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Morphology and Morphogenesis of *Strobilidium caudatum* (Fromentel), *Meseres corlissi* N. Sp., *Halteria grandinella* (Müller), and *Strombidium rehwaldi* N. Sp., and a Proposed Phylogenetic System for Oligotrich Ciliates (Protozoa, Ciliophora)[1]

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ABSTRACT. The morphology and morphogenesis of some oligotrichs were investigated using protargol impregnation, silver carbonate impregnation and scanning electron microscopy. The somatic kineties of *Strobilidium caudatum* form a spiral at the posterior pole. Strobilidiids without such a spiral are transferred to the genus *Rimostrombidium*. Fourteen new combinations and a nomen novum, *Strobilidium kahli*, are necessary, *Meseres corlissi* n. sp. is characterized by eight somatic kineties composed of long cilia which are not fused to "bristles" as they are in *Halteria*. *Strombidium oblongum* shows similar characteristics and is thus combined with *Meseres*. *Strombidium rehwaldi* n. sp. has an anterior and an equatorial girdle of extrusomes. The morphogenesis of *Meseres* and *Halteria* is very similar, i.e. the entire somatic ciliature and the oral primordium originate apokinetally on the cell surface; the parental somatic ciliature is resorbed. In strobilidiids and tintinnids, the oral anlagen develop in a subsurface pouch and the parental somatic kineties, which are not resorbed, elongate by intrakinetal proliferation of basal bodies. In strombidiids, the oral primordium develops in an intracellular sac or tube. These morphogenetic peculiarities and distinct morphologic characters (e.g. arrangement of adoral membranelles) were applied in constructing a phylogenetic system for oligotrichs using hypotrichs as outgroup. This shows that halteriids are more closely related to hypotrichs than they are to other oligotrichs. The Halteriidae are thus raised to ordinal and subclass ranks, Halteriida n. ord., Halteriia n. subcl.

Key words. Halteriidae, infraciliature, *Rimostrombidium*, Strobilidiidae, Strombidiidae, systematics, taxonomy, Tintinnina.

OLIGOTRICH ciliates usually dominate marine planktonic ciliate communities [49, 52]. Although comparatively few species occur in freshwater, they also play an important role in the planktonic food webs of lakes [20, 58]. Only recently, some oligotrichs have been investigated with silver impregnation and electron microscopy [10, 19, 21, 25, 26, 29–32, 42–45, 49, 52, 57]. However, the last detailed studies on morphogenesis date back to Fauré-Fremiet [17], Kormos & Kormos [41] and Deroux [10]! Even the morphogenesis of such a common oligotrich as *Halteria grandinella* is still controversial [17, 21, 74]. A detailed knowledge of the morphology and morphogenesis is indispensable for many ecological investigations and for reliable classification. In order to contribute to this goal, we studied four representative oligotrichs. These investigations, along with some preliminary observations on *Tintinnidium* and *Pelagostrombidium*, and data from the literature provide a reliable basis for a phylogenetic classification of the main oligotrichs, i.e. Halteriidae, Strombidiidae, Strobilidiidae, and Tintinnina.

MATERIALS AND METHODS

Strobilidium caudatum was found in a forest pond near the Grabensee, Flachgau, Salzburg, Austria, 47° 59′ N, 13° 05′ E.

Halteria grandinella and *M. corlissi* occurred in an infusion of dried mud from an astatic meadow-pond between the so-called Henkerhaus and the Peterweiher, City of Salzburg, Austria, 47° 47′ N, 13° 02′ E.

Strombidium rehwaldi was found in the benthos of the River Amper at 70.4 km. This is about 2 km downriver from the sewage plant at Geiselbullach, east of Fürstenfeldbruck, southern Germany, 48° 13′ N, 11° 21′ E.

Material from raw cultures was used. All species were studied in vivo and on protargol silver-impregnated slides. Furthermore, *S. caudatum* was treated with the pyridinated silver carbonate method. This species, *H. grandinella* and *M. corlissi* were also investigated with the scanning electron microscope (SEM). See Foissner [24] for detailed protocols of all of these methods.

Counts and measurements on silvered specimens were performed at a magnification of ×1,000. In vivo measurements were conducted at a magnification of ×100–200. Although these provide only rough estimates, it is convenient to give such data as specimens usually shrink in preparations or may even contract during fixation. Standard deviation and coefficient of variation were calculated following Sokal & Rohlf [71]. Drawings of impregnated specimens were made with a camera lucida.

RESULTS

Strobilidiidae Kahl in Doflein & Reichenow, 1929

Strobilidium Schewiakoff, 1892

Synonymy. *Strobilidium* Schewiakoff, 1892 (type species [by monotypy]: *S. adhaerens*); *Turbilina* Enriques, 1908 (type species [by monotypy]: *T. instabilis*); *Strombilidium* Schewiakoff, 1892—Neave, 1940 (subsequent incorrect spelling).

Improved diagnosis. Strobilidiidae with several somatic kineties, some of which form a spiral at posterior end of cell.

Type species. *Strombidium caudatum* Fromentel, 1876.

Remarks. *Strobilidium* is the type genus of the family Strobilidiidae, suborder Strobilidiina Jankowski, 1980, order Oligotrichida Bütschli, 1887. Claparède & Lachmann [7] used both spellings, *Strombidion* and *Strombidium* (in this order), when

[1] Dedicated to Professor Dr. John O. Corliss on the occasion of his 70th birthday.

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they established the genus. However, the spelling *Strombidium* succeeded. This can be justified with a very broad interpretation of Art. 24c and 32b of the International Code of Zoological Nomenclature (ICZN), saying that the correct spelling is that of the 1st reviser [34], i.e. [8, 37, 72]. Thus, *Strombidion* should be considered a nomen oblitum and the correct spelling of the type species of *Strobilidium* is *Strombidium caudatum*.

Lynn & Montagnes [49] consider the arrangement of the somatic kineties to be an important generic criterion in strobilidiids. We agree and thus use the characteristic spiralling of the somatic kineties at the posterior pole as genus character of *Strobilidium*. Strobilidiids lacking such a caudal spiral can be transferred to the ill-defined "desk-genus" *Rimostrombidium* Jankowski, 1978, for which the original definition [35] is: "with ribbed cortex." Jankowski [35] fixed as type *Strobilidium velox* Fauré-Fremiet, 1924, which is rather similar to, e.g. *Strobilidium lacustris* Foissner et al., 1988. This kind of strobilidiid has slightly spiralling somatic kineties which do not extend to the posterior end of the cell, i.e. do not form a caudal spiral. Based on this improved definition, the following nominal species of *Strobilidium* are combined (in alphabetical order) with *Rimostrombidium* Jankowski: *R. conicum* (Kahl, 1932) n. comb.; *R. epacrum* (Lynn & Montagnes, 1988) n. comb.; *R. humile* (Penard, 1922) n. comb.; *R. hyalinum* (Mirabdullajev, 1985) n. comb.; *R. kahli* n. comb. (original nomenclatural act, see below); *R. lacustris* (Foissner et al., 1988) n. comb.; *R. lineolatum* (Tucolesco, 1962a) n. comb.; *R. marinum* (Fauré-Fremiet, 1924) n. comb.; *R. mirabile* (Vuxanovici, 1962) n. comb.; *R. multinucleatum* (Lynn & Montagnes, 1988) n. comb.; *R. polyhalinum* (Tucolesco, 1962b) n. comb.; *R. saltans* (Vuxanovici, 1962) n. comb.; *R. sphaericum* (Lynn & Montagnes, 1988) n. comb.; *R. sulcatum* (Tucolesco, 1962b) n. comb. Several other poorly described species might also belong to *Rimostrombidium* [see 37, 53].

Strobilidium thus remains monotypic; the populations studied by Deroux [10] and Fernandez-Leborans [21] are, however, probably further new species.

Strobilidium caudatum (Fromentel, 1876) Foissner, 1987

Synonymy. (?) *Trichoda cometa* Müller, 1773; (?) *Trichoda bomba* Müller, 1773; (?) *Trichoda trochus* Müller, 1786; *Strombidion caudatum* Fromentel, 1876; *Strombidium claparèdi* Kent, 1881; *Strombidium gyrans* Stokes, 1887; *Strombidium intermedium* Maskell, 1887; *Strobilidium adhaerens* Schewiakoff, 1892; *Strombidium velox* Beardsley, 1902, (partim, Fig. 5b); *Turbilina instabilis* Enriques, 1908; *Strombidium gyrans* Stokes var. *transsylvanicum* Lepsi, 1926; *Strobilidium cometa* (Müller, 1786) Dingfelder, 1962; (?) *Strobilidium gyrans* Schewiakoff, 1893—Deroux 1974; (?) *Strombilidium gyrans* Schewiakoff, 1893—Fernandez-Leborans 1983; *Strobilidium caudatum* (Fromentel, 1874) Foissner, 1987; nec: *Strobilidium caudatum* Kahl, 1932.

Remarks. There is some confusion about the taxonomy of *S. caudatum* [23]. Dingfelder [11] synonymized *S. gyrans* with *Trichoda cometa*. This is uncertain because shape (spherical) and movement (not fast) of *T. cometa* differ from *S. caudatum*. The movement and shape of *T. trochus* and *S. caudatum* are quite similar [59, 60]. However, *T. trochus* and *T. bomba* are questionable synonyms for *Halteria verrucosa* [28]. These three poorly described ciliates are best considered nomina dubia.

The outline of *Strombidium velox* is very similar to *S. caudatum*. In addition, *S. velox* forms a thread with which it fixes to the substrate and on which it gyrates [3]. However, Beardsley's Fig. 5a [3], which clearly shows a *Strombidium*, indicates that he mixed two different species. *Strobilidium caudatum* Kahl, 1932 is certainly a different species. As a secondary homonym of *S. caudatum* (Fromentel, 1876) Foissner, 1987, it has to be renamed: *Strobilidium kahli* nom. n. The other synonymy is according to [37, 53]. As concerns some other populations [10, 21] see below.

Neotype material. Two slides of protargol impregnated cells have been deposited in the collection of microscope slides of the Oberösterreichisches Landesmuseum in Linz, Austria. Accession numbers: 1,2/1991.

Redescription (Fig. 1–5, 9–17; Table 1). In vivo 50–65 × 40–50 μm ($\bar{x}$ = 56 ± 6.7 × 42 ± 5.0 μm, n = 8). Turbinate to inverted pyriform, slightly asymmetric, posterior end tapering and obliquely truncate, transverse section circular. Macronucleus horse shoe-shaped, close beneath zone of external adoral membranelles (external polykinetids), with opening in cytopharyngeal region (Fig. 2). One spherical micronucleus adjacent to macronucleus (rarely stained with protargol; position probably variable). Contractile vacuole at left side in posterior third of cell. Feeds on diatoms and flagellates.

Movement very rapid, rotating about main body axis. When undisturbed for a longer while, cell secretes a thin, mucous thread at caudal end ("scopula"), often very long [32], and attaches to a substrate. Thread hardly recognizable unless small particles adhere to it (Fig. 1, 17). Frequently, cells swing on thread ("stalk") in a waving motion, still rotating. Disturbed individuals detach immediately and dart away.

Somatic kineties restricted to posterior half of cell, composed of closely spaced cilia, very likely monokinetids (Fig. 2, 3, 12–15; Table 1). On ventral side usually two, rarely three, shortened somatic kineties which do not reach posterior pole; remaining kineties extend to caudal end where they form a distinct spiral (Fig. 14, 15). Cilia directed to left, 2–3 μm long, shortened stubs in anterior portion of kineties often separated by small gap; proximal third of cilia covered by cytoplasmic flap (Fig. 13).

External adoral membranelles on continuous cytoplasmic ridge; zone therefore appears as closed circle in top view, as stated previously [9, 10, 18, 70]. However, 4–6 increasingly elongated external membranelles and two very short internal adoral membranelles (internal polykinetids) extend into oral cavity, clearly showing that external membranelles form a spiral (Fig. 4, 11). In scanning electron micrographs, the external adoral membranelles are usually in furrows, which are, however, probably produced by a slight contraction of the oral ridge as we could not recognize them in living specimens (Fig. 16). External membranelles composed of two long (ca. 10 μm) and one shorter kinety (ca. 8 μm; Fig. 5), cilia about 25 μm long and only proximally fused. Internal membranelles each consist of two rows of basal bodies. Anterior surface (peristomial bottom) slightly vaulted, with very short, funnel-shaped, acentric oral cavity defining ventral side and containing above mentioned elongated external and very small internal membranelles as well as single-rowed paroral membrane extending to center of anterior surface (Fig. 2, 10). A long bundle of pharyngeal fibers extends to posterior portion of cell (Fig. 2, 9).

Comparison with data from literature. The behavior of *S. caudatum* and the structure of the somatic kineties are well comparable with data by Grim & Halcrow [32], i.e. cells attach with a mucous thread to the substrate, disturbed specimens leave their thread immediately, the somatic ciliature consists of short cilia which are proximally covered by a cytoplasmic flap, and three somatic kineties form a distinct spiral at the posterior end of the cell. We did, however, not observe mucous material at the posterior pole.

Strobilidium caudatum has been repeatedly investigated, but only some redescriptions are based on silver impregnation [10, 21]. However, the populations these authors studied differ from our isolate in some features, indicating that they might not be conspecific. The population of Deroux [10] differs markedly

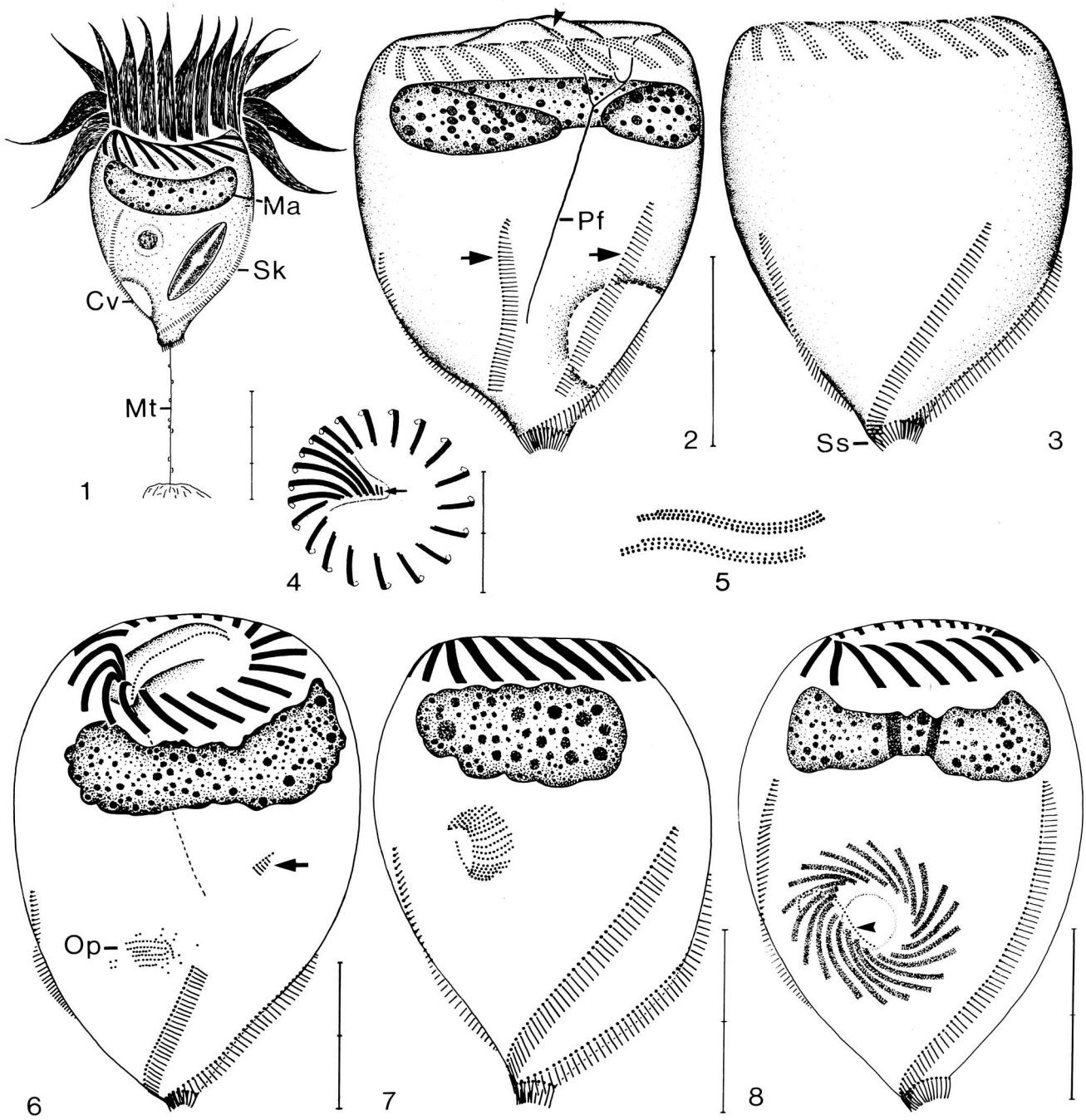

Fig. 1–8. Morphology and morphogenesis of *Strobilidium caudatum* (Fig. 1, from life; Fig. 2–8, protargol impregnation). **1**. Dorsal view of settled specimen. **2**. Infraciliature and somatic cilia of ventral side. Arrows mark shortened ventral kineties, arrowhead points to paroral membrane. **3**. Dorsal view of specimen shown in Fig. 2. Lateral and dorsal somatic kineties form distinct spiral on posterior pole. **4**. Top view of adoral zone of membranelles. Note elongated external membranelles and two very short internal membranelles (arrow). **5**. Detail of external adoral membranelles. **6**. Very early divider showing anarchic field of basal bodies between dorsal somatic kineties. Arrow marks short kinety fragment seen only in this specimen. **7**. Early divider showing oral primordium composed of anlagen for adoral membranelles and paroral membrane. Somatic kineties elongate by intrakinetal proliferation. **8**. Late divider. Adoral membranelles of opisthe form "closed" circle; the two very small internal membranelles were not clearly seen and have thus been omitted. Arrowhead marks paroral membrane. Scale bar, each division = 10 μm.

Cv, contractile vacuole; Ma, macronucleus; Mt, mucous thread; Op, oral primordium; Pf, pharyngeal fibers; Sk, somatic kinety; Ss, spiral of somatic kineties.

from our *S. caudatum* by its occurrence (brackish water), by some morphologic characters (three of the five somatic kineties extend almost to the external adoral membranelles; adoral zone separated head-like from postoral portion), and by the site of the formation of the oral primordium (close beneath zone of external membranelles). Fernandez-Leborans' [21] specimens differ by the larger size (in vivo 85–90 μm) and by the higher number (29–30) and greater length (14 μm) of the external mem-

Table 1. Morphometric data of *Strobilidium caudatum*.[a]

Character	$\bar{x}$	SD	CV	Min	Max
Body, length	49.8	5.0	10.0	43	65
Body, width	40.6	2.8	6.8	36	49
Macronuclear figure, diam.	32.2	3.4	10.4	23	38
Macronucleus, width	9.2	2.1	22.4	6	14
Micronucleus, length	3.2	1.0	29.9	2	5
Micronucleus, width	3.0	0.8	27.0	2	5
Number					
Macronuclei	1.0	0.0	0.0	1	1
External membranelles	20.0	1.0	5.2	18	22
Somatic kineties	5.3	0.6	11.1	5	7
Distance, ant. end of somatic kineties to posterior pole	27.7	5.5	19.8	21	43

[a] All data are based on the investigation of 30 randomly selected, protargol impregnated and mounted non-dividers. All measurements in μm. Abbreviations: ant, anterior; CV, coefficient of variation in %; diam, diameter; Max, maximum; Min, minimum; SD, standard deviation; $\bar{x}$, arithmetic mean.

branelles; whether the four short, three-rowed "buccal membranelles" of this population are part of the elongated external membranelles or are internal membranelles cannot be seen from the figures provided. Further populations of *S. caudatum* should be studied to elucidate the identity of the isolates studied by Deroux [10] and Fernandez-Leborans [21].

Morphogenesis (Fig. 6–8, 16, 18, 19). The morphogenesis of *S. caudatum* was studied in detail by Deroux [10]. Despite some doubts concerning the identification (see above), the morphogenetic events are rather similar to those of our population. Therefore, we illustrate only an early (Fig. 6), an intermediate (Fig. 7, 18, 19), and a late divisional stage (Fig. 8, 16) for comparison with the similar mode of stomatogenesis found in *Tintinnidium* (Fig. 35) and the rather different types occurring in *Meseres* (Fig. 28–33), *Halteria* (Fig. 44–47), and *Pelagostrombidium* (Fig. 34).

In short, the adoral membranelles and the paroral membrane differentiate in a subsurface pouch from an anarchic field in dorsal position, which is an uncommon location for oral primordium formation (Fig. 6–8, 16, 18, 19). The somatic kineties simply elongate by addition of new basal bodies and are divided during cytokinesis (Fig. 6–8) [10]; we did not find very late dividers in our material. Whether the basal bodies proliferate within or at the ends of the parental kineties must be clarified by transmission electron microscopy. They certainly do not originate apokinetally as in the halteriids. Two macronuclear replication bands are recognizable during morphogenesis (Fig. 8).

The most important difference to literature data [10, 41] concerns the site of origin of the oral primordium. In our population, stomatogenesis occurs roughly in mid-body (Fig. 6), whereas Deroux [10] and Kormos & Kormos [41] state that it commences slightly below the external membranelles. Possibly, this position is variable or a species-specific character, as also indicated by the morphologic differences mentioned above.

Halteriidae Claparède & Lachmann, 1858

Meseres corlissi n. sp.

Diagnosis. In vivo about 70–90 × 60 μm, acontractile. Eight slightly shortened somatic kineties in equatorial portion; cilia long, not fused to "bristles." Sixteen anterior and 15 ventral adoral membranelles on average.

Type location. Dried mud from an astatic meadow-pond between the so-called Henkerhaus and the Peterweiher, City of Salzburg Austria, 47° 47′ N, 13° 02′ E.

Type specimens. A holotype and a paratype of *M. corlissi* as two slides of protargol impregnated cells have been deposited in the collection of microscope slides of the Oberösterreichisches Landesmuseum in Linz, Austria. Accession numbers: 3, 4/1991.

Dedication. We dedicate this new species to Professor John O. Corliss as a small token of appreciation for his friendship and encouraging discussions over many years.

Description (Fig. 20–27, 37, 41; Table 2). Broad-ellipsoid, widest close below anterior adoral membranelles (anterior polykinetids), rarely slightly tapering posteriorly. Transverse section circular. Macronucleus ovoid to slightly reniform, approximately in mid-body left of cytostome, contains small and large, globular to band-like nucleoli (Fig. 23, 27). Single, spherical micronucleus in indentation of macronucleus. Contractile vacuole ventro-laterally left of oral cavity in anterior body half; temporary excretory pore between 2nd and 3rd somatic kinety (Fig. 41). Cytopyge near posterior end (Fig. 23), disproving the assumption that it is entirely absent in oligotrichs [9]. Cortex thin, flexible, with plate-like layer of, probably, numerous mitochondria (2–3 × 1–2 μm; Fig. 24). Cytoplasm usually packed with food vacuoles containing green algae (4–7 μm in diameter), some greasy shining globules (1–3 μm in diameter), and irregularly shaped crystals (ca. 1 μm). These inclusions render cells almost black at low magnification. Some individuals with vacuolized cytoplasm. Movement gyrating and jumping, never rests.

Somatic kineties slightly spiralling, composed of rather closely spaced cilia, take clockwise turn when viewed from anterior to posterior pole (Fig. 20, 21). Close to each ciliated basal body is a smaller, non-ciliated granule from which (as from the ciliated basal body) a long, lateral fiber originates, indicating that the somatic kineties are very likely composed of dikinetids (so designated in the further description). Fibers, like those found in *Halteria* [30], sometimes extend more than half the distance to adjacent kineties but, apparently, are not connected (Fig. 22, 25). The non-ciliated basal bodies are sometimes recognizable as very small knobs in the SEM. Cilia about 16 × 0.5 μm, remarkable both in structure (uniformly thick; cp. more needle-like cilia in *Halteria*, Fig. 43–45) and physiology (rather stiff, do not beat like normal cilia). One to two dikinetids with one cilium each (ca. 15 μm long) in small fold close to lower right

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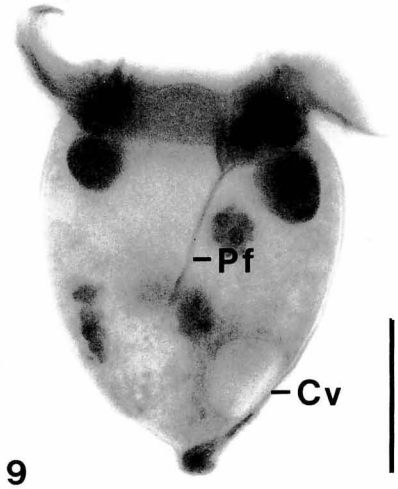
Fig. **9–15.** Morphology of *Strobilidium caudatum* (Fig. 9, 10, 15, protargol impregnation; 11, silver carbonate impregnation; 12–14, scanning micrographs). **9.** Ventral view of slightly asymmetric specimen. **10.** Oral infraciliature. Arrowhead marks shortened row of basal bodies. **11.** Top view of adoral membranelles. Arrow marks site where adoral spiral commences. **12.** Dorsal view of interphasic individual. **13.** Shortened cilia (arrow) at anterior portion of somatic kinety are separated by small gap (arrowhead) from other cilia partially covered by cytoplasmic flap. **14.** Lateral and dorsal somatic kineties extend in deep furrows and form distinct spiral on posterior pole. **15.** Spiral of somatic kineties on posterior pole.

Fig. 9, 12, bars = 20 μm; 13, 14, bars = 4 μm; 10, 11, 15, purposely without scale bars since the applied staining technique (squashed, unmounted specimens) leads to unavoidable distortions of the cells which would give meaningless measurements.

Cf, cytoplasmic flap; Cv, contractile vacuole; Em, external membranelles; Pf, pharyngeal fibers; Pm, paroral membrane; Sk, somatic kinety.



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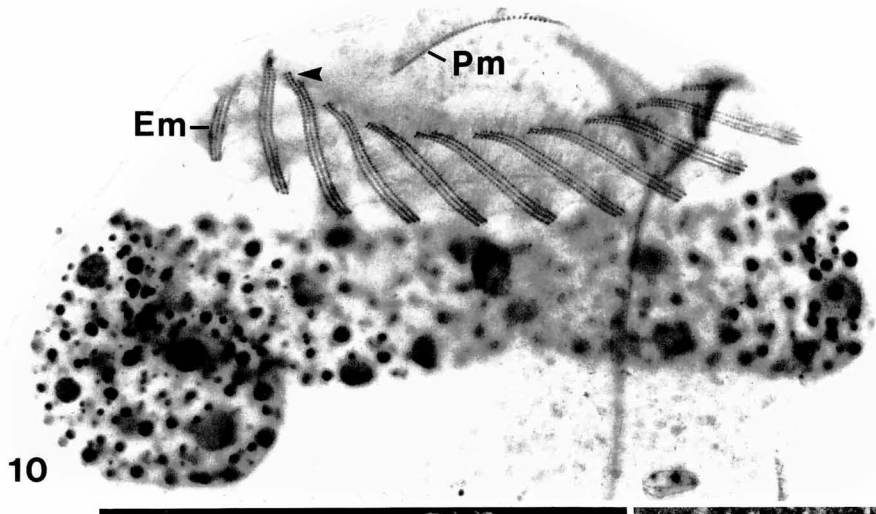

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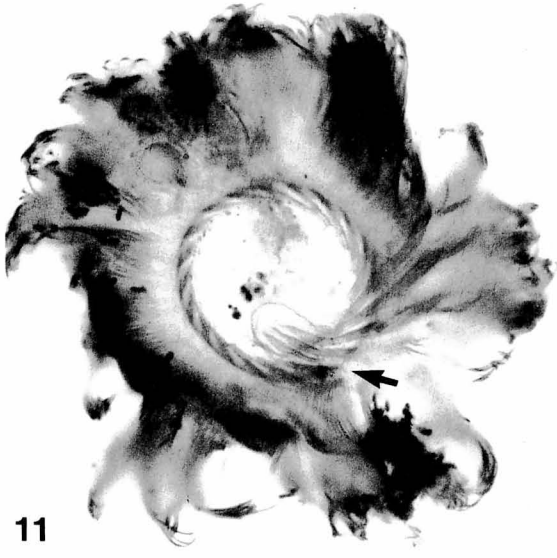

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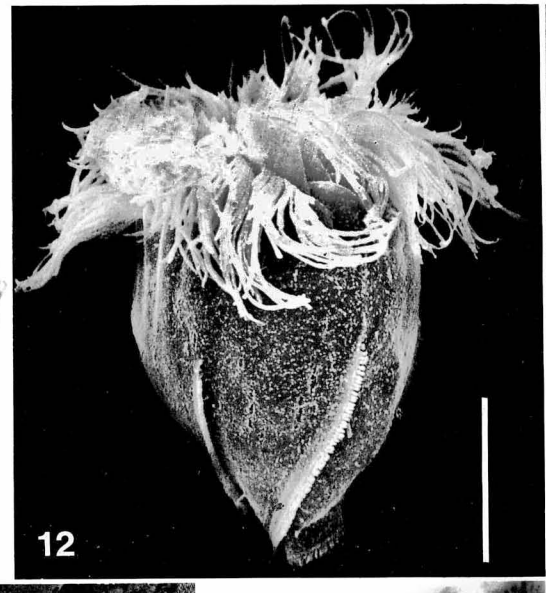

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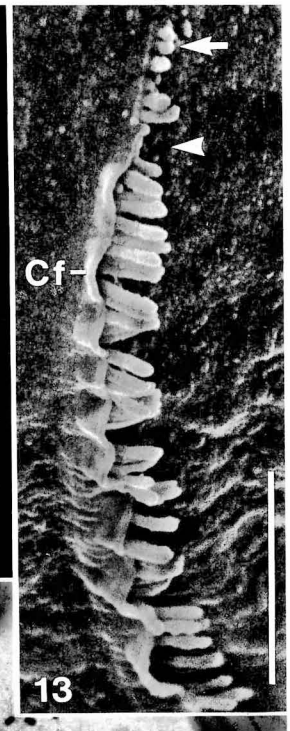

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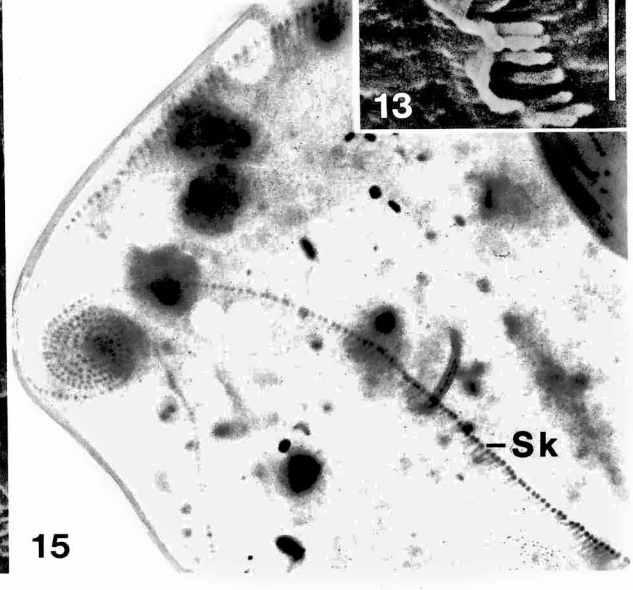

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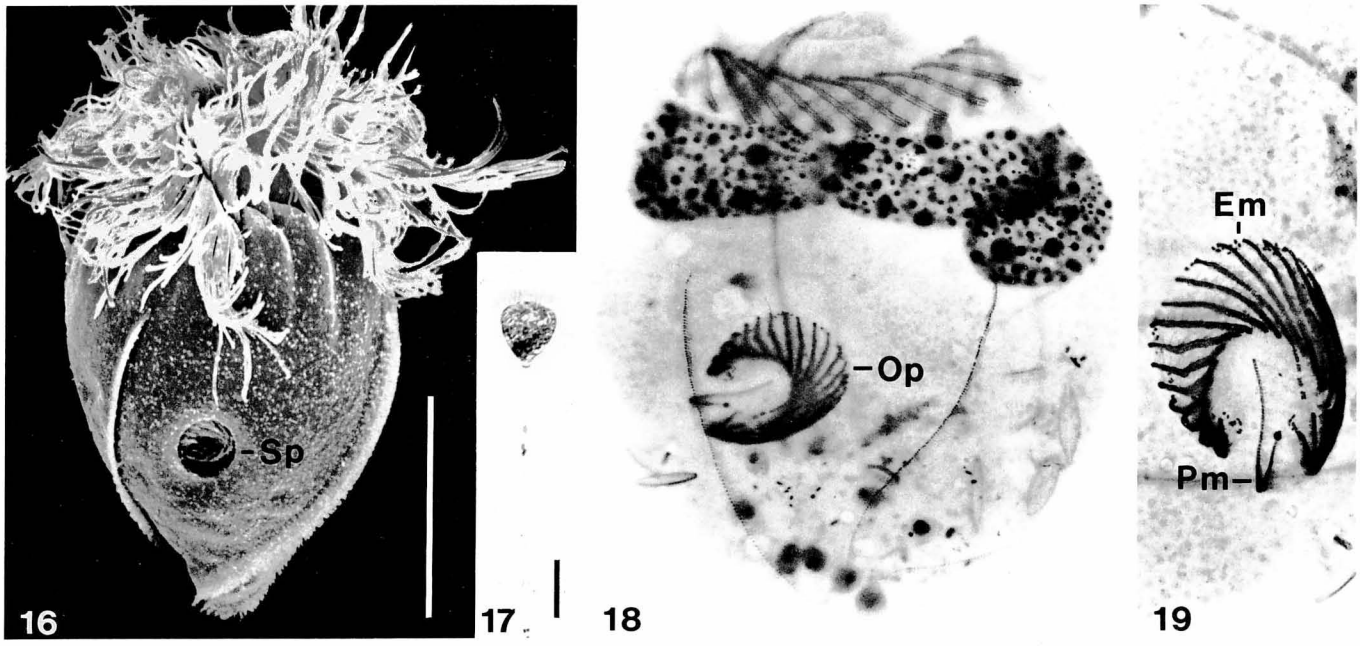


Fig. **16–19**. Morphology and morphogenesis of *Strobilidium caudatum* (Fig. 16, scanning micrograph; 17, bright field micrograph; 18, 19, protargol impregnation). **16**. Late divider showing opening of subsurface pouch. Bar = 20 μm. **17**. Attached, living specimen with fine mucous thread to which detritus adheres. Bar = 50 μm. **18**. Dorsal view of intermediate divider with almost completed oral structures. **19**. Higher magnification of oral apparatus of specimen shown in Fig. 18. Fig. 18, 19, purposely without scale bars since the applied staining technique (squashed, unmounted specimens) leads to unavoidable distortions of the cells which would give meaningless measurements.

Em, external membranelles; Op, oral primordium; Pm, paroral membrane; Sp, opening of subsurface pouch.

margin of oral opening; they possibly possess a long, anteriorly extending fiber (Fig. 23, 25, 26, 37).

Anterior adoral membranelles distinctly separate from ventral membranelles, conspicuous, surround anterior end of cell; cilia about 35 μm long, fused proximally, frayed distally. Each anterior membranelle composed of three equally long ciliary rows (about 12–14 μm; Table 2); first membranelle to right of oral cavity slightly shortened ($\bar{x}$ = 10.7 μm; Fig. 26, Table 2). Ventral adoral membranelles consist of four rows of basal bodies each: two equally long, one shorter and one very short row (Fig. 26); cilia about 10 μm long. Ventral and anterior membranelles each connected by system of fibers (Fig. 25). Paroral membrane on inner right side of oral cavity, extends to center of peristomial surface. Cytopharynx lined by few, short fibers.

Occurrence and ecology. Abundant in February 1990 in an infusion of dried mud from an astatic meadow pond. Occurred together with, e.g. *Colpoda magna, Epistylis alpestris* and other ciliates.

Generic position and comparison with related species. Schewiakoff [68] diagnosed *Meseres* as follows (translated from German): "As regards the oral organization, *Meseres* is a typical Oligotricha and is most similar to *Halteria* or *Strombidium*. However, it differs markedly from these genera by its complete somatic ciliature which, although sparse, has not entirely vanished." Our species matches this diagnosis perfectly.

Meseres differs from the genera *Halteria* Dujardin, 1841 and *Pelagohalteria* Foissner et al., 1988 by its much more complete, non-polymerized somatic ciliature. The somatic kineties of *Halteria* are very short and most of the cilia are fused to so-called "bristles" ([21, 29, 30, 75]; Fig. 42, 43). *Pelagohalteria* possesses fused cilia like *Halteria* and an additional horizontal row close below each "bristle complex" [26]. The few cilia to the right of the oral opening in *H. grandinella* (Fig. 43) and *M. corlissi* (Fig. 37) confirm their close relationship.

Meseres cordiformis Schewiakoff and *M. stentor* Schewiakoff differ from *M. corlissi* by having a higher number of somatic kineties (usually 16 or more), shorter somatic cilia, and a pronounced contractility (about 40% of body length [67, 68]).

Another species, *Strombidium oblongum* (syn. *Halteria oblonga* [37]), shares the peculiar somatic ciliature with *M. corlissi* [37, 38]. Although a detailed study of its infraciliature is lacking, the data indicate that it should be transferred to *Meseres*: *M. oblongus* (Kellicott, 1885) n. comb. This species is distinctly smaller (25–45 μm) and has 6–7 somatic kineties with "soft" (flexible) and widely spaced cilia. Trailing cilia, as long as the body, are at its posterior end. Like *M. corlissi*, it is acontractile. *Meseres oblongus* is associated with the algae *Chaetophora* [37, 38, 63].

Mirabdullajev illustrates *Metastrombidium nigrum* as having long somatic kineties (Fig. 5 in [56]). In the description, however, he states that it has "no somatic ciliature." Thus, it cannot be definitely assigned to *Meseres*.

Morphogenesis (Fig. 28–33, 36–41). Numbering of kineties follows [10]. Row one is nearest to the cytostomial region and counting continues clockwise around the cell when ciliate is viewed from posterior.

The oral primordium originates apokinetally slightly below mid-body between the 1st and the 2nd somatic kinety, i.e. in a ventro-lateral position. Very early stages show only a few basal bodies which soon develop to a falciform, posteriorly narrowed anarchic field (Fig. 28). The adoral membranelles begin to differentiate at the anterior end and on the right side of the anlage, respectively (Fig. 29, 36). During this process a short row of single granules develops as an anlage for a somatic kinety between the posterior ends of parental kineties 2 & 3 (Fig. 29). Resorption of the non-ciliated granules starts at the aboral ends of somatic kineties 1 & 2 (Fig. 29). In the next stage, the anterior and ventral membranelles can be distinguished. Right of these,

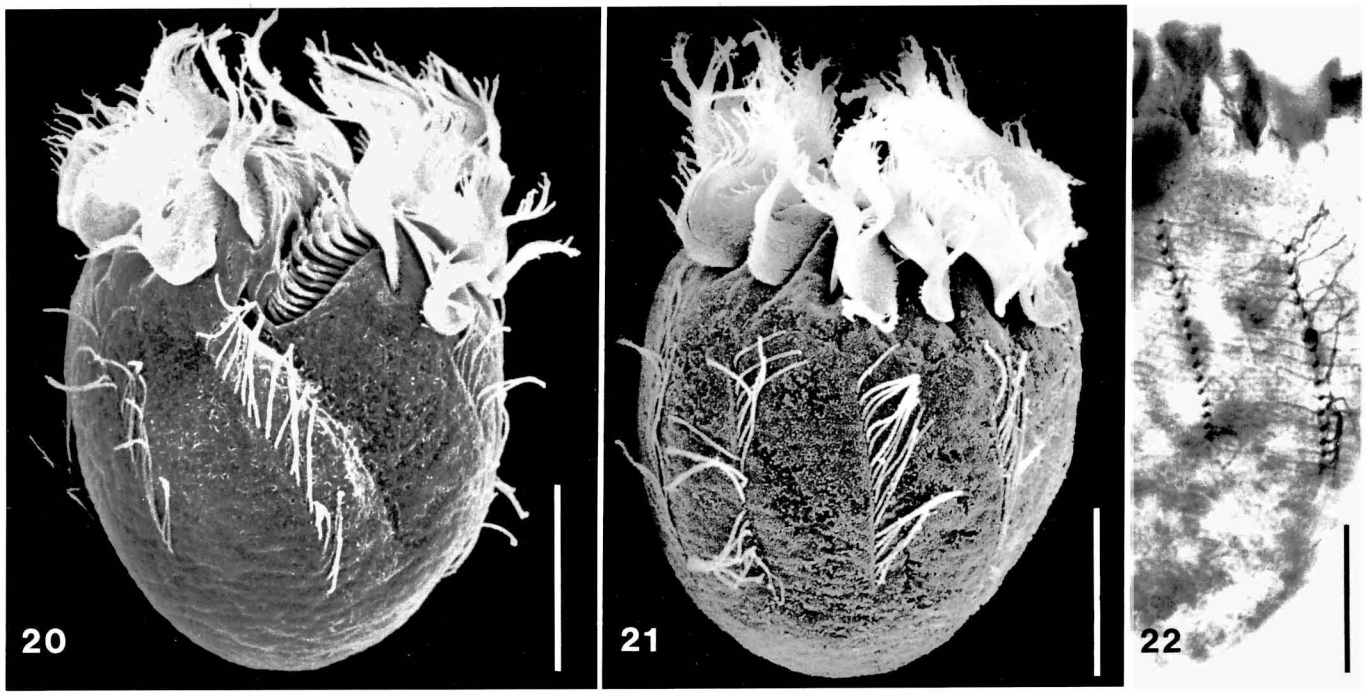


Fig. **20–22**. Morphology of *Meseres corlissi* n. sp. (Fig. 20, 21, scanning micrographs; 22, protargol impregnation). **20**. Ventral view. **21**. Dorsal view. **22**. Lateral fibers extend between two somatic kineties. Bars = 20 μm.

the paroral membrane forms without apparent contact with the adoral membranelles, indicating a likely de novo origin (Fig. 30). The resorption of the non-ciliated basal bodies (granules) is now recognizable in all somatic kineties and proceeds anteriad (Fig. 30). Except between kineties 8 & 1 and 1 & 2, two somatic anlagen originate de novo between each of two parental rows (Fig. 30, 31, 38, 39). Between kineties 8 & 1 only one row of basal bodies is formed which later becomes the opisthe's kinety 1 (Fig. 30). The anlage for the proter's kinety 1 develops left of the anterior end of the parental kinety 1 which is very close to the posterior rim of the oral cavity. Thus, three somatic anlagen are recognizable between kineties 1 & 2 (Fig. 30, 39). Subsequently, the somatic anlagen, which bear already short cilia, elongate and a smaller granule (another kinetosome?) appears very close to each basal body (Fig. 31–33); these granules are sometimes visible in the SEM as very small knobs, as in *H. grandinella* (Fig. 46). The granules from the parental kineties and from the dikinetids near the oral cavity are by now entirely absent, leaving ciliated monokinetids which are apparently resorbed during the very last stages of cytokinesis (Fig. 32, 38, 40). Next, the ventral adoral membranelles of the opisthe rotate clockwise about 90–100° and invaginate; the anterior membranelles spread to enclose the apparently fully differentiated peristomial surface in an incomplete circle (Fig. 32, 33, 40, 41). A very prominent spiral of adoral membranelles is now visible on the posterior ventral side of the cell (Fig. 41). During this rotation, the anlage left of the ventral membranelles moves onto the ventral side and becomes the opisthe's kinety 2 (Fig. 32, 33); the anlage between parental kineties 8 & 1 rotates about 90° and becomes somatic kinety 1 (Fig. 32, 33). The basal bodies near the opisthe's oral cavity develop de novo (Fig. 33). Apparently, the parental oral ciliature (anterior and ventral membranelles, paroral membrane) is not renewed. The micronucleus has divided and the distinctly elongated macronucleus is filled with chromatin filaments (Fig. 33). A macronuclear replication band was only rarely found in early and late divisional stages. Such nuclei occasionally contain one large, elongated nucleolus. We did not find very late dividers.

Halteria grandinella (Müller, 1773) Dujardin, 1841

Morphogenesis (Fig. 44–47). The division of *H. grandinella* is very similar to that of *Meseres*, i.e. the oral primordium forms on the cell surface between somatic kineties 1 & 2 (Fig. 44). The anterior membranelles of the opisthe encircle the new peristomial surface near the parental aboral pole (Fig. 47). Two somatic anlagen each develop de novo between the parental kineties (Fig. 45, 46). This agrees with observations by Szabo [74]. Descriptions stating a division of the parental kineties are thus obviously incorrect [17, 21]. The anlagen consist of elongating cilia adjacent to distinct knobs (Fig. 46). These knobs are possibly short ciliary stubs which are subsequently resorbed because they are not recognizable in interphasic individuals (Fig. 42, 43). The few cilia near the opisthe's oral cavity originate de novo (Fig. 47); those of the proter are possibly reorganized, because the twofold number of kinetids sometimes occurs only in very late dividers (observation from another population).

Strombidiidae Fauré-Fremiet, 1970

Strombidium rehwaldi n. sp.

Diagnosis. In vivo about 40 × 30 μm. Ellipsoid, prominent protuberance on anterior right end. One discontinuous equatorial and one ventral kinety. Ten to 14 anterior and 8–10 ventral adoral membranelles. One anterior and one equatorial girdle of extrusomes.

Type location. River Amper about 2 km downriver from the sewage plant at Geiselbullach, east of Fürstenfeldbruck, Germany, 48° 13′ N, 11° 21′ E.

Type specimens. A holotype and a paratype of *S. rehwaldi* as two slides of protargol impregnated cells have been deposited

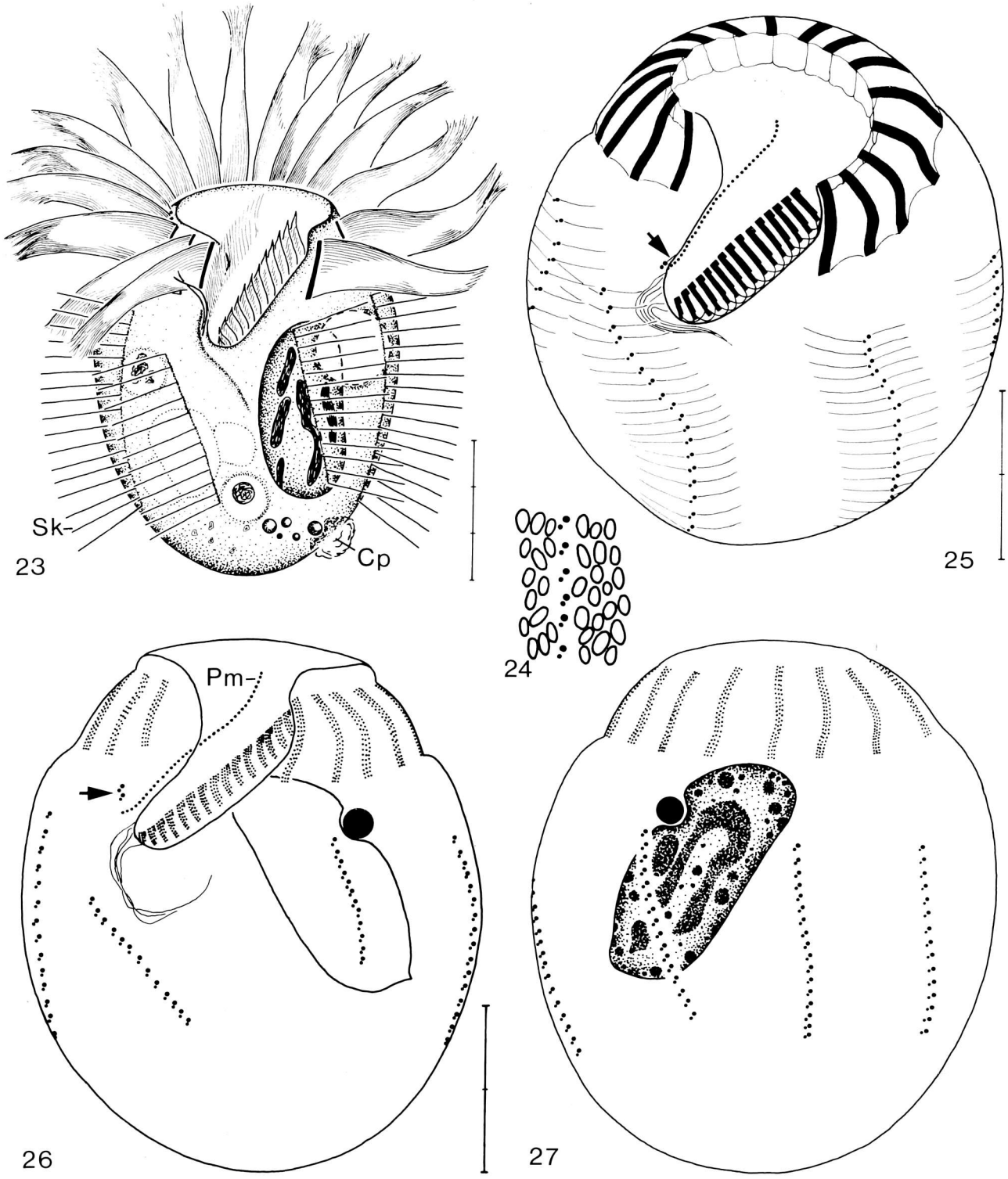


Fig. 23–27. Morphology of *Meseres corlissi* n. sp. (Fig. 23, 24, from life; 25–27, protargol impregnation). **23**. Ventral view of interphasic specimen. **24**. Cortical layer of mitochondria. **25**. Oblique view showing system of oral and somatic fibers. Arrow points to anteriorly extending fiber originating from basal bodies at right margin of oral opening. **26**. Infraciliature of ventral side. Arrow marks dikinetids near oral cavity. **27**. Dorsal view of specimen shown in Fig. 26. Scale bar divisions = 10 μm.

Cp, cytopyge; Pm, paroral membrane; Sk, somatic kinety.

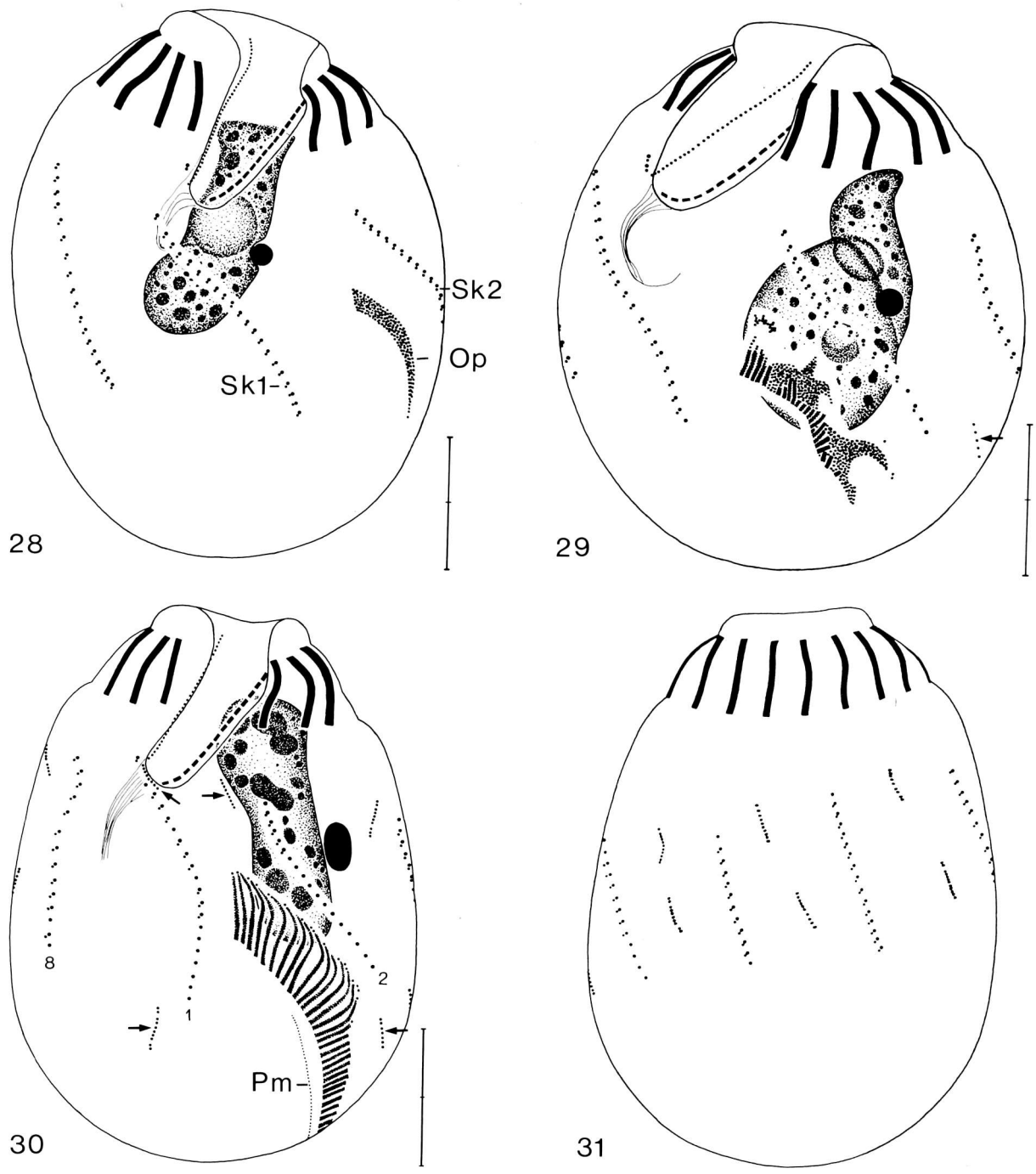


Fig. **28–31**. Morphogenesis of *Meseres corlissi* n. sp. (protargol impregnation). **28**. Very early divider with oral primordium between first and second parental somatic kinety. **29**. Early divider differentiating oral membranelles from anarchic field of basal bodies. Arrow marks somatic anlage. **30**. Ventral view of middle stage showing developing oral and somatic (arrow) anlagen. Numbers denote parental kineties 1, 2 & 8. **31**. Somatic anlagen on dorsal side of specimen shown in Fig. 30. Scale bar divisions = 10 μm.

Op, oral primordium; Pm, paroral membrane; Sk1, Sk2, somatic kineties 1, 2.

in the collection of microscope slides of the Oberösterreichisches Landesmuseum in Linz, Austria. Accession numbers: 5, 6/1991.

Dedication. This new species is dedicated to Dipl.-Ing. H. Rehwald (Wasserwirtschaftsamt München), the co-ordinator of the Amper-Sonderprogramm, in appreciation of his continuous support.

Description (Fig. 48–60; Table 3). Outline broadly oval to elliptical, anterior membranelles on prominent protrusion slanted ventrally and leftwards (Fig. 48, 59). Slightly flattened dorsoventrally. Posterior half of cell broadly rounded, with polygonal, subpellicular platelets (ca. 2–4 μm across; Fig. 48) which are difficult to recognize because of their transparency. Macronucleus ellipsoid, in left half of cell in mid-body (Table 3), contains small and large nucleoli. Micronucleus lenticular, attached to

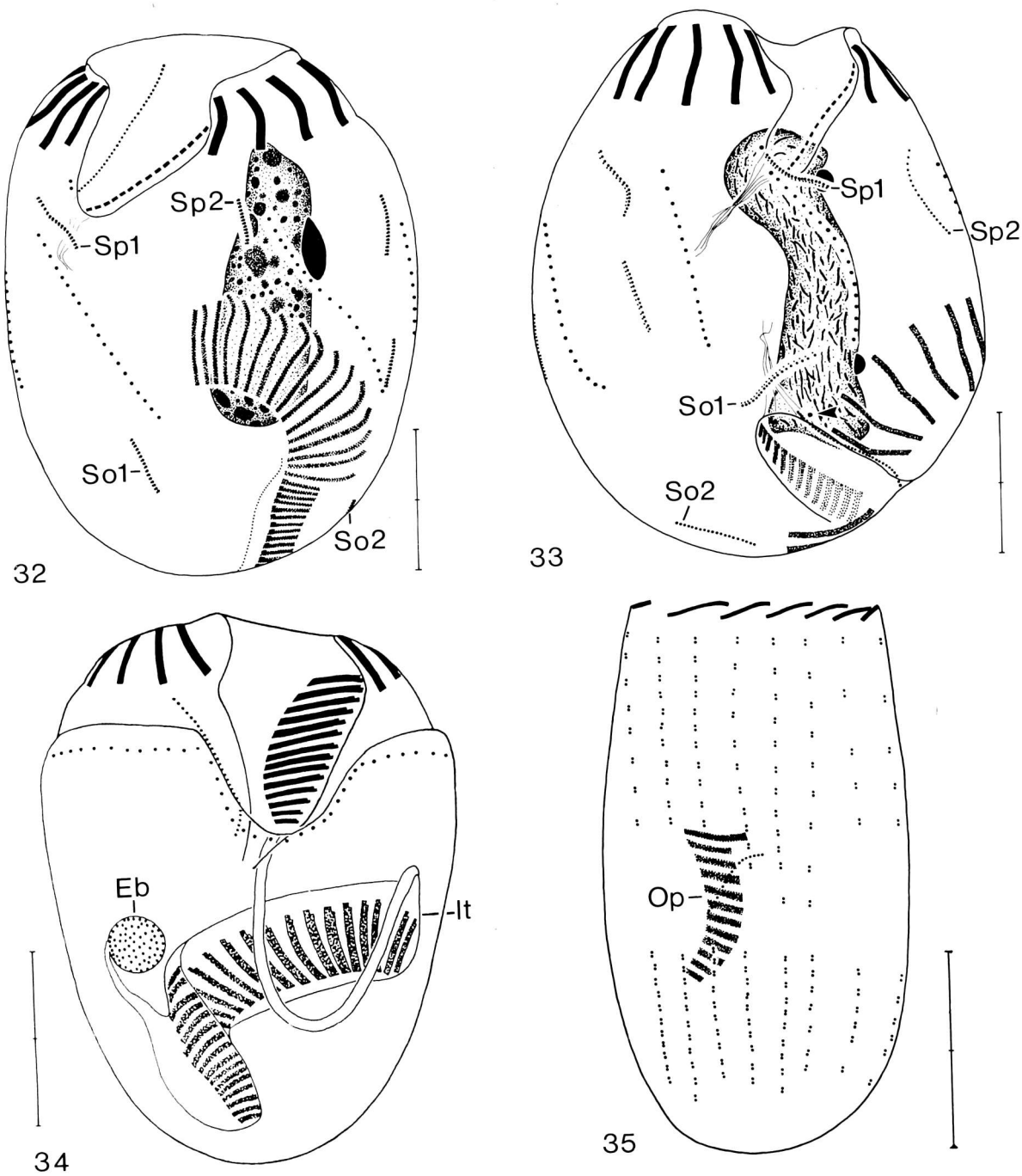


Fig. 32–35. Morphogenesis of some oligotrich ciliates (protargol impregnation). **32**. Ventral view of late divider of *Meseres corlissi* n. sp. Parental somatic kineties consist of single, ciliated granules. **33**. Ventral view of very late divider of *M. corlissi* n. sp. Arrowhead points to new basal body near opisthe's oral cavity. **34**. Ventral view of middle divider (mid-stage of division) of *Pelagostrombidium fallax* showing oral anlage in intracellular tube. **35**. Dorso-lateral view of middle divider of *Tintinnidium pusillum* showing oral anlage in subsurface pouch. Somatic kineties elongate by intrakinetal proliferation and divide. Scale bar divisions = 10 μm.

Eb, embryonic body; It, intracellular tube; Op, oral primordium; So1, So2, anlage of opisthe's somatic kineties 1, 2; Sp1, Sp2, anlage of proter's somatic kineties 1, 2.

macronucleus, usually does not impregnate with protargol (Fig. 48). Contractile vacuole in upper third of cell, left of ventral membranelles. Cytoplasm with few, colourless, greasy shining globules 2–4 μm in size (Fig. 59). Feeds on chrysomonads. Movement not particularly rapid, sometimes slightly jumping.

Extrusomes arranged in two distinct girdles, indistinctly grouped but apparently not in isolated bundles; not very firmly anchored, easily detached and displaced if cells are arrested for observation. Anterior girdle inserts close beneath anterior membranelles, discontinuous at oral cavity (Fig. 48, 58–60). Equatorial girdle inserts at edge of platelet layer (Fig. 58–60). Extrusomes almost parallel to cell surface, in resting state 12–13 ×

Table 2. Morphometric data of *Meseres corlissi*.[a]

Character	$\bar{x}$	SD	CV	Min	Max
Body, length	65.6	10.7	16.3	53	78
Body, width	55.9	4.6	8.2	47	66
Macronucleus, length	33.8	4.6	13.7	24	41
Macronucleus, width	17.7	3.0	17.0	12	23
Micronucleus, diameter	3.5	0.4	11.3	3	4
Length					
Base 1st ant. membranelle	11.8	0.8	6.9	10	13
Base 2nd ant. membranelle	12.2	0.8	6.9	10	14
Base 14th ant. membranelle	13.8	0.8	5.8	12	16
Base 15th ant. membranelle	12.7	1.0	7.6	10	15
Base 16th ant. membranelle	10.7	1.0	8.9	9	13
Number					
Macronuclei	1.0	0.0	0.0	1	1
Anterior membranelles	16.0	0.0	0.0	16	16
Ventral membranelles	14.6	1.7	11.7	10	18
Somatic kineties	8.0	0.0	0.0	8	8
Cilia, somatic kinety 2	18.1	2.0	11.1	12	22
Cilia, somatic kinety 4	16.6	1.1	6.8	15	19
Cilia, somatic kinety 8	15.2	1.5	10.0	12	18

[a] All data are based on the investigation of 30 randomly selected, protargol impregnated and mounted non-dividers. All measurements in μm. Abbreviations as in Table 1.

Table 3. Morphometric data of *Strombidium rehwaldi*.[a]

Character	$\bar{x}$	SD	CV	Min	Max
Body, length	40.6	3.9	9.6	33	46
Body, width	30.2	2.8	9.3	26	36
Macronucleus, length	17.2	2.9	17.1	11	21
Macronucleus, width	10.2	1.8	18.1	8	15
Distance apex to macronucleus	14.4	2.9	19.8	9	19
Distance apex to cytostome	16.4	2.7	16.2	12	21
Number					
Macronuclei	1.0	0.0	0.0	1	1
Anterior membranelles	11.4	1.3	11.0	10	14
Ventral membranelles	9.2	0.6	6.7	8	10
Dikinetids, equatorial kinety	45.1	6.5	14.5	34	64
Dikinetids, ventral kinety	13.6	2.9	21.0	10	18

[a] All data are based on the investigation of 18 randomly selected, protargol impregnated and mounted non-dividers. All measurements in μm. Abbreviations as in Table 1.

0.5 μm, cone-shaped, tapering posteriorly (Fig. 51, 55). Several other shapes, probably partially extruded or developing extrusomes with a distended anterior end, have been observed (Fig. 52, 53, 56). Triggered extrusomes elongate at posterior end to about 35 μm (Fig. 54, 57).

Equatorial and ventral kinety composed of dikinetids, only one basal body of each with a short cilium (ca. 2 μm long; Fig. 49, 50). Equatorial kinety at edge of platelet layer, discontinuous on ventral side, slightly spiralling, right end shifted somewhat posteriad. Ventral kinety in shallow groove, extends from posterior region almost to equatorial kinety whose right end sometimes appears continuous with it (preparation artifact?; Fig. 48, 49); absent (or not stained) in some specimens.

Peristomial field conspicuous, surrounded by anterior adoral membranelles each comprising three equally long basal body rows (about 6 μm) which bear about 20 μm long cilia (Fig. 48, 49). Base of left-most anterior membranelle slightly shortened (ca. 5 μm; Fig. 49). Ventral membranelles continuous with anterior membranelles, invaginated, longest bases about 4 μm, comprising three ciliary rows each, longest cilia about 7 μm; last two (proximal) ventral membranelles perhaps double-rowed. Oral cavity acentric, with paroral membrane along right border. A complex system of fibers lining the cytopharynx originates from the basal bodies of the paroral membrane and the adoral membranelles (Fig. 49).

Occurrence and ecology. *Strombidium rehwaldi* was fairly numerous in the green layer covering the underwater river sediment on March 8, 1989. The coating consisted of *Oscillatoria* and other filamentous bacteria, filamentous green algae, and diatoms. It is, however, doubtful whether this is its preferred habitat. It was probably washed out from a lake about 30 km upstream or from a stabilization pond, and colonized the lentic zone of this slowly running (about 0.2 m/sec), beta- to alpha-mesosaprobic river only by chance. All other known freshwater species of *Strombidium* occur in the pelagial of lakes and ponds. Only exceptionally, e.g. *S. viride,* are they found in small rivers [27].

Comparison with related species. According to the revision by Maeda & Carey [54] there is only one marine strombidiid species, *Strombidium cinctum* Kahl, 1932, which supposedly has two transverse girdles of extrusomes on the dorsal side. However, these are only part of one long extrusome band which extend around the cell in the shape of a number 6 [37]. Several other species have helicoidal extrusome bands [54]. There is some resemblance in size, shape, and extrusomes to *S. fourneleti,* which has, however, two curious thigmotactic membranelles and inhabits marine sand and brackish pools [13].

None of the few freshwater species possesses two extrusome girdles. However, *Pelagostrombidium mirabile* has two to four supraequatorial bundles, which may resemble a girdle, and a posterior group of extrusomes which is not always present [42, 62]. Penard [62] mentions that the extrusomes are very easily displaced if cells are slightly squeezed for observation. This indicates that the additional posterior group could be a displaced anterior bundle. *Pelagostrombidium mirabile* [42, 62] differs distinctly from *S. rehwaldi* by the more clearly separated anterior and ventral membranelles, the more posteriorly located extrusome girdle, the exit canal of the neoformation organelle[3] and the embryonic body[3] both of which could not be observed in *S. rehwaldi.*

Morphogenesis. Only a few stages were found which resemble those known from other strombidiids [17, 41, 63]. They show that the oral primordium originates de novo in a ventral, subsurface position. A paroral membrane forms near the longitudinally aligned, slightly curved adoral anlage. The ventral kinety is resorbed very early (or at least not impregnated), while the equatorial row still persists. A macronuclear replication band is recognizable.

DISCUSSION

Morphogenesis in oligotrich ciliates. The following considerations include unpublished observations on the morphogenesis of *Pelagostrombidium* and *Tintinnidium* (Fig. 34, 35). A more detailed study is in progress.

The main morphogenetic events in halteriids are apparently identical. The oral primordium develops on the cell surface and the entire somatic ciliature originates de novo between the pa-

[3] The neoformation organelle is a permanent, tube-like structure found in several strombidiids; in some species its inner end widens to a large vesicle, the embryonic body [42, 62]. During morphogenesis, at least the oral anlagen originate in this organelle (Fig. 34).

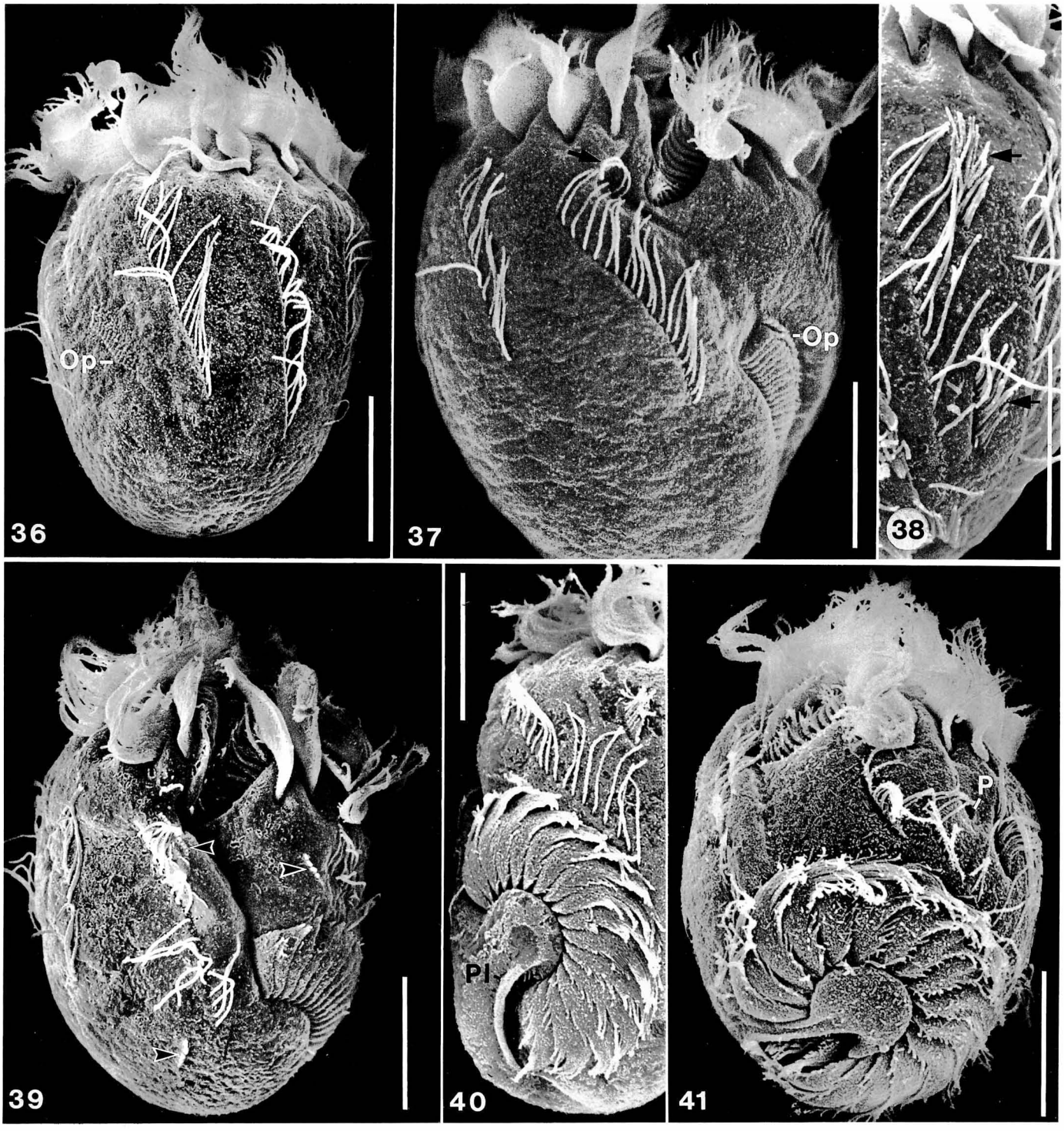


Fig. **36–41**. Morphogenesis of *Meseres corlissi* n. sp. (scanning micrographs). **36**. Early divider with oral primordium on cell surface. **37**. Middle divider. Arrow marks two cilia near oral cavity. **38**. Late divider showing two ciliated somatic anlagen (arrows) between parental kineties. **39**. Intermediate divider with anlagen of somatic kineties (arrowheads). **40**. Ventral view of late divider with invaginating ventral membranelles. **41**. Frontal view of very late divider with fully differentiated adoral zone of membranelles; ventral membranelles have invaginated. Bars = 20 μm.

Op, oral primordium; P, pore of contractile vacuole; Pl, right peristomial lip.

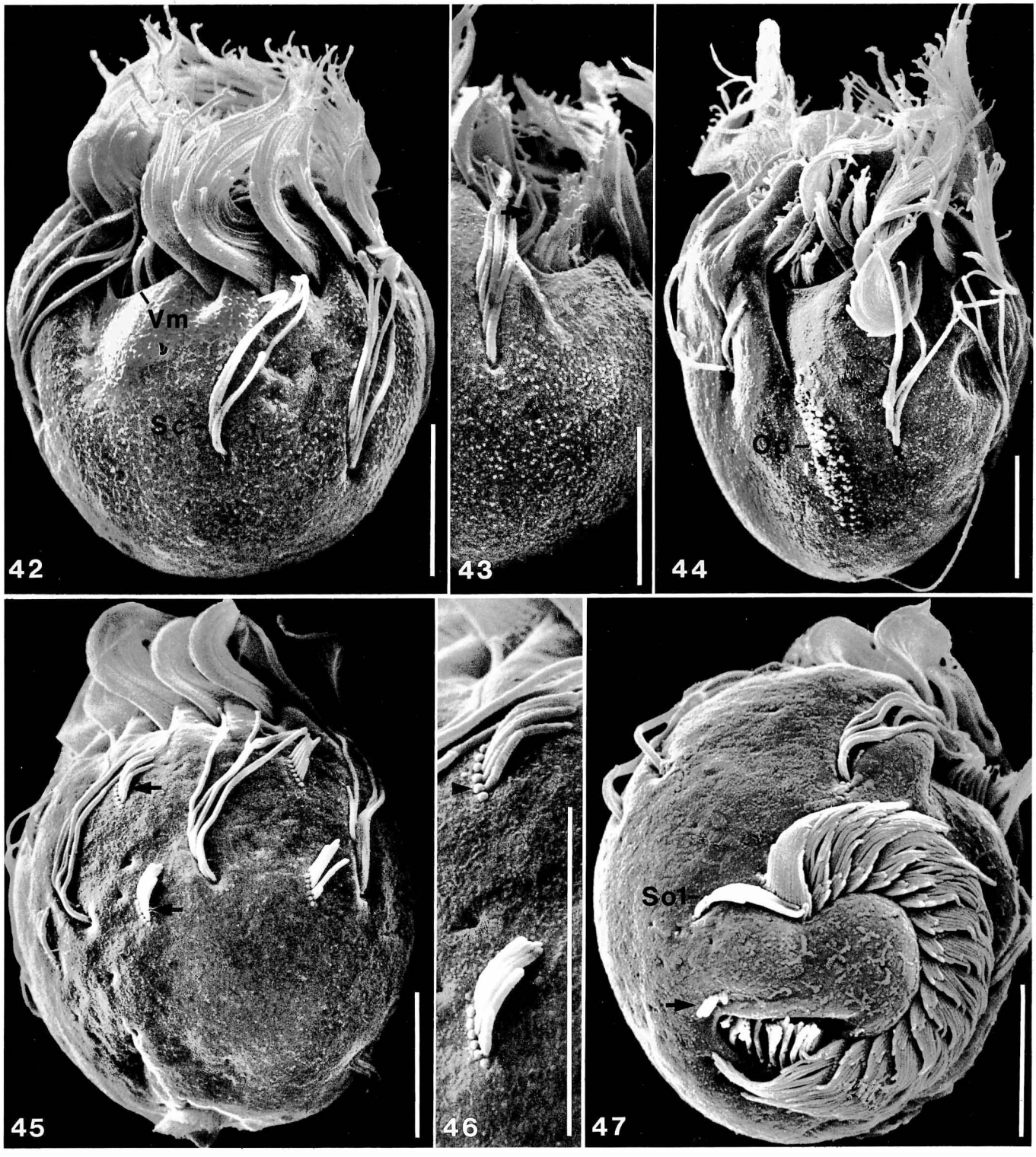


Fig. **42–47**. Morphology and morphogenesis of *Halteria grandinella* (scanning micrographs). **42**. Ventro-lateral view of interphasic specimen showing that last two bristles of each somatic kinety consist of fused cilia; however, bristles sometimes disintegrate due to the preparation procedure. **43**. A very short kinety is found near the oral cavity (arrow). **44**. Ventral view of early divider showing oral primordium. **45**. Dorsal view of middle divider showing anlagen of somatic kineties (arrows). **46**. Somatic anlagen have distinct knobs nearby (arrowhead). **47**. Posterior view of late divider. Arrow marks very short kinety near opisthe's oral cavity. Bars = 10 μm.

Op, oral primordium; Sc, fused somatic cilia ("bristles"); So1, opisthe's somatic kinety 1; Vm, ventral adoral membranelles.

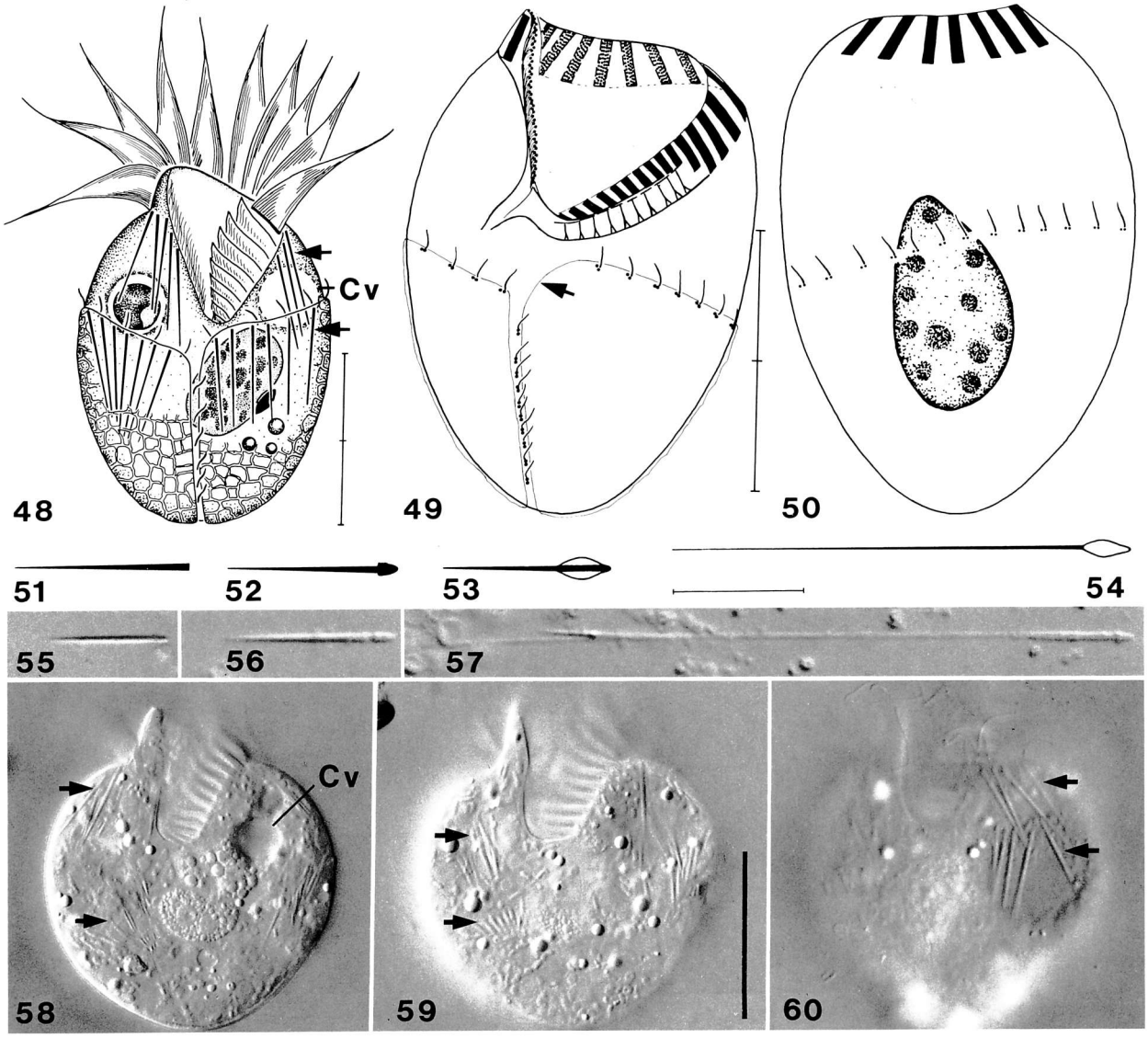


Fig. **48–60**. Morphology of *Strombidium rehwaldi* n. sp. (Fig. 48, 51–54, from life; 49, 50, protargol impregnation; 55–60, interference contrast). **48**. Ventral view of interphasic individual showing species-specific extrusome girdles (arrows). **49**. Infraciliature and somatic cilia of ventral side. Subpellicular platelet layer is outlined (arrow). **50**. Dorsal view of specimen shown in Fig. 49. **51**, **55**. Resting extrusomes. **52**, **53**, **56**. Partially extruded or developing extrusomes. **54**, **57**. Released extrusomes. **58**, **59**. Same specimen at different focus levels showing extrusome girdles (arrows). **60**. Specimen focussed to plane where the two extrusome girdles (arrow) are recognizable. Fig. 48–54, scale bar divisions = 10 μm; 58–60, bar = 20 μm.

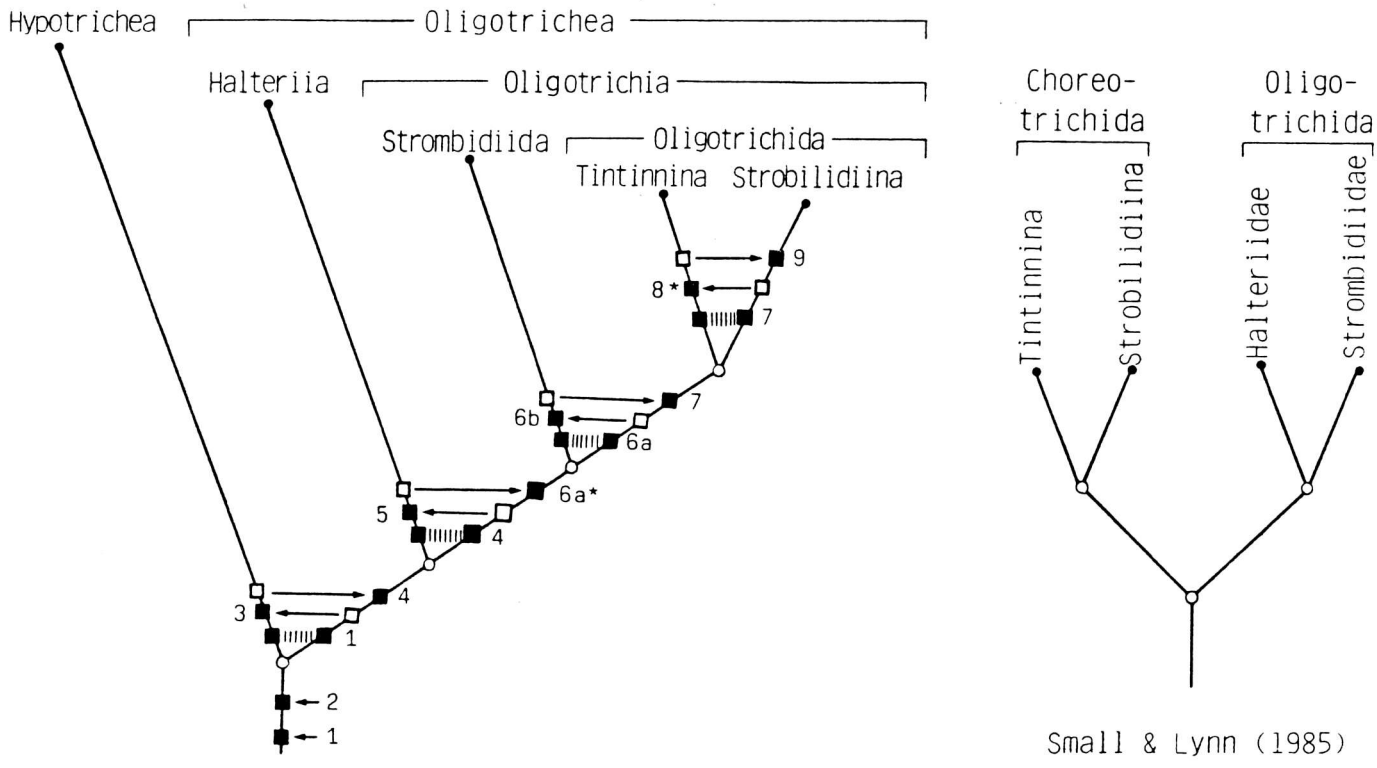
Cv, contractile vacuole.

rental ciliary rows (Fig. 38, 45). The division in strobilidiids and tintinnids is also quite similar. The oral primordium develops in a subsurface pouch and the entire somatic ciliature originates by intrakinetal proliferation of basal bodies. The elongated kineties are simply divided during cytokinesis. The oral anlage of the tintinnids develops more laterally than that of the strobilidiids (Fig. 6, 35).

The strombidiid stomatogenesis is different from those of halteriids, tintinnids and strobilidiids, i.e. the oral anlagen form in a long intracellular sac or tube (Fig. 34) [41, 62]. The equatorial kinety of the opisthe of *P. fallax* is also formed de novo in this tube.

The parental oral ciliature (paroral membrane, adoral membranelles) is not renewed during morphogenesis in the oligotrich taxa investigated so far.

Character states. Only synapomorphies should be used in reconstructing phylogenetic relationships [1, 33]. The plesiomorphic or apomorphic state of a character can be determined by an outgroup comparison, i.e. characters or character states occurring in the outgroup, which should be closely related to the investigated ingroup, are considered to be plesiomorphic [1]. The hypotrichs (euplotids and stichotrichs), which we and others [69] consider as a monophyletic lineage, served as outgroup for our analysis because they share an important synapomorphy with the oligotrichs, viz. the macronuclear replication band [65]. Another, however still doubtful, synapomorphy might be the perilemma, an additional layer covering the plasma membrane, which is found only in some stichotrich hypotrichs and in some oligotrichs [2]. However, too few data are available concerning this enigmatic structure. Lynn & Corliss [48] even



	Character	
	Apomorph ■	Plesiomorph □
1	Macronuclear replication band	Without
2	Perilemma	Without
3	Cirri	Cilia
4	Morphogenesis enantiotropic	Homeotropic
5	Entire somatic ciliature originates de novo on cell surface between parental ciliature	Entire somatic ciliature originates intrakinetal or in subsurface tube[a]
6a*	Oral primordium in subsurface pouch	On cell surface
6b	Oral primordium in intracellular tube	In subsurface pouch
7	Anterior adoral membranelles form a "closed" circle	"Open" circle
8*	Lorica	Without
9	Loss of postciliodesmata	Postciliodesmata

[a] Uncertain in strombidiids, since their morphogenesis has not yet been studied in detail.

* Convergence

Fig. **61**. Phylogenetic relationships of oligotrich ciliates compared with the classification of Small & Lynn [70]. Main character states used to separate taxa in the phylogenetic approach are listed.

suppose that it might be a special fixation artifact of the glycocalyx. Therefore, hypotrichs and oligotrichs are more closely related than, e.g., heterotrichs and oligotrichs [cp. 43, 44, 50]. This is also corroborated by a comparative analysis of the 16S-like rRNA [51].

The oral primordium of halteriids and stichotrich hypotrichs forms on the cell surface. Compared to this ancestral (plesiomorphic) state, the subsurface development of the oral ciliature in the Strombidiida, Strobilidiina, and Tintinnina is an apomorphy. The intracellular sac or tube, which occurs in strombidiids, can be considered as a transformation (second derived state) of the rather shallow subsurface pouch found in strobilidiids and tintinnids. The subsurface pouch of oligotrichs is very likely convergent to that occurring in euplotids [66] because a "subsurface" development of the oral anlagen occurs also in other groups, e.g. entodiniomorphids [9]. This explanation is more parsimonious than to suppose a common ancestor of euplotids and oligotrichs, which would require the assumption of other convergences. For example, the cirri in the euplotids would be either an independent autapomorphy (convergent to sticho-

trichs; with oligotrich cilia plesiomorphic) or the cilia in the oligotrichs would be convergent to that occurring in other, e.g. heterotrich, ciliates (with euplotid cirri plesiomorphic).

The de novo origin of the entire somatic ciliature in the halteriids is regarded as an autapomorphy because at least part of the hypotrich somatic ciliature, e.g. marginal and dorsal rows, originate from parental cilia. The origin of the somatic kineties in strombidiids is still dubious.

The ultrastructure of the adoral membranelles is very similar in oligotrichs and hypotrichs [29, 31, 47]. However, in strobilidiids and tintinnids the external membranelles form a flat spiral around the peristomial surface; this is the derived character state compared to the hypotrichous adoral zone of membranelles which extends as curved ribbon onto the ventral side.

The lorica, which is an apomorphy for the Tintinnina, is obviously convergent to that found in some hypotrichs, e.g. *Stichotricha* [22].

Compared to the hypotrichs and other oligotrichs the loss of postciliodesmata in *Strobilidium* is classified as an autapomorphy. Very probably, this is related to a secondary reduction of somatic dikinetids to monokinetids [31].

Phylogenetic relationships. In a recent classification of the phylum Ciliophora, suprafamilial relationships were mainly based on ultrastructural similarities of the somatic kinetid patterns [70]. The ultrastructure of the oligotrich kinetid is, however, poorly investigated and probably not conservative. Therefore, it cannot contribute substantially to a higher level classification at present [31].

Morphogenesis, on the other hand, has been comparatively well researched and can be applied to elucidate the phylogenetic relationships of oligotrichs using Hennig's method [33]. Some oligotrich genera, e.g. *Strombidinopsis, Laboea, Tontonia,* are excluded because they are insufficiently known. Recent evidence clearly suggests that at least *Strombidinopsis gyrans* is a synonym of *Tintinnidium semiciliatum* [4]. The foundation of the suborder Strombidinopsina and the family Strombidinopsidae by Small & Lynn [70] therefore seems very premature.

The monophyletic origin of the oligotrichs is founded on the following apomorphies: (i) absence of an endoral membrane; (ii) the oral primordium is not involved in the formation of somatic ciliature; (iii) enantiotropic division, i.e. the daughter cells are connected with their aboral parts, whereas hypotrichs and many other ciliates divide homeotropically (homothetogenic fission), viz. the proter's posterior pole is joined with the opisthe's anterior region [17, 41]. This special mode of division is the most important apomorphy as the other two occur also in heterotrichs.

Of the investigated "choreotrich" groups [70], the Halteriidae appear to be the nearest relatives of the hypotrichs (Fig. 61). Besides morphogenetic similarities (oral primordium on cell surface, macronuclear replication band), both groups have some common morphologic features, e.g. four-rowed ventral adoral membranelles and compound somatic ciliary structures, viz. cirri in hypotrichs and "bristles" in *Halteria* (Fig. 42, 43) and *Pelagohalteria* [26]; however, a homology of cirri and bristles has yet to be proved. It may be speculated that the few basal bodies near the oral cavity in *Halteria* and *Meseres* could be a strongly reduced endoral membrane (Fig. 37, 43).

Small & Lynn [70] assume in their classification that Halteriidae and Strombidiidae are adelphotaxa (Fig. 61). The phylogenetic approach, however, shows that strombidiids are more closely related to tintinnids and strobilidiids (Fig. 61). Thus, the new order Choreotrichida [70] is superfluous, since the taxa in question can be well included in the time-honoured Oligotrichida [5]. Consequently, the same of the subclass, Choreotrichia, can be replaced by a simple rank elevation of the order, i.e. Oligotrichia, as proposed earlier [64]. According to our system, the Oligotrichia are the adelphotaxon of the Halteriia which are therefore elevated to subclass, too (Fig. 61).

Table 4. A revised classification for oligotrich ciliates.

Class Oligotrichea Bütschli, 1887
Subclass I. Halteriia n. subcl.
Order Halteriida n. ord.
Subclass II. Oligotrichia Bütschli, 1887
Order Strombidiida Jankowski, 1980[a]
Order Oligotrichida Bütschli, 1887
Suborder Tintinnina Kofoid & Campbell, 1929[b]
Suborder Strobilidiina Jankowski, 1980[c]

[a] Previously mentioned, but not diagnosed [Jankowski, A. W. 1975. *In:* Balashov, U. S. (ed.), Account of Scientific Sessions on Results of Scientific Work, Year 1974: Abstracts of Reports, pp. 26–27].
[b] Established by Jankowski [36] as new suborder, too.
[c] Established by Small & Lynn [70] as new suborder, too.

Our scheme shows that either most taxa must be raised by one rank or that the many tintinnid families have to be lumped into a single family or superfamily (Fig. 61). We suggest raising the taxa because 1) the tintinnids and the hypotrichs are very voluminous groups, and 2) the hypotrichs achieve class rank, which is indicated by the considerable divergence of stichotrichids and euplotids. Our classification corroborates the close relationship of tintinnids and strobilidiids [9, 31, 44]. Grim [31], however, suggests separating strobilidiids and tintinnids at the ordinal level; this would demand a further rank elevation of all taxa. The system resulting from our phylogenetic approach is summarized in Table 4. Since a sister group relationship between oligotrichs and hypotrichs has not yet been conclusively proven, we leave the monophyletic taxon shown in Fig. 61 unranked.

DIAGNOSES OF THE NEW HIGHER TAXA

Class Oligotrichea Bütschli, 1887. Body typically small, ovoid to elongate. Perilemma present in some (all?) species. Somatic ciliature commonly reduced, rarely absent. Adoral zone of membranelles conspicuous, forms flat spiral on peristomial surface ("closed" circle in top view; Strobilidiina, Tintinnina) or extends as curved ribbon onto ventral side ("open" circle; Halteriia, Strombidiida); paroral membrane monostichomonad; no endoral membrane. Morphogenesis enantiotropic; stomatogenesis apokinetal on or below cell surface; somatic ciliature originates de novo (Halteriia) or by intrakinetal proliferation (Strobilidiina, Tintinnina; uncertain in Strombidiida); macronucleus with one or two replication bands. Mainly planktonic in marine and freshwater habitats.

Subclass Halteriia n. subcl. Body small, ovoid. Adoral zone of membranelles extends as curved ribbon onto ventral side. Oral primordium develops on cell surface; entire somatic ciliature originates de novo. Predominantly freshwater species, some also edaphic.

Order Halteriida n. ord. With characteristics of the subclass. For diagnoses of other oligotrichs see [6, 7, 9, 36, 40, 49, 64, 70].

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