62).

The dikinetidal row of the postoral complex originates as described above in Development of somatic kinety 10. Briefly, the three portions of kinety 10 align, producing a straight kinety that splits in the middle, producing a new kinety 10 in both proter and opisthe (Fig. 54, 57, 58, 69). The five anterior monokinetids become dikinetidal (Fig. 60, 62): the anterior two dikinetids migrate left of the adoral membranelles, forming the group C basal bodies, while the other dikinetids migrate posterior to the membranelles, forming the right row of the postoral complex (Fig. 64).

Development of the contractile vacuole. In early dividers, a new contractile vacuole appears as a short tube posterior to the proter's adoral membranelles, while there is no change in the parental contractile vacuole, which is taken over by the opisthe (Fig. 46). During the division process, the contractile vacuoles of proter and opisthe are marked by a short excretory tube and/or the circular opening posterior to kinety 1 (Fig. 48, 50–54, 57, 58, 60, 68).

Division of nuclear apparatus. *Leptopharynx costatus* has a homomeric macronucleus, which divides transversely like the micronucleus. Briefly, the micronucleus becomes fusiform in very early dividers, while there is no change in the shape of the macronucleus and the infraciliature (Fig. 45, 65, 66). In early mid-dividers, the micronucleus divides into two ovate pieces connected by a membranous strand (Fig. 50, 67), while the macronucleus becomes ellipsoidal (Fig. 50–53, 68). In mid-dividers, both the micronucleus and the macronucleus are dumbbell-shaped (Fig. 54, 55, 69, 70); they begin to separate in late dividers (Fig. 61, 63).

DISCUSSION

Comparison with congeners and changes in the descriptive morphology. The most detailed redescriptions of *L. costatus* are those of Prelle (1961), Njiné (1979), and Foissner (1979, 1989). Their data match our observations on the microstome morph of the German population. However, these authors did not observe macrostome or other morphs, either because they did not use cultures or because they did not study declining and old cultures, where macrostomes are most common. The isolate of Njiné has a specific adoral membranelle 1, which is absent from the *L. costatus* populations investigated by us and from those described in the literature (Table 2). Thus, Dragesco and Dragesco-Kernéis (1986) might be correct in establishing a new species, *L. ambiguus*, for Njiné's *L. costatus*. Njiné (1979) concomitantly described a new macrostome species, *L. macrostoma*, having the same membranellar structure as his *L. costatus*. As this pattern is definitely different from our and other *L. costatus* populations (Table 2), Njiné's *L. costatus* might be indeed a distinct species: the microstome of his *L. macrostoma*. This is indicated by the occurrence of both species in the same sample and the ignorance of macrostomy in *L. costatus* at that time.

There are three congeners, which are similar or even synonymous with *L. costatus*: *Leptopharynx eurystoma* (Kahl, 1931) Foissner et al., 2011 is likely a macrostome of *L. costatus* (Omar & Foissner, 2012); *Leptopharynx agilis* (Savoie, 1957) Foissner et al., 2011; which supposedly lacks extrusomes, is a misidentified *L. costatus* because Savoie (1957) described "cigar-shaped" structures in the cytoplasm, perfectly matching *Leptopharynx* extrusomes; and *Leptopharynx stenostomatus* (Gellért, 1942) Foissner et al., 2011, which is likely a distinct species because it has six monokinetids in kinety 6.

According to the data obtained from five populations of *L. costatus*, four morphs occur (Table 2). All populations have a small morph with narrow oral basket (MI). They are very similar in most features, including the average total of 181–190 basal bodies excluding those of the adoral membranelles. The large morphs (MA) of both the German neotype and the

Table **2.** Comparison of main characteristics in four *Leptopharynx costatus* populations (from Omar and Foissner 2011). Dotted features define distinct morphs.

Characteristics	*L. costatus costatus* (Germany)	*L. costatus costatus* (Mexico)	*L. costatus costatus* (Austrian Alps)	*L. costatus costatus* (Brazil)	*L. costatus gonohymen* (Florida)
• Small morph with narrow oral basket (MI)	Present	Present	Present	Present	Present
• Large morph with wide oral basket (MA)	Present	Present	Absent	Not observed	Absent
Large morph with narrow oral basket	Absent	Absent	Does not apply	Not observed	Present
Adoral membranelle 1 in small morph with narrow oral basket	Absent	Absent	Absent	Absent	Absent
• Adoral membranelle 1 in large morph with wide oral basket	Present	Absent	Does not apply	Does not apply	Does not apply
Adoral membranelle 1 in large morph with narrow oral basket	Does not apply	Does not apply	Absent	Does not apply	Absent
Adoral membranelle 1 in dividers	Present	Present	Present	Not observed	Present
• Orientation of membranelles 2 and 3	Flat	Flat	Flat	Flat	Right-angled
Average total number of basal bodies in small morph	190	185	187	186	162
Average total number of basal bodies in large morph	264	248	Does not apply	Does not apply	256

Table **3.** The origin of main organelles in microthoracid and nassulid taxa.

Characteristics	*Leptopharynx costatus*	*Pseudomicrothorax dubius* (Peck 1974)	*Drepanomonas revoluta* (Antes & Wilbert 1987)	*Colpodidium caudatum* (Foissner et al. 2002)	*Nassula citrea* (Eisler & Bardele 1986)	*Furgasonia blochmanni* (Eisler & Bardele 1986)
Stomatogenic mode	Mixokinetal	Mixokinetal	Mixokinetal	Mixokinetal	Mixokinetal	Mixokinetal
Adoral membranelles	Mixokinetal	Mixokinetal	Mixokinetal	Mixokinetal	Telokinetal	Telokinetal
Membranelle 1	Oral primordium	Oral primordium	Oral primordium	Nasse kinetosomes	Somatic kinety	Somatic kinety
Membranelle 2	Oral primordium	Oral primordium	Oral primordium	Nasse kinetosomes	Somatic kinety	Somatic kinety
Membranelle 3	Somatic kinety 1	Somatic kinety 1	Somatic kinety 1?	Somatic kinety 1	Somatic kinety	Somatic kinety
Other membranelles	Does not apply	Does not apply	Does not apply	Does not apply	Somatic kineties	Does not apply
Nasse kinetosomes	Oral primordium	Oral primordium[a]	?	Nasse kinetosomes	Nasse kinetosomes	Nasse kinetosomes
Oral primordium	Nasse kinetosomes	Nasse kinetosomes	Oral primordium?	Nasse kinetosomes	Nasse kinetosomes and somatic kineties	Nasse kinetosomes and somatic kineties
Oral primordium, permanent	Yes	Yes	Yes	Yes	No	No
Preoral kineties	De novo	Does not apply	?	Does not apply	Does not apply	Does not apply
Postoral complex/ kineties	Somatic kineties 9 and 10	Does not apply	?	Somatic kineties and nasse kinetosomes	Does not apply	Does not apply

[a]As supposed by Eisler and Bardele (1986).

Mexican population are very similar in having a wide oral basket and a total of 248–264 basal bodies on average. However, they differ from the microstomes in the presence (vs. absence) of adoral membranelle 1. The large morph of *L. costatus gonohymen* Foissner & Omar, 2012 differs from those of *L. costatus costatus* mainly in the arrangement of adoral membranelles 2 and 3 (i.e. right-angled vs. flat) and the size of the oral basket (i.e. narrow vs. wide).

Kinety 6 of *Leptopharynx* consists of more monokinetids than previously recognized (Foissner 1989; Njiné 1979; Omar and Foissner 2011, 2012). After proliferation of kinety 6, the two pair-like anterior monokinetids of the opisthe migrate to the anterior end of kinety 7. Thus, we suggest adding these monokinetids to kinety 6 in previously investigated species, which will now have 4 kinetids in kinety 6 rather than 2 (i.e. in *L. costatus, L. costatus gonohymen, L. bromeliophilus*, and *L. australiensis*) or 8 kinetids rather than 6 (i.e. *Leptopharynx brasiliensis*). A further change concerns preoral kinety 4, where the ontogenetic analysis shows that it belongs to somatic kinety 9, which is thus composed of an anterior portion (formerly

"preoral kinety 4") and a posterior one, forming the left row of the postoral complex.

Comparative ontogenesis. Members of the class Nassophorea share the mixokinetal mode of stomatogenesis, where both somatic and oral ciliary structures contribute to the oral ciliature of the opisthe (Foissner 1996) (Table 3). With the exception of the Synhymeniida, ontogenetic data are available for all nassophorean orders (i.e. the Nassulida, Microthoracida, and Colpodidiida), while such data are lacking from half of the families recognized by Lynn (2008). As concerns *Leptopharynx*, only the study by Njiné (1979) was available. Unfortunately, it contains some mistakes and did not describe the origin of the preoral kineties and the postoral complex, two very important structures. He correctly recognized the mixokinetal stomatogenesis, the preservation of the parental adoral membranelles, and the origin of the opisthe nasse kinetosomes from the anterior portion of the oral primordium.

The origin of key organelles in *L. costatus* and other microthoracid and nassophorean ciliates is collated in Table 3. This shows that *Leptopharynx* matches the microthoracid pattern because it develops preoral kineties and a postoral complex. Within the supposed nassulids, *Colpodidium caudatum* represents a remarkable exception (Foissner et al. 2002): in the proter, kineties 1–3 originate from parental postoral kineties, while kinety 4 is produced by the left row of nasse kinetosomes; the opisthe obtains the parental postoral kinety 4. Thus, the classification in the nassulids may be questioned. An analogous case is known from a hymenostome scuticociliate, *Dexiotrichides pangi*, which develops the paroral membrane of the opisthe from somatic kinety 1, while the adoral membranelles are generated by the scutica (Song et al. 2005). These authors suggest exclusion of *D. pangi* from the "true" scuticociliates.

Alveolocysts and intraordinal classification. Alveolocysts are a special cortex pattern as yet found in *Furgasonia blochmanni*, *Nassula aurea*, *N. citrea*, *N. ornata*, *N. tumida*, and *Pseudomicrothorax dubius* (Eisler & Bardele 1983). Based on Corliss (1979), who classified *Pseudomicrothorax* and *Leptopharynx* in the same family, Leptopharyngidae Kahl, 1926; Eisler and Bardele (1983), Lynn (2008), and Gong et al. (2009) obviously assumed that *Leptopharynx* has alveolocysts. However, they did not know the study by Njiné and Didier (1980), who showed by transmission electron microscopy the absence of alveolocysts in *Leptopharynx*. This and the recent molecular data, which show *Pseudomicrothorax* at the base of the microthoracid clade with high bootstrap support (Foissner et al. 2011), suggest quite different relationships with the microthoracids (Fig. 71). Briefly, these data support the classification of Foissner (1985): *Pseudomicrothorax* represents a distinct family (Jankowski 1975; Foissner 1985) and *Leptopharynx* belongs to the microthoracids, likely together with the genera *Drepanomonas*, *Helicyclium*, *Microthorax*, *Stammeridium*, and *Trochiliopsis* (Augustin et al. 1987).

Classification of the Nassophorea. Recently, Gong et al. (2009) found evidence for a nonmonophyly of the class Nassophorea, using the small subunit rRNA and phenotypic and ontogenetic characteristics. The conclusion of Gong et al. (2009) has been supported by Foissner et al. (2011), providing full bootstrap support for both, the Nassulida and Microthoracida and, less clearly, also for a class Nassophorea containing the orders Microthoracida and Synhymenida. The present study adds an ontogenetic feature, viz., the telokinetal vs. mixokinetal origin of the adoral membranelles (Table 3). The only problem is the classification of the Colpodidiida, which are ontogenetically nearer to the microthoracids than to the nassulids because of the mixokinetal origin of the adoral membranelles. Further, the colpodidiids have a rather unique organization: they have a distinct buccal cavity lacking in the nassulids but present in microthoracid genera like *Microthorax* and *Drepanomonas*.

TAXONOMIC SUMMARY

Class Nassophorea Small & Lynn, 1981

Order Microthoracida Jankowski, 1967

Family Microthoracidae Wrześniowski, 1870

Improved diagnosis. Small (< 20 μm) to medium-sized (up to 100 μm) ellipsoidal to semidiscoidal Microthoracida with single macronucleus and micronucleus. Exploded trichocysts with four rod-shaped arms distally. Cortex rigid, with or

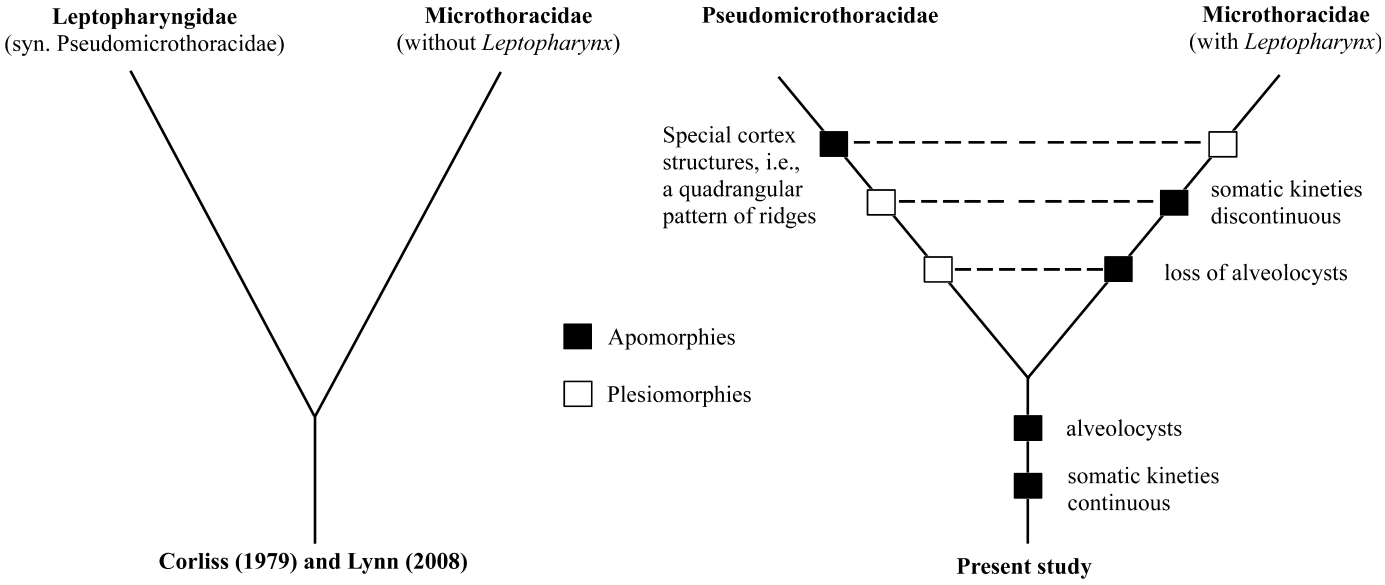

Fig. **71.** Classifications of the Microthoracida. Names of families in bold.

without distinct ridges and/or furrows containing or accompanying ciliary rows. Somatic kineties partially without cilia and/or kinetids in middle third of body, especially on left side; three preoral kineties of which kineties 1 and 3 originate de novo, while kinety 2 is generated by somatic kinety 8. Oral apparatus near anterior or posterior end of body, oral basket composed of nematodesmata bundles; two to three adoral membranelles with membranelles 1 and 2 originating from oral primordium, and membranelle 3 from somatic kinety 1.

Type genus (by tautonymy). *Microthorax* Engelmann, 1862

Remarks. The diagnosis follows Wrześniowski (1870), Kahl (1931), Foissner (1985), Lynn (2008), and the present investigations on the ontogenesis of *Leptopharynx*. As detailed ontogenetic data are lacking from all other genera, the diagnosis may change with further knowledge.

Neither Wrześniowski (1870) nor any other person fixed a type genus for the family Microthoracidae. Wrześniowski (1870) included two genera in this "Microthoracina": *Microthorax* and *Cinetochilum*. Thus, *Microthorax* becomes the type genus of the family Microthoracidae by tautonymy (*Int. Code Zool. Nomenclature* 1999, article 68.4). *Cinetochilum* is now in a distinct family belonging to the Scuticociliatia (Lynn 2008).

Genera assignable. *Drepanomonas* Fresenius, 1858; *Hemicyclium* Eberhard, 1862 (will be redescribed in a forthcoming paper), *Leptopharynx* Mermod, 1914; *Microthorax* Engelmann, 1862; *Stammeridium* Wenzel, 1969; and *Trochiliopsis* Penard, 1922.

Genus *Leptopharynx* Mermod, 1914

Improved diagnosis. Microthoracidae with 10 (microstomes "MI") and 10 or 11 (macrostomes "MA") somatic kineties and a postoral complex generated by kineties 9 and 10. Oral apparatus in anterior half of body, with two or three adoral membranelles; membranelle 1, if present, consisting of < 10 barren basal bodies. Produces MI and MA morphs. In limnetic and terrestrial habitats.

Type species (by monotypy). *Leptopharynx costatus* Mermod, 1914

Species assignable. Eleven species, as discussed by Foissner et al. (2011) and above.

Remarks. For family classification, see Comparative ontogenesis. *Leptopharynx* can be easily distinguished from most other microthoracid genera by the position of the oral apparatus: in anterior third or in second quarter of body in *Leptopharynx*, between middle and posterior third of body in *Drepanomonas*, in the posterior third of body in *Microthorax*, near the anterior body end in *Stammeridium* and *Trochiliopsis* (Foissner 1985; Augustin et al. 1987).

Species *Leptopharynx costatus* Mermod, 1914

Diagnosis (includes four morphs described in Table 2). Size of microstomes (MI) in vivo on average about 40 × 25 μm (35–50 × 20–35 μm; 20–50 × 15–35 μm when literature data are included), that of macrostomes (MA) 55 × 40 μm (40–70 × 30–50 μm). Body outline elliptical to broadly elliptical with moderately oblique preoral region in MI, broadly elliptical to semidiscoidal with slightly oblique preoral region in MA. Microstomes with 10 somatic kineties, MA with 10 or 11. Kineties 1, 2, and 3 with dikinetids anteriorly; kinety 1 consisting of narrowly spaced, ciliated dikinetids in MI and of narrowly or widely spaced dikinetids in MA; kinety 6 composed of four monokinetids; kinety 10 far underneath of adoral membranelles and without dikinetids; a total average of 162–190 and 248–264 basal bodies in MI and MA, respectively. Preoral kineties on ventral side. Two adoral membranelles in MI, two or three in MA, membranelles 2 and 3 form a flat field in MI and a flat or right-angled field in MA. Oral basket narrow in MI and narrow or wide in MA. Oral primordium left of kinety 1.

Remarks. This is an improved version of the diagnosis given by Omar and Foissner (2012). We distinguish two subspecies (diagnosis below). Possibly, a third subspecies is warranted for the population from a Mexican bromeliad whose macrostomes lack adoral membranelle 1.

Subspecies *Leptopharynx costatus costatus* Mermod, 1914

Improved diagnosis. Ten somatic and three preoral kineties with an average of 181–190 basal bodies in MI, while 10 or 11 kineties and 248–264 basal bodies in MA. Kinety 1 consisting of narrowly spaced dikinetids in both morphs. Adoral membranelle 1 absent in MI, while present or absent in MA; membranelles 2 and 3 form a flat ciliary field. Oral basket on average 5 and 15 μm wide in MI and MA, respectively.

Neotypification. No original type material is available from *L. costatus*. Now, its identity is threatened by the discovery that it has four morphs and two subspecies not recognized in previous studies. Further, there are three congeners that are similar or even synonymous with *L. costatus costatus* (see above). Thus, neotypification is required (Foissner 2002; Foissner et al. 2002).

Foissner (1979) deposited a "paratype" (actually a voucher) slide with silver nitrate-impregnated specimens from the Austrian Central Alps in the Biology Centre of the Museum of Upper Austria (Aescht 2008). Recently, Omar and Foissner (2012) deposited in the same repository voucher protargol slides from a Brazilian population and from the Austrian population studied by Foissner (1989). All these slides are based on environmental material and contain only microstomes. Accordingly, the German population, which has been fully investigated in the present study and was sequenced by Foissner et al. (2011), should serve as a neotype of *L. costatus costatus*. This population, which is polymorphic, makes microstomes and macrostomes, of which the former match previous descriptions of "*L. costatus*." Furthermore, it is from the same biogeographic region as the type locality (i.e. Switzerland, Central Europe) (Mermod 1914).

Neotype locality. The exact locality is unknown, as explained in the Material and Methods, Terminology section. Thus, we fix as neotype locality Germany, the country where the neotype was found.

Neotype material. Two hapantotype slides with protargol-impregnated microstome and macrostome specimens of *L. costatus costatus* have been deposited in the Biology Centre of the Museum of Upper Austria, Linz (LI). Further, 13 paratype slides with protargol and Klein-Foissner silver nitrate-impregnated morphostatic and dividing cells have been deposited in the same repository. Hapantotypes, paratypes, and other relevant specimens have been labeled and marked by black ink circles on the coverslip. The GenBank accession number for the 18S rDNA is HQ668467.

Subspecies *Leptopharynx costatus gonohymen* Foissner & Omar, 2012

Improved diagnosis. Ten somatic and three preoral kineties with an average of 162 and 256 basal bodies in small and large morphs, respectively. Kinety 1 consisting of widely spaced dikinetids in large morphs. Adoral membranelle 1 absent in small and large morphs; membranelles 2 and 3 right-angled to each other in large morphs. Oral basket on average 3 and 5 μm wide in small and large morphs, respectively.

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