536

Arch. Protistenkd. **135** (1988): 213–235
VEB Gustav Fischer Verlag Jena

Institut für Zoologie und Institut für Pflanzenphysiologie der Universität Salzburg, Austria

The Fine Structure of *Fuscheria terricola* BERGER et al., 1983 and a Proposed New Classification of the Subclass Haptoria CORLISS, 1974 (Ciliophora, Litostomatea)[1]

By WILHELM FOISSNER and ILSE FOISSNER

With 31 Figures

Key words: Ciliophora; Haptoria; *Fuscheria terricola;* Ultrastructure; Classification; Phylogeny; Toxicysts

Summary

The general fine structure of *Fuscheria terricola* BERGER, FOISSNER and ADAM, 1983 is very similar to that of other haptorid ciliates. However, a tela corticalis and parasomal sacs are absent. *Fuscheria terricola* has doughnut-shaped mucocysts and unique nail-shaped toxicysts. Their nail-like appearance is due to a conspicuous posterior thickening of a fibro-granular material surrounding the rod-shaped center which is very similar to the pexicysts of *Acropisthium* and *Didinium*. The somatic kinetids are monokinetids with the classical haptorian fibrillar associates. In addition, the upper 4 to 7 somatic kinetids in each kinety possess nematodesmal bundles. At the base of the oral cone there is a circumoral kinety composed of typical haptorian dikinetids. Their nematodesmal bundles and those from the upper somatic kinetids form a highly characteristic irregular rhabdos. *Acropisthium* and *Actinorhabdos* show the same oral organization as *Fuscheria*. Hence, these 3 genera are united in the new family Acropisthiidae nov. fam.

The rhabdos of most members of the subclass Haptoria is built up of 3 microtubular components: a) the transverse microtubular ribbons which originate from the nonciliated kinetosomes of oral dikinetids or from ciliated or nonciliated oralized somatic kinetids and turn to the center of the oral bulge, where they plunge inwards to support the cytopharynx; b) the nematodesmal bundles which form an "outer rhabdos"; and c) the vertically oriented bulge microtubules which are distributed rather regularly in the marginal area of the oral bulge and grouped in nematodesmata-like bundles in the lower oral region, where they form a more or less pronounced "inner rhabdos". Exceptions from this pattern are the Cyclotrichina which lack nematodesmata and the Archistomatida which lack bulge microtubules, probably because of the absence of toxicysts.

The term "oralized somatic kinetids" is suggested for such kinetids which lie within somatic kineties, but bear nematodesmal bundles contributing to the rhabdos. Such kinetids may be monokinetids or dikinetids; they may or may not be associated with normal haptorid oral dikinetids; and they may be ciliated or nonciliated. The different kinds of kinetids which contribute to the rhabdos and the dorsal brush (presence/absence) are the clue characters for a revised classification of the Haptoria. The following new higher taxa are erected: Enchelyina nov. subord. (with nonciliated oralized somatic monokinetids), Acropisthiina nov. subord. (with oral dikinetids and ciliated oralized somatic monokinetids), Spathidiida nov. ord. (with oral dikinetids only), Litonotina nov. subord. (right oral kinety associated with somatic monokinetids), Pseudoholophryida nov. ord. and Pseudoholophryina nov. subord. (dorsal brush absent or highly aberrant), Helicoprorodontina nov. subord. (oralized somatic dikinetids, dorsal brush probably absent).

1. Introduction

During the last decades a bulk of light and electron microscopical evidence has accumulated showing that the "primitive" rhabdophorine ciliates are much more differentiated than earlier workers supposed. The first effort to classify this diversity was undertaken by CORLISS (1974, 1979), who erected the new order Haptorida for ciliates with a terminally located cytostome and

---

[1] The photographical assistance of Mrs. KARIN BERNATZKY is greatly acknowledged. This study was supported by the "Fonds zur Förderung der wissenschaftlichen Forschung, Projekt Nr. P 5889".

toxicysts. This characterization, which is still of use, was improved by Jankowski (1980); Foissner (1984 a), and especially Small and Lynn (1981, 1985), who added important characters on the fine structure of the somatic and oral kinetids and ranked the Haptorida as separate subclass in the class Litostomatea. However, taxonomy at ordinal, familial, and genus level is still poor because only a few out of nearly 100 genera, which are included in the Haptoria at present, have been investigated in greater detail. We have studied many haptorian genera during the last few years (e.g. Foissner 1983 a, 1984 a, b, 1987; Foissner and Foissner 1985) and found that the diversity within the group is still immense. This is fully confirmed by the present study on *F. terricola* which exhibits a new way of building the rhabdos. Thus, time is ripe for a revised classification of the Haptoria. We hope that the thoughts and evidence presented here will stimulate discussion and render with time a more natural classification of this fascinating group of predominantly free-living, rapacious carnivores.

2. Material and Methods

Fuscheria terricola Berger et al., 1983 occurred in the same soil sample as *Enchelydium polynucleatum*. Thus, "material and methods" are the same as described in Foissner and Foissner (1985).

3. Results

3.1. General organization

A detailed description of *F. terricola* has been published by Berger et al. (1983) and Foissner (1984 a). Therefore, we repeat only the most important light microscopical characters and refer to Figs. 1–3.

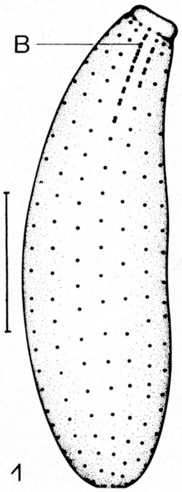
Fuscheria terricola is a cylindrical to bottle-shaped soil ciliate which is slightly curved anteriorly. Its length amounts up to 100 µm, the diameter is about 27 µm. The macronucleus is mostly horseshoe-shaped, the micronucleus spherical. The contractile vacuole is terminally situated. The oral area contains many genus-specific nail-shaped toxicysts.

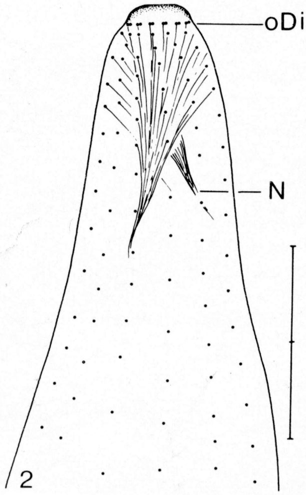
There are about 15 bipolar somatic kineties. Two of these bear anteriorly the brush which is composed of paired kinetosomes. At the base of the oral cone there is a circumoral kinety composed of dikinetids (Foissner 1984 a).

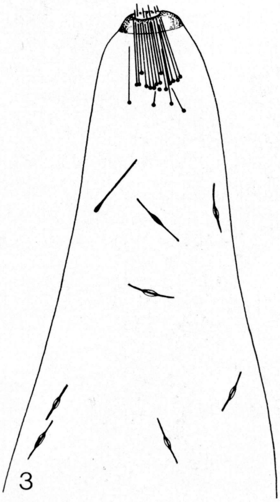
3.2. Somatic cortex and somatic kinetids

The ciliate is bounded by a plasmalemma which is underlined by alveoli that are often lens-like (Figs. 8, 13 b). A tela corticalis seems to be absent except for the filamentous annulus in the oral region (see below). However, more posteriorly the cortex can be well distinguished from the endoplasm because of 2 cisternae of rough endoplasmic reticulum which are located beneath and between the kinetosomes, extrusomes and microtubular ribbons (Fig. 8).

The somatic kinetids are composed of a single kinetosome and its fibrillar associates and are thus monokinetids (Lynn 1981). There are, however, 2 types of somatic monokinetids, namely ones with and others without nematodesmal bundles. The monokinetids with the nematodesmal bundles are restricted to the anterior 4 to 7 kinetosomes of each kinety (Figs. 2, 4, 5). These monokinetids are ciliated and show the same common set of fibrillar associates as those without nematodesmata (Figs. 4–6, 13–15): a) a kinetodesmal fibril which originates near triplets 6 and 7 and extends laterally and to the right at an angle of about 70° to the longitudinal axis; b) a postciliary ribbon of about 6 microtubules which originates in dense material at triplet 9 and extends posteriorly and to the right to course beneath the cortical alveoli (Figs. 8, 13 b) where, in the interkinetal ridge, it becomes associated with the postciliary ribbons of more anterior kinetids; c) a primary transverse ribbon of about 6 microtubules which originates near triplets 2, 3 and 4 and extends to the left







Figs. 1−29. *Fuscheria terricola.* 1−3: Protargol stained specimens. 4−29: TEM-micrographs.

Fig. 1. Infraciliature of the dorsal side. B = dorsal brush. Bar = 15 μm. From Berger et al. (1983).

Fig. 2. Infraciliature in the anterior region of the ventral side at higher magnification. N = nematodesmal bundle, oDi = oral dikinetids. Bar = 15 μm. From Foissner (1984a).

Fig. 3. Same individual as in Fig. 2 showing the nail-shaped toxicysts. Bar = 15 μm. From Foissner (1984a).

anteriorly (but not over the oral cone) into the interkinetal ridges; d) a secondary transverse ribbon of about 3 microtubules which originates near triplet 5 and curves to extend to the lateral left into the interkinetal ridge; and e) a group of about 4 loosely associated microtubules which originate at the left side of the kinetosome and extend anteriorly to the next kinetid. These microtubules are also present in the nematodesmata bearing kinetids (Fig. 13a).

The nematodesmata of the anterior somatic kinetids originate from the same electron-dense material as the transverse ribbons (Figs. 4, 5, 14). They are displaced from their kinetid by half a kinetosome. The angle between kinetosome and nematodesmal bundle is about 40°. The same inclination of all nematodesmata in relation to the longitudinal axis of the cell is therefore achieved by the inclination of the anterior kinetosome of the oral dikinetid relative to the posterior kinetosome or the inclination of the nematodesmal bundle itself in relation to the kinetosome of the anterior somatic monokinetid respectively.

3.3. Dorsal brush

The kinetosomes of the brush are mostly paired and connected by desmoses. Triplets have been observed occasionally (Figs. 1, 16−18). A zig-zag pattern as e.g. in *Enchelydium* (Foissner and Foissner 1985) is not found. Both kinetosomes bear short cilia with a slender membrane. The anterior kinetosome lacks all fibrillar associates. The posterior one is equipped with a kinetodesmal fibril and a postciliary ribbon, 2 transverse ribbons (4 and 3 microtubules respectively) and a nematodesmal bundle that is inclined to the longitudinal axis of the kinetosome by about 40°. Vesicles encircle the kinetosomes (Fig. 17, arrows).

Parasomal sacs could not be identified unequivocally, neither in the brush nor in other kinetids.

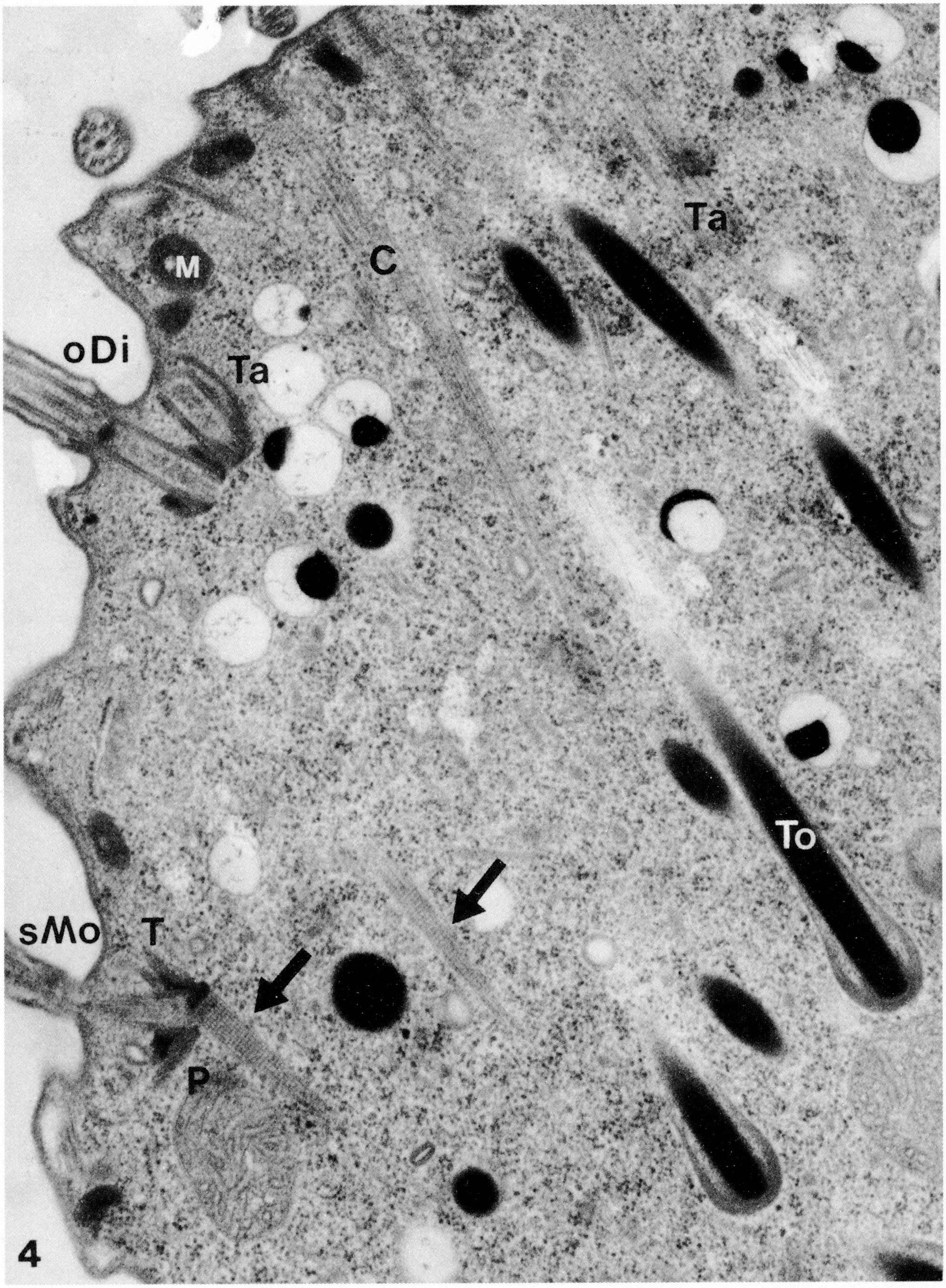


Fig. 4. Longitudinal section through the center of the oral area. Nematodesmal bundles (arrows) originate from the nonciliated kinetosomes of the oral dikinetids (oDi) and the anterior oralized somatic monokinetids (sMo). Transverse ribbons (Ta) of the anterior kinetosomes of the oral dikinetids and cone microtubules (C) support the cytopharynx which is filled with long toxicysts (To). M = mucocyst, P = postciliary ribbon of an oralized somatic kinetid, T = transverse ribbon of an oralized somatic kinetid. ×24,000.

3.4. Oral cortex and oral kinetids

The oral region of *F. terricola* is a sharply truncated cone at the extreme anterior end of the cell (Figs. 1–5). Its posterior limit is defined by a ring of oral kinetids which are composed of 2 kinetosomes and their fibrillar associates and are thus termed dikinetids (LYNN 1981). The oral dikinetids are associated with a ring of filamentous material, the filamentous annulus, which reaches the first monokinetid of the somatic kineties. This annulus is perforated by cone microtubules and has small projections which accompany the transverse ribbons of the anterior kinetosomes of the oral dikinetids for a short distance (Fig. 7). The 2 kinetosomes of the oral kinetids, one slightly anterior and one slightly posterior, are inclined to each other and are linked by 2 filamentous desmoses (Figs. 4, 9, 10, 11). The posterior kinetosome of each dikinetid is ciliated,

---

Fig. 5. Longitudinal section through the peripheral oral area showing nematodesmata (arrows) of the nonciliated kinetosome of the oral dikinetid (oDi) and of oralized somatic monokinetids (sMo). Cone microtubules (C) are oriented perpendicularly to the anterior transverse ribbons (Ta). M = mucocyst, P = postciliary ribbon of an oralized somatic kinetid, T = transverse ribbon of an oralized somatic kinetid. ×40,000.

Fig. 6. Cross-section through posterior somatic monokinetids. An additional nonciliated kinetosome (nK) devoid of any fibrillar associates is found occasionally. K = kinetodesmal fibril, P = postciliary ribbon, T1 = primary transverse ribbon, T2 = secondary transverse ribbon. ×100,000.

Fig. 7. Cross-section through the oral cone. The oral dikinetids are connected by a fibrillar annulus (F). The center (Ce) of the oral cone is slightly indented. C = cone microtubules, Ta = transverse ribbon of the anterior kinetosome of an oral dikinetid, To = toxicysts, Tp = transverse ribbon of the posterior kinetosome of an oral dikinetid. ×26,000.

Fig. 8. Cross-section through the cortical region showing the pellicle, alveoli (A), postciliary microtubules (P), and a mucocyst (M). ×58,000.

Fig. 9. Cross-section through the oral region at a slightly deeper level than Fig. 7. Transverse ribbons of the anterior (Ta) and posterior (Tp) kinetosomes of the oral dikinetids, nematodesmal bundles (arrows) and loose bundles of cone microtubules (C), which form a distinct "inner rhabdos", support the cytopharynx which is filled with toxicysts (To) and vesicles (V). M = mucocyst. ×36,000.

Fig. 10. Enlarged detail of Fig. 9. Cross-sectioned oral dikinetid with anterior (Ta) and posterior (Tp) transverse ribbon. nK = nonciliated kinetosome. ×82,000.

Fig. 11. Enlarged detail of Fig. 9. Cross-section through the anterior nonciliated kinetosome (nK) of an oral dikinetid with transverse (Ta) ribbon, postciliary microtubules (arrow-head), and a nematodesmal bundle (arrow). The posterior kinetosome is tangentially sectioned and shows the postciliary ribbon (P). M = mucocyst. ×82,000.

Fig. 12. Section near the posterior end showing food vacuoles (fV) and the contractile vacuole (cV) with its surrounding tubular network. ×11,000.

Fig. 13a. Anterior oralized somatic monokinetid with nematodesmal bundle (N) and subkinetal microtubules (lines). ×42,000.

Fig. 13b. Organization of the somatic cortex. A = pellicular alveoli, K = kinetodesmal fibril, M = mucocysts. ×50,000.

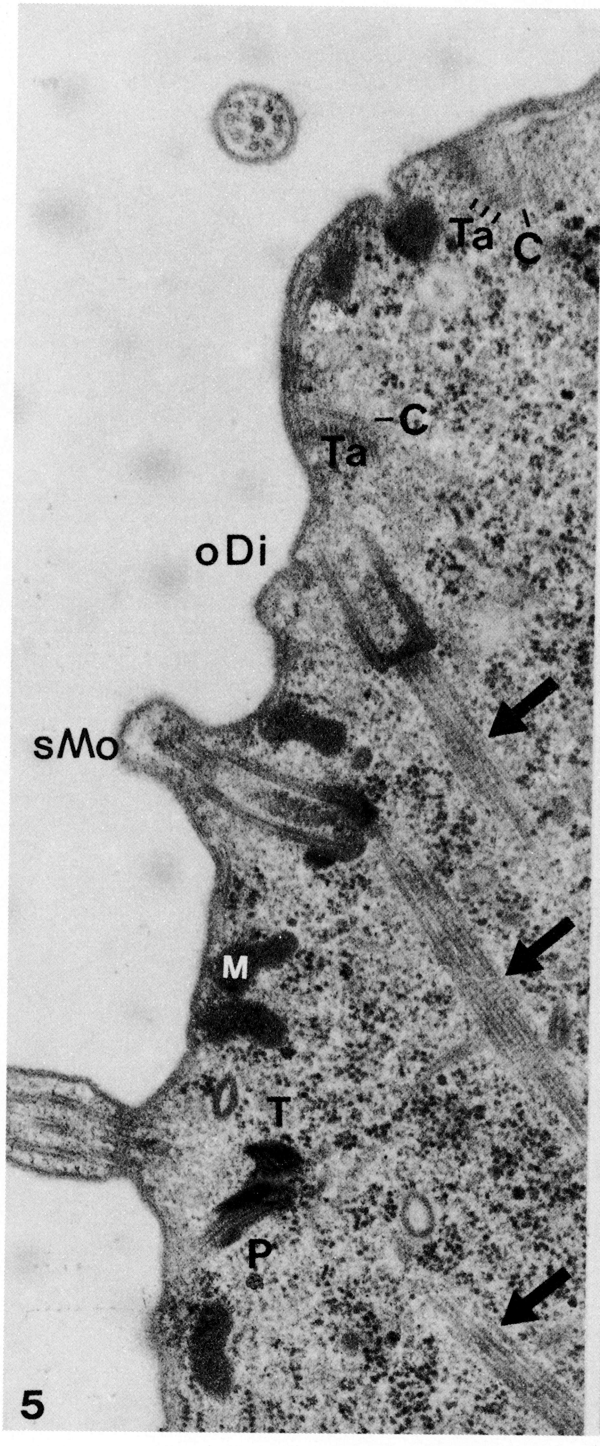
Fig. 14. Transverse microtubules (T) and a nematodesmal bundle (N) of an anterior oralized somatic monokinetid. ×56,000.

Fig. 15. Cross-section through a posterior somatic monokinetid. K = kinetodesmal fibril, P = postciliary ribbon, T1 = primary transverse ribbon, T2 = secondary transverse ribbon. ×65,000.

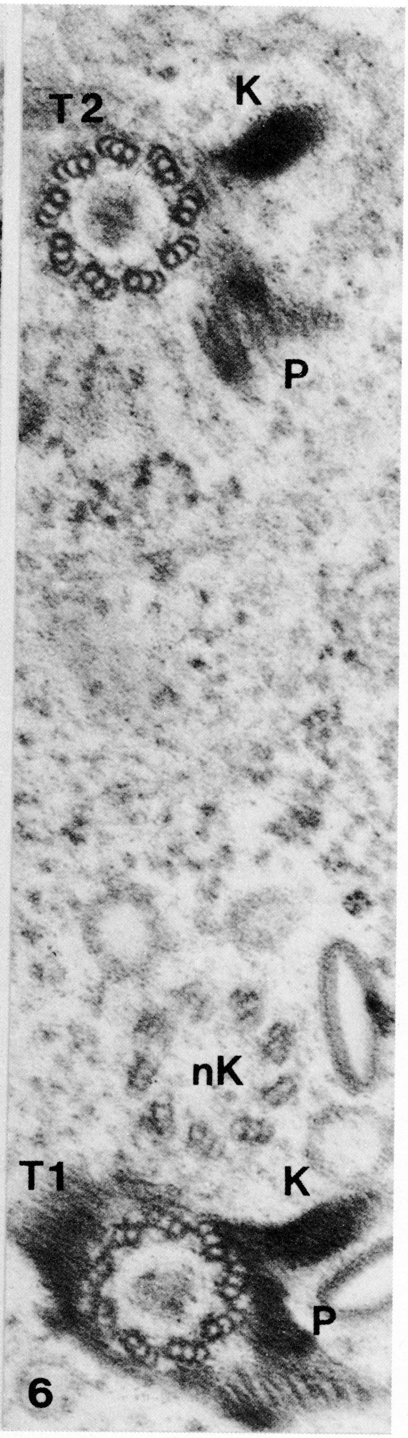
Fig. 16. Longitudinal section through the paired kinetosomes of the dorsal brush. Nematodesmal bundles (arrow) originate at the posterior kinetosome. T1 = primary transverse ribbon of the posterior kinetosome. ×35,000.

Fig. 17. Slightly tangentially sectioned dorsal brush. Kinetosome pairs or triplets are joined by electron dense desmoses (D). Vesicles surround the kinetosomes (arrows). Transverse ribbons (T1, T2) are found only at the posterior kinetosome. ×42,000.

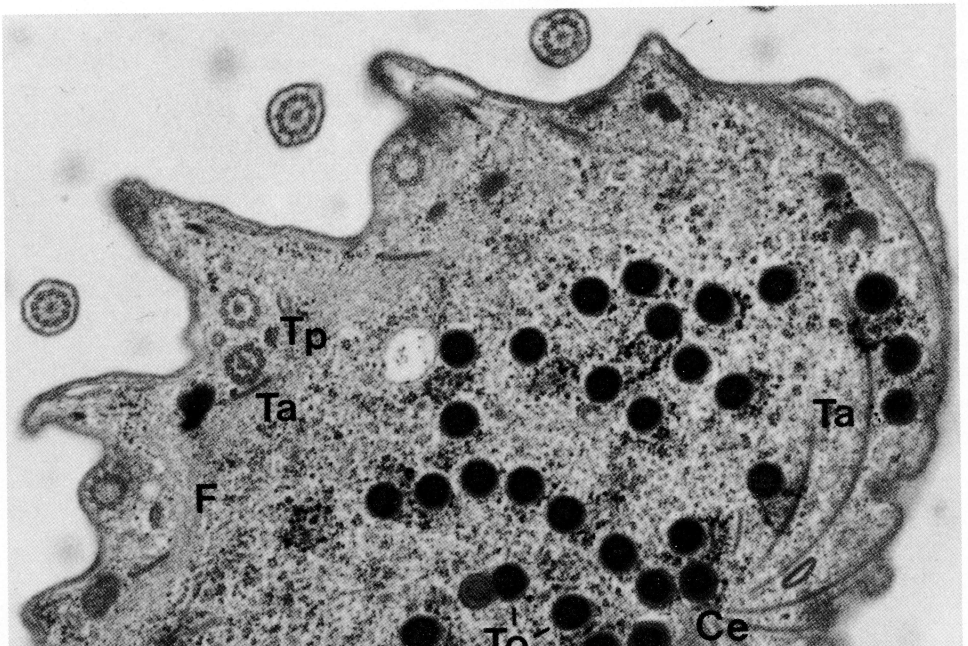
Fig. 18. Tangential section through the brush showing transverse ribbons (T1, T2), kinetodesmal fibril (K), postciliary ribbon (P), and nematodesmal bundle (arrow) of the posterior kinetosome. ×51,000.



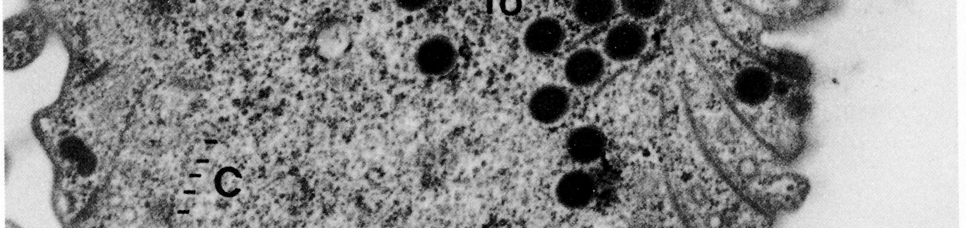
5



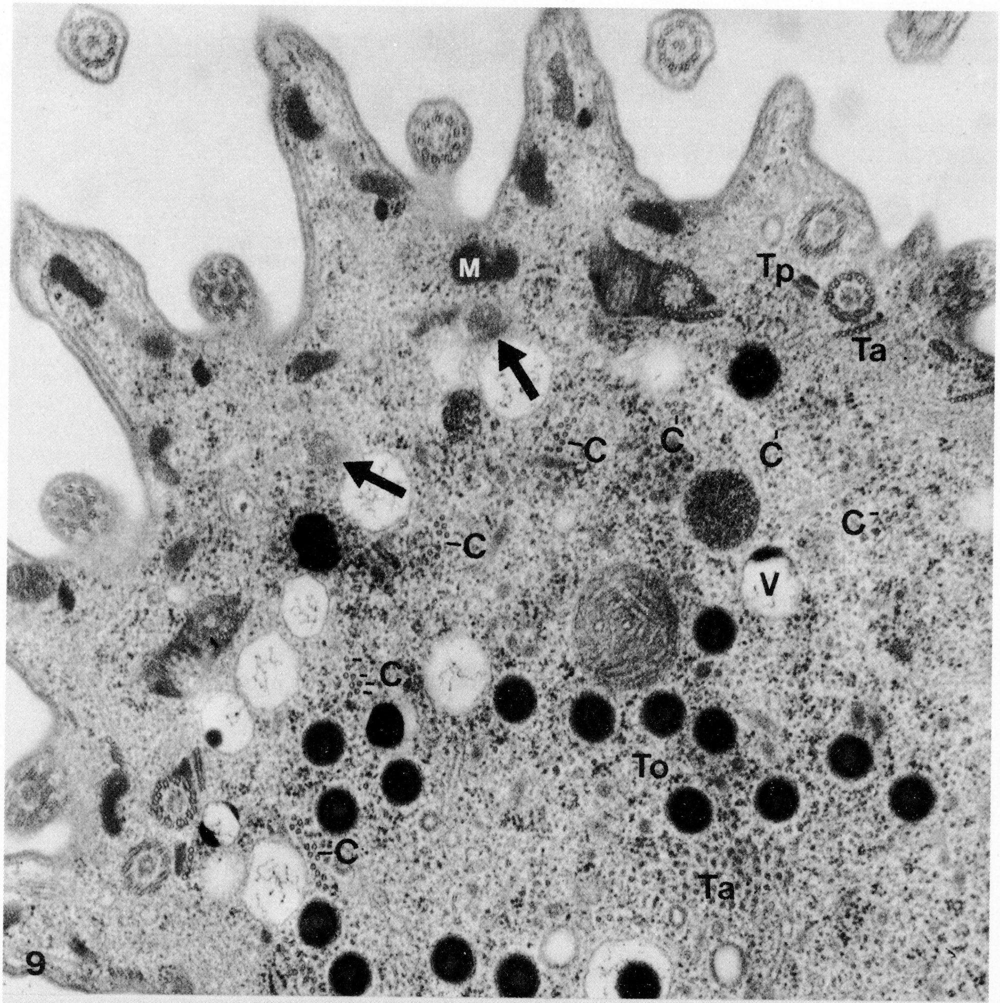
6



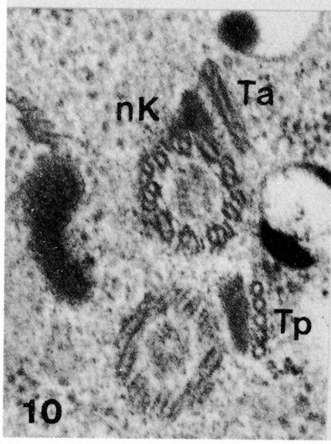
7



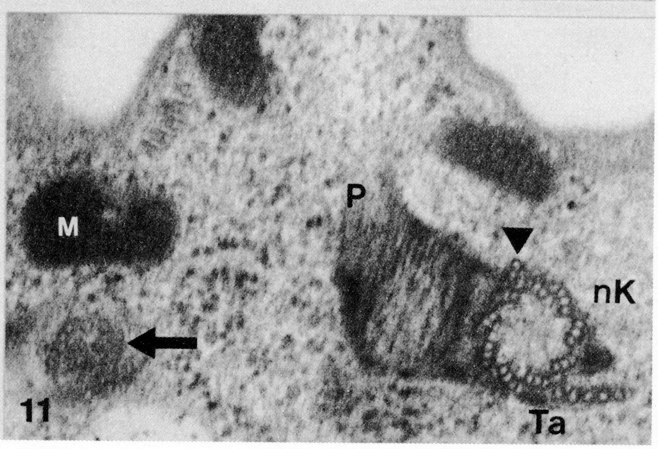
8



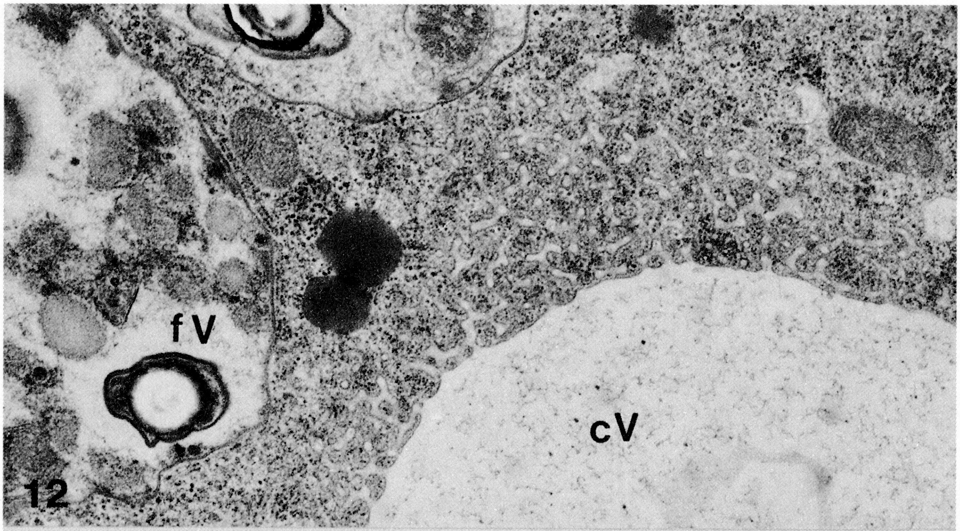
9

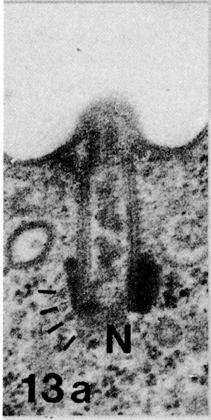


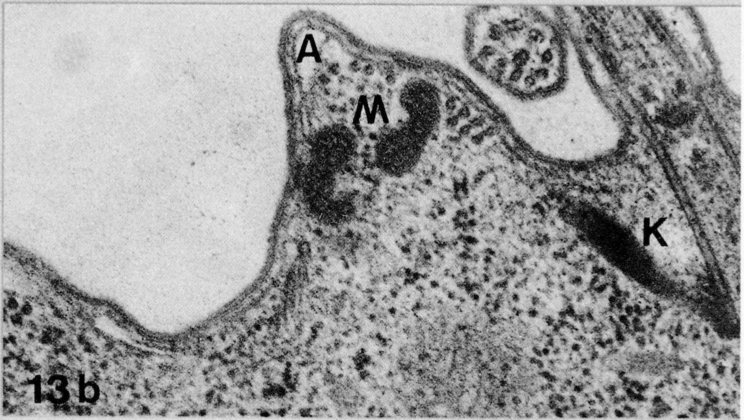
10

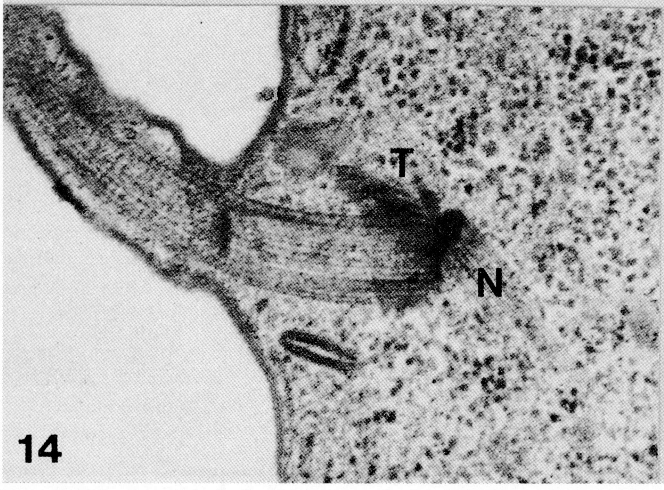


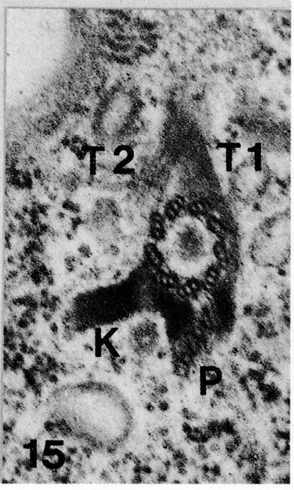
11


fV
cV
12

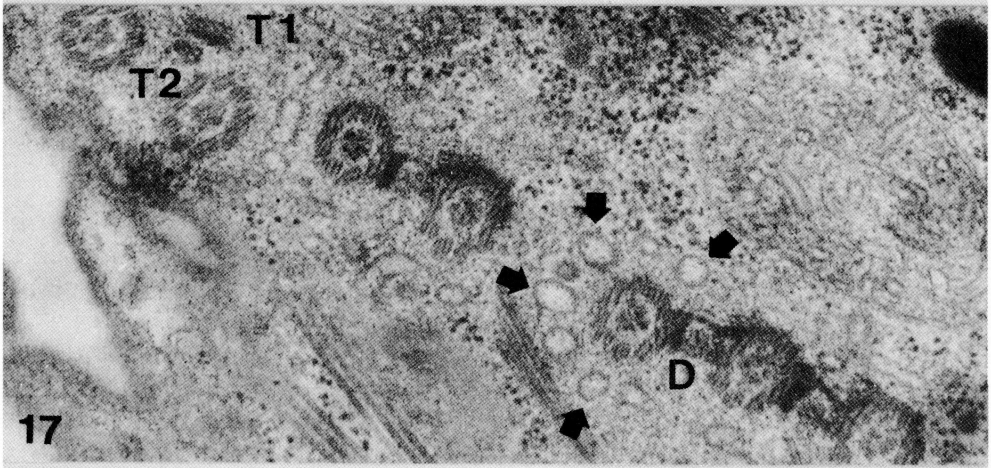

N
13a

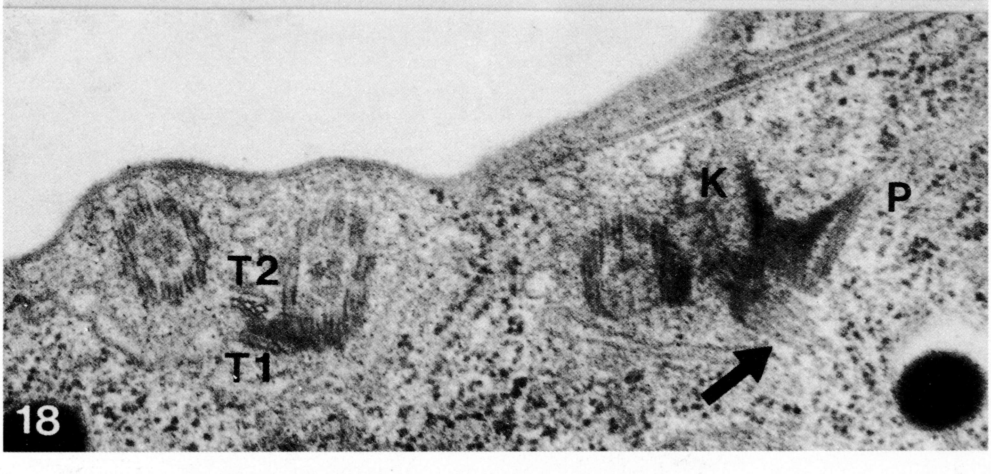

A
M
K
13b


T
N
14


T2
T1
K
P
15


16
T1


T1
T2
D
17


K
P
T2
T1
18

the anterior kinetosome is nude, but bears a hexagonally packed nematodesmal bundle composed of 9–18 microtubules. The bundle originates from a dense layer at the basis of the kinetosome and runs parallel to its longitudinal axis. Electron-dense lines in the upper part of the bundle as in *Enchelydium* (FOISSNER and FOISSNER 1985) are not visible (Figs. 4, 5, 9). There are no kinetodesmal fibrils associated with the oral dikinetids.

The fibrillar associates of the anterior nonciliated kinetosome of the oral dikinetids include the following: a) 1 to 3 postciliary microtubules associated with triplet 9. They are probably very short because they have been seen only in appropriate sections at the level of the cartwheel structure (Figs. 9, 11); and b) a transverse ribbon of about 6 microtubules which originates at the proximal end of the kinetosome, extends out- and upwards to the rim of the oral cone where it runs perpendicularly to the pellicle and plunges inwards thereby forming the slightly indented center of the cone (Figs. 4, 5, 9, 10, 11). The transverse ribbon is accompanied by widely spaced long cone microtubules and a short dense fiber running between the basal body and the ribbon. The cone microtubules are perpendicularly oriented to the transverse ribbons and form small loose bundles in deeper regions of the cytopharynx (Figs. 7, 9, 10, 11). The fibrillar associates of the posterior ciliated kinetosome include the following: a) a long postciliary ribbon of about 6 microtubules which originates at triplet 9 and extends to the right and posteriorly into the interkinetal space (Fig. 11); and b) a very short (about 2 μm) transverse ribbon of about 4 microtubules which originates near triplets 4, 5, and 6 and runs anteriorly beneath and parallel to the pellicle and ends in the oral cone (Figs. 7, 9, 10).

3.5. The rhabdos

The rhabdos of *F. terricola* is made of 3 microtubular components: a) the transverse ribbons of the anterior kinetosomes of the dikinetids which line the center of the cytopharynx (Figs. 4, 5, 7); b) the nematodesmal bundles ("outer rhabdos") which originate from the anterior kinetosomes of the oral dikinetids and from the anterior oralized somatic monokinetids (Figs. 2, 4, 5, 9); and c) the cone microtubules which are distributed rather regularly in the marginal area of the oral cone and form bundles ("inner rhabdos") in the deeper regions of the cytopharynx (Figs. 4, 7, 9).

3.6. Internal organization

The oral region is filled with conspicuous toxicysts which have a length of about 7 μm. They are spaced regularly between the transverse ribbons of the anterior basal bodies of the oral dikinetids and the cone microtubules respectively (Figs. 4, 7). The center-to-center spacing between adjacent toxicysts of one row is 250–350 nm. The toxicysts are slightly curved. The diameter of the inner electron dense tube is about 200 nm, except for the anterior end, which is slightly constricted (Figs. 19, 20). Both ends of the tube are truncated. The anterior two thirds of the tube have a complex structure, which can be best seen in cross-sections. These show concentric lines of different electron density (Figs. 21, 22, 24, 25). The posterior third of the tube is of uniform electron density without recognizable substructure (Figs. 23, 26–29). The tube is surrounded by a fibro-granular material which is slightly thickened at the anterior end but very conspicuously so at the posterior end. The diameter of the whole toxicyst in the middle region is thus about 200 nm but up to 450 nm posteriorly. The inner region of the inflation is more loosely structured than the laminated periphery (Figs. 19, 20, 28). Fine filaments extending from the membrane of the capsule into the clear region (halo) around the tube can be seen in tangential sections. The inflated posterior ends of the toxicysts are visible also in the light microscope the more so because they stain well with protargol (BERGER et al. 1983; FOISSNER 1983a, 1984a; Fig. 3).

Another type of extrusomes is doughnut-shaped with an indented center (Figs. 4, 8, 9, 11, 13b). The longer axis is about 300 nm, the shorter about 130 nm. They are found occasionally between the long extrusomes in the periphery of the oral region but also in the somatic cortex in and between the pellicular crests. They do not have a special orientation and may be attached to the pellicle in any position.

The chromatin of the micronucleus is more heavily stained than that of the macronucleus. Many diffuse nucleoli are present in the macronucleus and at the least one in the micronucleus.

Spherical, electron-lucent vesicles with dense droplets and fibrillar material are especially abundant in the oral region (Figs. 4, 9). They have a diameter of about 300–500 nm. Smaller irregularly shaped vesicles which appear double-membraned are often associated with the kinetids as well as vesicles with a "coated surface" (Figs. 6, 15).

Fuscheria terricola feeds on ciliates. The membrane of the food vacuoles is generally smooth (Fig. 12). Protuberances as in *Enchelydium* (Foissner and Foissner 1985) can be rarely seen. The contractile vacuole contains membranous and fuzzy material and is surrounded by numerous tubules which form an extensive network (Fig. 12).

4. Discussion

4.1. Comparative fine structure

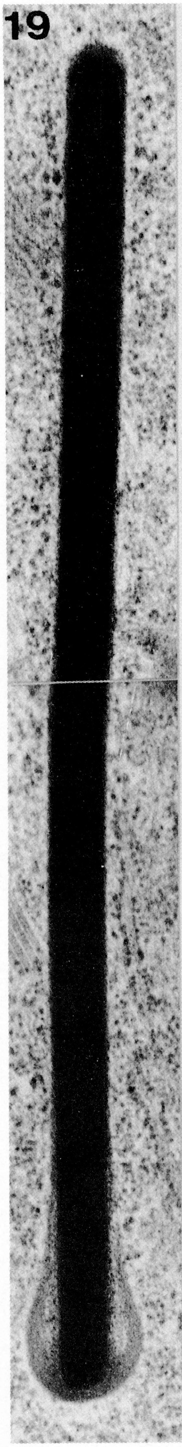
The general fine structure of *F. terricola* is very similar to that of other haptorids like *Lagynophrya* (Grain, 1970), *Spathidium* (Bohatier et al. 1978; Williams et al. 1981), *Enchelydium* (Foissner and Foissner 1985), and *Lepidotrachelophyllum* (Lynn and Nicholls 1985). These and related contributions have been carefully reviewed by Foissner and Foissner (1985), Lynn and Nicholls (1985), and Lynn (1981, 1985). Thus, we restrict this part of the discussion to a few points which are either special to the genus *Fuscheria* or which need some reinterpretation.

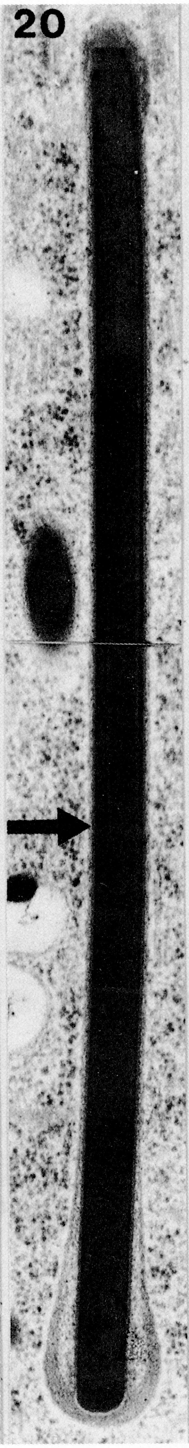
A tela corticalis is present in all haptorids so far investigated. However, we could not find it in *F. terricola,* either because it is really absent or because it is very inconspicuous or did not withstand the preparation procedure.

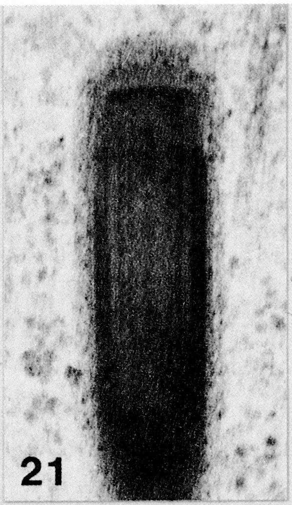
There is a great diversity of extrusomes (toxicysts and mucocysts) in the haptorid ciliates (Puytorac and Kattar 1969; Hausmann 1978; Foissner 1984a). Certainly, this can be used to separate genera (Foissner 1983a, 1984a). The nail-shaped toxicysts, the main character of the genus *Fuscheria* (Foissner 1983a, 1984a), are unique within the known haptorids. From the light microscopical observations it was not evident that their nail-shaped appearance is due to a fibrogranular material which encloses otherwise typical toxicysts that look rather similar to the pexicysts of *Didinium* (Wessenberg and Antipa 1968) and *Acropisthium* (Bohatier and Detcheva 1973). The doughnut-shaped mucocysts of *F. terricola* resemble the type 2 mucocysts of *Lagynophrya fusidens* (Grain 1970).

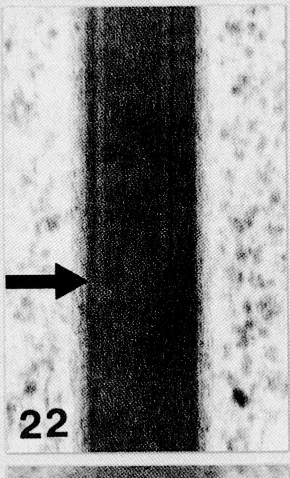
Lynn and Nichols (1985) and Foissner and Foissner (1985) presented schematic figures of the oral area of *Lepidotrachelophyllum* (suborder Spathidiina) and *Enchelydium* (suborder Enchelyina) respectively. These diagrams differ in 2 important details. The cone microtubules of *Lepidotrachelophyllum* are said to be anchored in the fibrillar annulus which binds together the oral dikinetids. In *Enchelydium,* which lacks a distinct fibrillar annulus, these cone (bulge) microtubules reach deeply into the cytopharyngeal plasm, where they form nematodesmata-like bundles. The same is evident in *F. terricola* (Figs. 4, 9). A closer examination of Fig. 15 in the paper of Lynn and Nicholls (1985) convincingly shows that this is also the case in *Lepidotrachelophyllum.* Very likely, the pronounced nematodesmata-like microtubular bundles in the proboscis of *Didinium* and *Monodinium* (Wessenberg and Antipa 1968; Rodrigues de Santa Rosa and Didier 1975) and

Figs. 19–29. Toxicysts in longitudinal sections (Figs. 19–23) and cross-sections (Figs. 24–29) of progressively deeper regions. Note the inflated end. Fig. 23 probably represents a developmental stage. The complex structure of the tube occupies the anterior 2 thirds of the whole toxicyst (arrows). Figs. 19, 20: ×38,000, Figs. 21–23: ×76,000, Figs. 24–29: ×80,000.

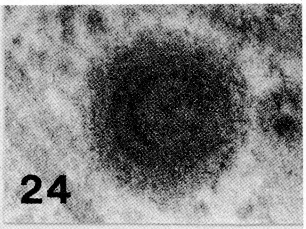

19

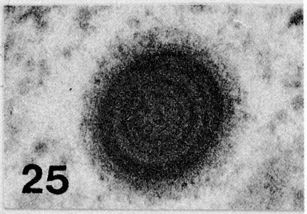

20

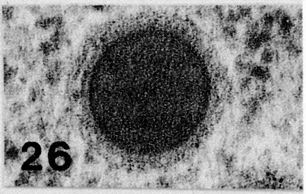

21

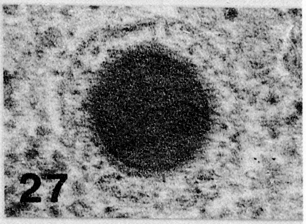

22

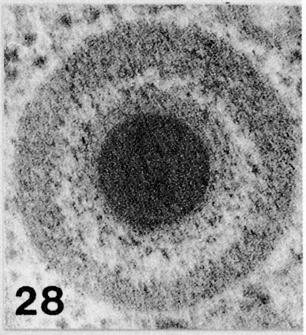

23

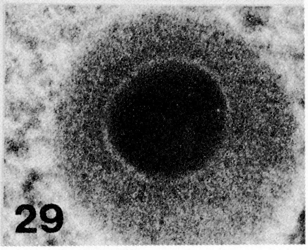

24


25


26


27


28


29

the inner wreath of nematodesmata in the cytopharynx of *Dileptus* (GRAIN and GOLINSKA 1969) are homologous to the bulge microtubules found in the above mentioned genera.

The oral transverse microtubular ribbons of *Helicoprorodon* (RAIKOV and KOVALEVA 1980), *Acropisthium* (BOHATIER and DETCHEVA 1973), *Enchelydium* (FOISSNER and FOISSNER 1985), and *Fuscheria* (Figs. 4, 7, 9) turn to the rim of the oral bulge and extend anteriorly to the center of the bulge, where they plunge inwards to support the cytopharynx. This is different from *Lepidotrachelophyllum,* where these ribbons are said to end at the tip of the oral cone. However, no clear evidence for this is given in the paper of LYNN and NICHOLLS (1985). We would interpret the central microtubules which are visible in Fig. 15 of the paper of LYNN and NICHOLLS (1985) as plunged transverse ribbons.

The above discussed data suggest that the rhabdos of most members of the subclass Haptoria is built up of the following 3 basic microtubular components: a) the transverse microtubular ribbons which originate from the nonciliated kinetosomes of oral dikinetids or from ciliated or nonciliated oralized somatic monokinetids and turn to the rim of the oral bulge, extend anteriorly to the center of the bulge, where they plunge inwards to support the cytopharynx; b) the nematodesmal bundles which originate from the nonciliated kinetosomes of the oral dikinetids and/or from the ciliated or nonciliated oralized somatic monokinetids form an "outer rhabdos"; and c) the cone or bulge microtubules which are distributed rather regularly in the marginal area of the oral cone and grouped in nematodesmata-like bundles in the lower oral region, where they form a more or less pronounced "inner rhabdos". Exceptions from this pattern are the Cyclotrichina which lack nematodesmata and the Archistomatida which lack bulge microtubules. Electron microscopical investigations on the morphogenesis of one of the above mentioned haptorids are necessary to elucidate the origin of the cone microtubules. From the interphasic stages investigated they seem to be of nonkinetosomal origin. Functionally, they could be a "guide" for the toxicysts because the cone microtubules and the transverse ribbons form a lattice-like structure (KUHLMANN et al. 1980). This interpretation is supported by their absence in the Archistomatida (GRAIN 1966 a, b) which do not possess toxicysts.

4.2. Phylogenetic and taxonomic implications

FOISSNER (1984 a) and LYNN (1985) presented phylogenies of selected rhabdophoran ciliates. In these suggestions, prostomate genera like *Coleps, Urotricha,* and *Placus* are the sister group of litostomatic genera like *Spathidium, Trachelophyllum,* and *Monodinium.* Further, the Archistomatids are said to be more closely related to the Trichostomatids and Entodiniomorphids than to the Haptorids (SMALL and LYNN 1981, 1985). Recent data strongly oppose these ideas. *Coleps* and very likely many other Prostomatea have been shown to belong to the Cyrtophora (HUTTENLAUCH and BARDELE 1987). Oral monokinetids, which were one reason to unite the Archistomatida, Trichostomatida, and Entodiniomorphida, have been discovered in typical free-living Haptorids (FOISSNER 1984 a; FOISSNER and FOISSNER 1985). Thus, these authors suggested including the Archistomatida into the Haptoria.

These and other new data are included in the following system of the subclass Haptoria CORLISS, 1974. Orders and suborders are defined by conventional characters and details of their oral and somatic infraciliature. Much weight is put on the nematodesmata (Fig. 30) and the presence/absence of a dorsal brush because the general kinetid structure is too similar within the subclass to be of use at the ordinal rank. Until recently, these characters were not used for taxonomic purposes, obviously because their high diversity had not been recognized. The term "oralized somatic kinetids" is suggested for such kinetids which lie within somatic kineties, but bear nematodesmal bundles contributing to the rhabdos. Such kinetids may be monokinetids *(Fuscheria, Enchelydium, Alloiozona)* or dikinetids *(Helicoprorodon);* they may *(Fuscheria)* or may not be *(Alloiozona, Enchelydium)* associated with normal haptorian oral dikinetids; and they may be ciliated *(Fuscheria, Alloiozona)* or nonciliated *(Enchelydium).*

A natural grouping of the orders and suborders within the subclass is at present almost

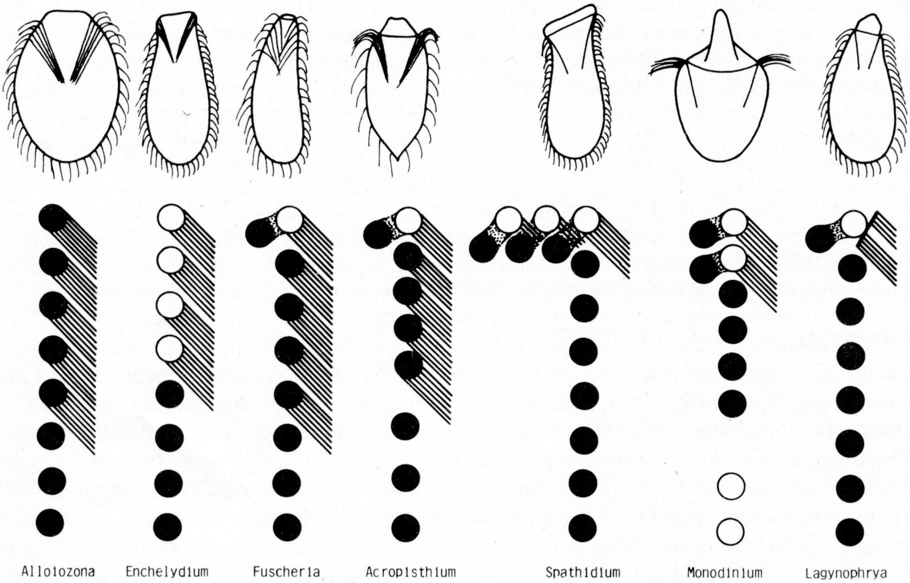


Fig. 30. Schematic drawings showing the oral and somatic infraciliature in representatives of the Archistomatida *(Alloiozona)* and the Haptoria. Ciliated kinetosomes are shown as black dots, nonciliated kinetosomes are drawn as open circles, and the nematodesmal bundles are depicted as slanting lines. Compiled from data of GRAIN (1966a, b); FOISSNER and FOISSNER (1985); BOHATIER and DETCHEVA (1973), BOHATIER et al. (1978); RODRIGUES DE SANTA ROSA and DIDIER (1975); GRAIN (1970), and especially of PUYTORAC and GRAIN (1976).

impossible because "hard" information about the apomorphic and plesiomorphic state of the main characters is still lacking. Thus, it might seem premature to propose new higher categories. We hope, however, that our effort is a first step to a more natural system of the Haptorids. The number of species, genera, and families within this group is much higher than most ciliatologists think. We have drawings and protargol slides of about ten new genera which will be described in the near future.

Subclass Haptoria CORLISS, 1974

Usually uniform holotrichous somatic ciliation; somatic kineties often longitudinally, rarely right-spiralling; somatic monokinetids with short kinetodesmal fibrils, 2 tangential transverse ribbons, and moderately overlapping, weakly convergent postciliary ribbons; cytostome usually apical, rarely subapical or antapical, round, oval or slit-like, not permanently open; oral kinetids are usually dikinetids whose transverse ribbons extend from the anterior kinetosomes to support the cytopharynx; in groups lacking oral dikinetids, the rhabdos is built from oralized somatic kinetids which have nematodesmal bundles and long transverse ribbons; bulge (cone) microtubules, tela corticalis, and toxicysts usually present; dorsal brush common, within somatic kineties, thus longitudinally oriented, consists of paired clavate cilia; silverline system fine-meshed, between brush kineties often platyophryid or colpodid; stomatogenesis telokinetal; most are free-living, rapacious carnivores, some are parasites or endocommensals.

Remarks: The characterization of the kinetids is based on LYNN (1981, 1985) and SMALL and LYNN (1981, 1985). The second tangential transverse ribbon of the somatic monokinetids has probably often been overlooked; it is, however, possible that it really is absent in some groups.

The Haptoria are divided into six orders, 2 of which are new. SMALL and LYNN (1985) established the new haptorid order Pharyngophorida which is characterized by a permanent cytopharynx and includes the families Actinobolinidae, Helicoprorodontidae, and Tracheliidae. Several problems exist with this suggestion. Firstly, there already exists the order Dileptida, which includes at least the Tracheliidae, and the suborder Belonophryina, which covers the Actinobolinidae (JANKOWSKI 1978, 1980). Secondly, one must ask, whether there really are Haptorids which do not have a "permanent cytopharynx lined by the transverse microtubular ribbons of the oral dikinetids". As far as we can see from our data and from the literature, this is not the case. The central area of the cytostome is always more *(Actinobolina, Enchelydium)* or less *(Helicoprorodon, Spathidium)* indented, lined by the more or less pronounced transverse ribbons of the oral kinetids, and surrounded or filled with phagoplasm. There exist certainly some variations in this pattern, but this seems to be due to the different shape and height of the oral bulge (cone) which are, however, often very different even within a single genus (FOISSNER 1984a). In addition, the families included in the Pharyngophorida seem to be a rather random assemblage. Are, for instance, the Tracheliidae really nearer to the Helicoprorodontidae than to the Enchelyina or Spathidiida? Altogether, we see no advantage of this order.

Order Haptorida CORLISS, 1974

Cytostome apical or subapical, round, oval or slit-like; rhabdos made of three microtubular components: transverse ribbons originating from the nonciliated oralized somatic monokinetids or oral dikinetids, nematodesmal bundles originating from the same source and/or from ciliated or nonciliated oralized somatic monokinetids, and bulge microtubules; somatic ciliation uniform; dorsal brush composed of two or more kineties; toxicysts localized, typically in or near oral area; free-living, suborder Dileptina with conspicuous proboscis. Type: Enchelyina nov. subord.

Remarks: This characterization is based on the studies of CORLISS (1979), FOISSNER and FOISSNER (1985) and the present investigation. The order Haptorida is best distinguished from all other haptorian taxa by the occurrence of oralized somatic monokinetids bearing nematodesmal bundles.

Suborder Enchelyina nov. subord.

Cytostome apical, round or oval; nematodesmal bundles originate exclusively from nonciliated oralized somatic monokinetids which bear also long transverse ribbons; dorsal brush consists of three kineties. Type: Enchelyidae EHRENBERG, 1838.

Remarks: This new suborder is based on the investigations of FOISSNER (1984a) and FOISSNER and FOISSNER (1985) which show that *Enchelys* and *Enchelydium* lack oral dikinetids. These 2 genera, and probably *Papillorhabdos* FOISSNER, 1984, may be united in the family Enchelyidae EHRENBERG, 1838. CORLISS (1979) assigns to this family a lot of other, mostly poorly described genera. Some of them (e.g. *Enchelyodon, Trachelophyllum, Lacrymaria*) are now considered to belong to other families (see below and FOISSNER 1984a).

Suborder Acropisthiina nov. subord.

Cytostome apical, round or oval; nematodesmal bundles originate from typical haptorid oral dikinetids and from ciliated oralized somatic monokinetids. Dorsal brush consists of two to three kineties. Type: Acropisthiidae nov. fam.

Remarks: This new suborder is based on the present investigations and those of BOHATIER and DETCHEVA (1973) and FOISSNER (1984a) which show that *Acropisthium, Fuscheria,* and *Actinorhabdos* (separated from *Fuscheria* by its graver-like toxicysts) have the same type of oral infraciliature (Fig. 31). Thus, these 3 genera are united in the new family Acropisthiidae nov. fam. (with the same characterization as the suborder; Type: *Acropisthium* PERTY, 1852).

Suborder Dileptina JANKOWSKI, 1978

Oral area bipartited in a proboscis bearing ciliated oral dikinetids without nematodesmata and in a subapical cytostomal-cytopharyngeal complex with nonciliated oralized somatic monokinetids bearing nematodesmata; dorsal brush usually consists of more than 3 kineties. Type: Tracheliidae EHRENBERG, 1838.

Remarks: This special oral pattern is evident from the studies of GRAIN and GOLINSKA (1969) and GOLINSKA (1986) and shows the need of a separate suborder for the Tracheliidae. JANKOWSKI (1980) even suggests a separate subclass for the Tracheliidae, the Rhynchostomata with the single order Dileptida. He gives, however, a very poor characterization of these taxa. We believe that at present the subordinal rank is more appropriate because the dorsal brush, the somatic infraciliature and the ecology of *Dileptus* and related genera are very near to many other members of the Haptorida (FOISSNER 1984a; DRAGESCO and DRAGESCO-KERNÉIS 1986).

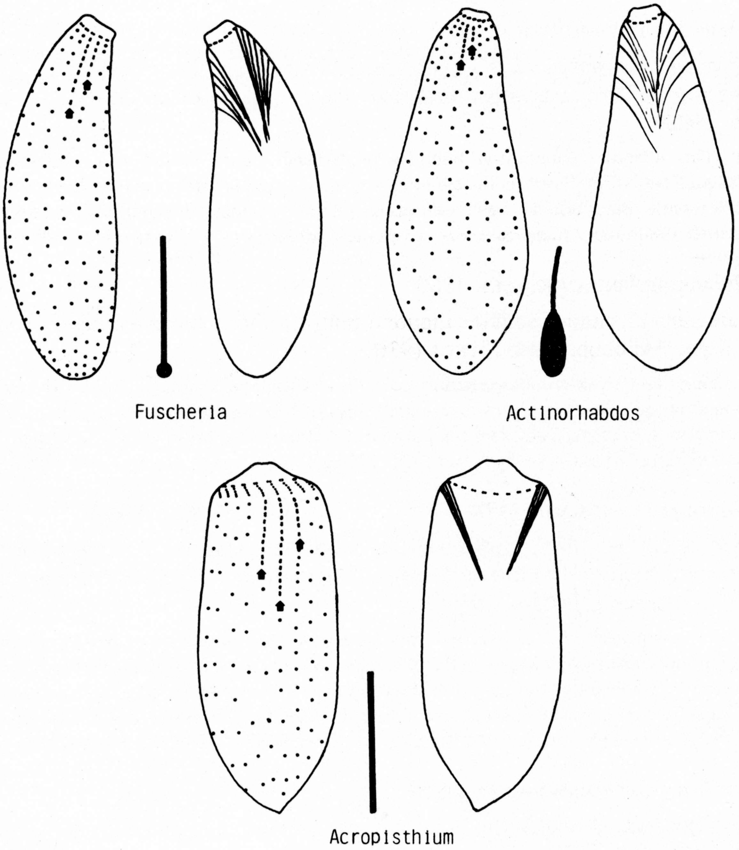


Fig. 31. Distinguishing characters of the genera of the family Acropisthiidae. Each genus is depicted in dorsal view (arrows denote the dorsal brush) and in a schematic drawing showing the nematodesmal bundles. The black figures between the pairs of graphs show the toxicysts at high magnification. Drawings of *Actinorhabdos* and *Acropisthium* are from Foissner (1984a).

Order Spathidiida nov. ord.

Cytostome apical, round or slit-like, in suborder Didiniina on top of cone-like proboscis; rhabdos made of three microtubular components: transverse ribbons originating from the nonciliated kinetosomes of the oral dikinetids, nematodesmal bundles originating exclusively from the same source, and bulge microtubules; somatic ciliation uniform or limited to dense bands which, however, rest within longitudinally running kineties composed of nonciliated kinetids; dorsal brush composed of 2 to many kineties; toxicysts localized, typically in or near oral area; free-living. Type: Spathidiina Jankowski, 1980.

Remarks: This new order is based mainly on the studies of Wessenberg and Antipa (1968); Bohatier (1970); Holt et al. (1973); Rodrigues de Santa Rosa and Didier (1975); Bohatier et al. (1978); Kuhlmann et al. (1980); Williams et al. (1981); Foissner (1984a) and Lynn and Nicholls (1985). The oral structures show a rather great uniformity within this order. Thus, the more differentiated somatic kinetids and other cortical structures are used to distinguish suborders.

Suborder Spathidiina Jankowski, 1980

Cytostome apical, round, oval or slit-like, in some genera covering the "ventral" body margin; somatic ciliation usually uniform. Type: Spathidiidae Kahl in Doflein and Reichenow, 1929.

Remarks: This suborder contains the families Spathidiidae Kahl in Doflein and Reichenow, 1929, Trachelophyllidae Kent, 1882, Lacrymariidae Fromentel, 1876, and Homalozoonidae Jankowski, 1980. Do the Homalozoonidae which have, like the Pleurostomatida, a rather distinct left-right differentiation of the somatic ciliation (Foissner 1984a) need a separate order or suborder as proposed by Jankowski (1980)?

Suborder Belonophryina Jankowski, 1980

Cytostome apical, round; somatic ciliation uniform; nonsuctorial tentacles widely distributed over body. Type: Actinobolinidae Kahl, 1930.

Remarks: This characterization is based mainly on the investigation of *Actinobolina* by Holt et al. (1973). This genus has some resemblance to *Fuscheria* because oral trikinetids (or oralized somatic monokinetids?) occur which bear 2 bundles of nematodesmata. The exact composition and shape of the brush are still unknown, but clavate cilia have been shown electron microscopically (Holt et al. 1973). Contains single family Actinobolinidae Kahl, 1930.

Suborder Didiniina Jankowski, 1978

Cytostome apical on conspicuous cone-like proboscis; somatic ciliation bipartited in one or more ciliated and nonciliated girdles which bear longitudinally arranged kineties with nonciliated kinetids. Type: Didiniidae Poche, 1913.

Remarks: The oral pattern of *Monodinium* bears some resemblance to that of *Helicoprorodon* (see below). There are, however, differences which suggest that this is an analogy. In *Monodinium* all somatic kineties bear 2 to 3 oral dikinetids causing a distinct "closed" circumoral kinety (Rodrigues de Santa Rosa and Didier 1975), whereas such kinetids are restricted to a few specialized kineties in *Helicoprorodon* which, thus has an "open" circumoral kinety (Raikov and Kovaleva 1980). Contains single family Didiniidae Poche, 1913.

Order Pleurostomatida Schewiakoff, 1896

Oral area flattened along ventral margin of laterally compressed body, surrounded by toxicysts; rhabdos made of three microtubular components: transverse ribbons originating from the oral dikinetids and in suborder Litonotina from somatic monokinetids too, nematodesmal bundles originating exclusively from the oral dikinetids, and bulge microtubules; somatic ciliature shows left-right differentiation; dorsal brush present; free-living and parasitic on other ciliates (especially peritrichs), often large, lengthy voracious carnivores, widely distributed and facultatively interstitial. Type: Amphileptina Jankowski, 1967.

Remarks: This characterization is based mainly on the studies of Bohatier and Njine (1973), Puytorac and Rodrigues de Santa Rosa (1975), and Corliss (1979). Small and Lynn (1985) give a wrong definition because the left oral kinety is never associated with somatic monokinetids. Although there is still some uncertainty about the exact composition of the oral structures of the Pleurostomatida, a large distinction is obvious, which suggests that the order should be divided into 2 suborders.

Suborder Amphileptina Jankowski, 1967

Cytostome surrounded by a right and a left oral kinety composed of dikinetids; right somatic infraciliature with "spica". Type: Amphileptidae Bütschli, 1889.

Remarks: To this suborder belong the genera *Amphileptus, Pseudoamphileptus, Opisthodon,* and *Loxophyllum* (see Puytorac and Rodrigues de Santa Rosa 1975; Foissner 1983b, 1984b) which are united in the family Amphileptidae Bütschli, 1889. *Loxophyllum* probably deserves a family of its own.

Suborder Litonotina nov. subord.

Cytostome surrounded by a right and a left oral kinety composed of dikinetids, right oral kinety continuous with (oralized?) somatic monokinetids (arranged in a distinct "perioral kinety

3") whose *transverse* ribbons contribute to the rhabdos; somatic kineties of the right side successively shortened along the cytostome. Type: Litonotidae KENT, 1882.

Remarks: To this suborder belong the genera *Litonotus* and *Acineria* (see BOHATIER and NJINE 1973; FOISSNER 1984b; AUGUSTIN et al. 1987) which are united in the family Litonotidae KENT, 1882.

Order Pseudoholophryida nov. ord.

Cytostome apical, round or oval; rhabdos made of the same microtubular components as in the Spathidiida; somatic ciliation uniform, but kineties more or less distinctly spirally arranged; dorsal brush absent or highly aberrant; toxicysts localized, typically in or near oral area; free-living. Type: Pseudoholophryina nov. subord.

Remarks: This characterization is based on the studies of PUYTORAC and KATTAR (1969); RAIKOV and KOVALEVA (1980), BERGER et al. (1984) and FOISSNER (1984a). Members of the Pseudoholophryina are known from light microscopical observations only. Thus, there is some uncertainty about their fine details. But oral dikinetids and transverse ribbons have been identified at least in *Paraenchelys* and *Ovalorhabdos* (FOISSNER 1984a). The main character of this new order is the absence of a typical haptorian dorsal brush, a feature which is shared by the Archistomatida and Cyclotrichida. Thus, these 3 orders could be united in a separate subclass, if further studies can prove that this absence is a true homology which is, however, not very likely.

Suborder Pseudoholophryina nov. subord.

Cytostome apical, round or oval; dorsal brush lacking or highly aberrant.Type: Pseudoholophryidae BERGER et al., 1984.

Remarks: This new suborder contains the single family Pseudoholophryidae BERGER et al., 1984, which includes 3 genera. *Pseudoholophrya* BERGER et al., 1984 and *Ovalorhabdos* FOISSNER, 1984 lack a dorsal brush. The "brush" of *Paraenchelys* FOISSNER, 1983 covers a large field in the anterior area of the cell and consists of many short arched kineties whose kinetosomes are not clearly paired.

Suborder Helicoprorodontina nov. subord.

Cytostome apical, round; oral dikinetids not arranged in a distinct circumoral kinety but at the top of some somatic kineties whose anterior ends spiral around the cytostome ("oralized somatic dikinetids"); exclusively in marine sands. Type: Helicoprorodontidae SMALL and LYNN, 1985.

Remarks: This characterization is based on the studies of PUYTORAC and KATTAR (1969) and RAIKOV and KOVALEVA (1980). The rhabdos of *Helicoprorodon* is very similar to that of the Spathidiina. The special kineties which spiral around the cytostome and bear the oral dikinetids are, however, such an extraordinary feature that a subordinal rank seems appropriate. No exact data are available concerning the dorsal brush and the arrangement of the somatic kineties. Contains the single family Helicoprorodontidae SMALL and LYNN, 1985 (the family is credited to these authors because JANKOWSKI 1975 did not give a diagnosis).

Order Archistomatida PUYTORAC et al., 1974

Cytostome apical, round or oval; rhabdos made of 2 microtubular components: transverse ribbons and nematodesmal bundles originating from ciliated oralized somatic monokinetids; somatic ciliation uniform or limited to tufts and bands; toxicysts and haptorid dorsal brush absent; concrement vacuole present; exclusively endocommensals, principally in horses and camels. Type: Buetschliidae POCHE, 1913.

Remarks: Characterization principally according to CORLISS (1979) and SMALL and LYNN (1985). Single family Buetschliidae POCHE, 1913. Many of the genera listed by CORLISS (1979) in this family are now considered to belong to other subclasses (JANKOWSKI 1980; SMALL and LYNN 1985). The rhabdos of the Archistomatida resembles that of the Enchelyina in the order Haptorida. It differs, however, by the absence of bulge microtubules and by the ciliated nematodesmata bearing oralized somatic monokinetids.

Order Cyclotrichida JANKOWSKI, 1980

Cytostomal-cytopharyngeal structures apical or antapical, in some genera strongly reduced and probably functionless; rhabdos without nematodesmata and bulge microtubules, but probably with transverse ribbons; somatic ciliation limited to 2 cirri-like girdles; dorsal brush absent; toxicysts present; often with incomplete cryptomonad symbionts. Type: Mesodiniidae JANKOWSKI, 1980.

Remarks: This characterization is based on the studies of BORROR (1963); TAYLOR et al. (1971); JANKOWSKI (1980); GRAIN et al. (1982) and WILBERT (1986). The absence of a dorsal brush and of nematodesmata (at least in *Myrionecta rubra;* see TAYLOR et al. 1971 and GRAIN et al. 1982) and the widely meshed silverline system in *Askenasia* (FOISSNER, unpubl.) suggest that this order probably belongs to another subclass. Details of the oral apparatus are, however, too poorly known to find a more meaningful affinity than that conventionally suggested. Contains single family Mesodiniidae JANKOWSKI, 1980 (first named, but not diagnosed in JANKOWSKI 1975).

4.3. Summary of the new classification of the Haptoria

Class Litostomatea SMALL and LYNN, 1981
  Subclass I. Haptoria CORLISS, 1974
    Order I. Haptorida CORLISS, 1974
      Suborder (1) Enchelyina nov. subord.
      Suborder (2) Acropisthiina nov. subord.
      Suborder (3) Dileptina JANKOWSKI, 1978
    Order II. Spathidiida nov. ord.
      Suborder (1) Spathidiina JANKOWSKI, 1980
      Suborder (2) Belonophryina JANKOWSKI, 1980
      Suborder (3) Didiniina JANKOWSKI, 1978
    Order III. Pleurostomatida SCHEWIAKOFF, 1896
      Suborder (1) Amphileptina JANKOWSKI, 1967
      Suborder (2) Litonotina nov. subord.
    Order IV. Pseudoholophryida nov. ord.
      Suborder (1) Pseudoholophryina nov. subord.
      Suborder (2) Helicoprorodontina nov. subord.
    Order V. Archistomatida PUYTORAC et al., 1974
    Order VI. Cyclotrichina JANKOWSKI, 1980
  Subclass II. Trichostomatia BÜTSCHLI, 1889 (not treated here)

Zusammenfassung

Fuscheria terricola BERGER, FOISSNER and ADAM, 1983 gleicht in der allgemeinen Feinstruktur anderen haptoriden Ciliaten. Es fehlen jedoch die tela corticalis und parasomale Säcke. Die Mucocysten sind krapfenförmig, die Toxicysten nagelartig. Die ungewöhnliche Form der Toxicysten wird durch eine kugelförmige Anschwellung des fibro-granulären Materials hervorgerufen, das den zentralen Teil der Organellen umgibt, der stabförmig ist und den Pexicysten von *Didinium* und *Acropisthium* ähnelt. Die somatischen Kinetiden sind Monokinetiden mit typischer fibrillärer haptorider Ausstattung. Die oberen 4 bis 7 somatischen Kinetiden besitzen jedoch Nematodesmen. An der Basis des Mundwulstes befindet sich eine circumorale Kinete, die aus typischen haptoriden Dikinetiden aufgebaut ist. Ihre Nematodesmen und jene der vorderen somatischen Monokinetiden bilden eine sehr charakteristische, irreguläre Reuse (Rhabdos). Die gleiche Merkmalskombination zeigen *Acropisthium* und *Actinorhabdos.* Diese 3 Genera werden daher in der neuen Familie Acropisthiidae nov. fam. vereinigt.

Die Reuse der meisten Haptorida ist aus 3 mikrotubulären Systemen aufgebaut: a) transversalen Mikrotubuli-Bändern, die von den unbewimperten Basalkörpern der oralen Dikinetiden oder von bewimperten oder unbewimperten oralisierten somatischen Kinetiden entspringen und zum Zentrum des Mundwulstes ziehen, wo sie umbiegen und den Cytopharynx auskleiden; b) Bündel von Nematodesmen, die eine „äußere Reuse“ bilden; und c) vertikal orientierte Wulst-Mikrotubuli, die im Randbereich des Mundwulstes ziemlich regelmäßig angeordnet sind, sich im hinteren Mundbereich aber zu nematodesmenartigen Bündeln vereinigen und auf diese Weise eine „innere Reuse“

bilden. Ausnahmen von dieser „Regel“ sind die Cyclotrichida und die Archistomatida. Ersteren fehlen die Nematodesmen, letzteren die Wulst-Mikrotubuli, vermutlich weil sie keine Toxicysten besitzen.

Für Kinetiden, die in somatischen Kineten liegen, aber Nematodesmen besitzen, die zum Aufbau der Reuse (Rhabdos) beitragen, wird der Terminus „oralisierte somatische Kinetiden“ eingeführt. Solche Kinetiden können Mono- oder Dikinetiden sein; sie können oder können nicht mit normalen oralen haptoriden Dikinetiden vergesellschaftet sein; und sie können bewimpert oder unbewimpert sein. Die verschiedenen Arten von Kinetiden, die zum Aufbau der Reuse beitragen und die Dorsalbürste (vorhanden bzw. fehlend) sind die Schlüsselmerkmale für eine revidierte Klassifikation der Haptoria. Folgende neue höhere Taxa werden errichtet: Enchelyina nov. subord. (mit unbewimperten oralisierten somatischen Monokinetiden), Acropisthiina nov. subord. (mit oralen Dikinetiden und bewimperten oralisierten somatischen Monokinetiden), Spathidiida nov. ord. (nur mit oralen Dikinetiden), Litonotina nov. subord. (rechte orale Kinete mit somatischen Monokinetiden assoziiert), Pseudoholophryida nov. ord. und Pseudoholophryina nov. subord. (Dorsalbürste fehlend oder sehr aberrant), Helicoprorodontina nov. subord. (oralisierte somatische Dikinetiden, vermutlich keine Dorsalbürste).

Literature

AUGUSTIN, H., FOISSNER, W., and ADAM, H. (1987): Revision of the genera *Acineria, Trimyema* and *Trochiliopsis*. Bull. Br. Mus. nat. Hist. (Zool.) **52**: 197–224.

BERGER, H., FOISSNER, W., and ADAM, H. (1983): Morphology and morphogenesis of *Fuscheria terricola* n. sp. and *Spathidium muscorum* (Ciliophora: Kinetofragminophora). J. Protozool. **30**: 529–535.

– (1984): Taxonomie, Biometrie und Morphogenese einiger terricoler Ciliaten (Protozoa: Ciliophora). Zool. Jb. Syst. **111**: 339–367.

BOHATIER, J. (1970): Structure et ultrastructure de *Lacrymaria olor* (O. F. M. 1786). Protistologica **6**: 331–342.

– et DETCHEVA, R. (1973): Observations sur la cytologie et sur l'ultrastructure du cilié *Acropisthium mutabile* PERTY 1852. C. r. Séanc. Soc. Biol. **167**: 972–976.

– et NJINE, T. (1973): Observations ultrastructurales sur le cilié holotriche gymnostome *Litonotus quadrinucleatus* DRAGESCO et NJINÉ, 1971. Protistologica **9**: 359–372.

– IFTODE, F., DIDIER, P., et FRYD-VERSAVEL, G. (1978): Sur l'ultrastructure des genres *Spathidium* et *Bryophyllum*, ciliés kinetophragmophora (DE PUYTORAC et al., 1974). Protistologica **14**: 189–200.

BORROR, A. C. (1963): Morphology and ecology of the benthic ciliated protozoa of Alligator Harbor, Florida. Arch. Protistenkd. **106**: 465–534.

BÜTSCHLI, O. (1887–1889): Protozoa. Abt. III. Infusoria und System der Radiolaria. In: BRONN, H. G. (ed.), Klassen und Ordnung des Thier-Reichs, Vol. I, pp. 1098–2035. Leipzig.

CORLISS, J. O. (1974): Remarks on the composition of the large ciliate class Kinetofragmophora DE PUYTORAC et al., 1974, and recognition of several new taxa therein, with emphasis on the primitive order Primociliatida n. ord. J. Protozool. **21**: 207–220.

– (1979): The ciliated protozoa. Characterization, classification and guide to the literature. 2nd ed. Oxford, New York, Toronto, Sydney, Paris, Frankfurt.

DOFLEIN, F., und REICHENOW, E. (1927–1929): Lehrbuch der Protozoenkunde. Eine Darstellung der Naturgeschichte der Protozoen mit besonderer Berücksichtigung der parasitischen und pathogenen Formen. 5. Aufl. Jena.

DRAGESCO, J., et DRAGESCO-KERNÉIS, A. (1986): Ciliés libres de l'Afrique intertropicale. Faune tropicale **26**: 1–559.

EHRENBERG, C. G. (1838): Die Infusionsthierchen als vollkommene Organismen. Leipzig.

FOISSNER, W. (1983a): Taxonomische Studien über die Ciliaten des Großglocknergebietes (Hohe Tauern, Österreich) I. Familien Holophryidae, Prorodontidae, Plagiocampidae, Colepidae, Enchelyidae und Lacrymariidae nov. fam. Annln naturh. Mus. Wien **84/B** (year 1980): 49–85.

– (1983b): Morphologie und Infraciliatur zweier ectocommensaler Ciliaten (Protozoa: Ciliophora) von *Cyprinus carpio* L. (Pisces: Cypriniformes): *Heteropolaria lwoffi* (FAURÉ-FREMIET, 1943) (Peritrichida: Epistylididae) und ihr Predator *Pseudoamphileptus macrostoma* (CHEN, 1955) nov. gen. (Pleurostomatida: Amphileptidae). Zool. Jb. Syst. **110**: 399–418.

– (1984a): Infraciliatur, Silberliniensystem und Biometrie einiger neuer und wenig bekannter terrestrischer, limnischer und mariner Ciliaten (Protozoa: Ciliophora) aus den Klassen Kinetofragminophora, Colpodea und Polyhymenophora. Stapfia, Linz **12**: 1–165.

– (1984b): Taxonomie und Ökologie einiger Ciliaten (Protozoa, Ciliophora) des Saprobiensystems. I: Genera *Litonotus, Amphileptus, Opisthodon*. Hydrobiologia **119**: 193–208.

– (1987): Neue terrestrische und limnische Ciliaten (Protozoa, Ciliophora) aus Österreich und Deutschland. Sber. Akad. Wiss. Wien **195**: 217–268.

– and FOISSNER, I. (1985): Oral monokinetids in the free-living haptorid ciliate *Enchelydium polynucleatum* (Ciliophora, Enchelyidae): ultrastructural evidence and phylogenetic implications. J. Protozool. **32**: 712–722.

FROMENTEL, E. DE (1874–1876): Études sur les microzoaires ou infusoires proprement dits comprenant de nouvelles recherches sur leur organisation, leur classification et la description des espèces nouvelles ou peu connues. Paris.

GOLINSKA, K. (1986): Modifications of size and pattern of microtubular organelles in overfed cells of a ciliate *Dileptus*. J. Embryol. exp. Morph. **93**: 85–104.

GRAIN, J. (1966a): Étude cytologique de quelques ciliés holotriches endocommensaux des ruminants et des équidés (Première partie). Protistologica **2**: 59–141.

– (1966b): Étude cytologique de quelques ciliés holotriches endocommensaux des ruminants et des équidés. Deuxième chapitre microscopie électronique. Protistologica **2**: 5–51.

– (1970): Structure et ultrastructure de *Lagynophrya fusidens* KAHL, 1927. Protistologica **6**: 37–51.

– et GOLINSKA, K. (1969): Structure et ultrastructure de *Dileptus cygnus* CLAPARÈDE et LACHMANN, 1859, cilié holotriche gymnostome. Protistologica **5**: 269–291.

– PUYTORAC, P. DE, et GROLIÈRE, C.-A. (1982): Quelques précisions sur l'ultrastructure et la position systématique du cilié *Mesodinium rubrum,* et sur la constitution de ses symbiontes chloroplastiques. Protistologica **18**: 7–21.

HAUSMANN, K. (1978): Extrusive organelles in protists. Int. Rev. Cytol. **52**: 197–276.

HOLT, P. A., LYNN, D. H., and CORLISS, J. O. (1973): An ultrastructural study of the tentacle-bearing ciliate *Actinobolina smalli* n. sp. and its systematic and phylogenetic implications. Protistologica **9**: 521–541.

HUTTENLAUCH, I., and BARDELE, C. F. (1987): Light and electron microscopical observations on the stomatogenesis of the ciliate *Coleps amphacanthus* EHRENBERG, 1833. J. Protozool. **34**: 183–192.

JANKOWSKI, A. W. (1967): A new system of ciliate protozoa (Ciliophora). Akad. Nauk SSSR, Trudy Zool. Inst. **43**: 3–54 (in Russian).

– (1975): A conspectus of the new system of subphylum Ciliophora DOFLEIN, 1901. In: BALASHOV, U. S. (ed.), Account of scientific sessions on results of scientific work, year 1974: Abstracts of reports. Akad. Nauk SSSR, Zool. Inst. Leningrad, pp. 26–27 (Abstr.) (in Russian).

– (1978): New higher taxa of ciliated protozoa (Ciliophora). In: Morphology, taxonomy and evolution of animals. Set of scientific papers. Akad. Sci. USSR, Zool. Inst. Leningrad, pp. 88–90 (Abstr.) (in Russian).

– (1980): Conspectus of a new system of the phylum Ciliophora. Proc. Acad. Sci. USSR **94**: 103–121 (in Russian with English title translation).

KAHL, A. (1930): Urtiere oder Protozoa I: Wimpertiere oder Ciliata (Infusoria) 1. Allgemeiner Teil und Prostomata. Tierwelt Dtl. **18**: 1–180.

KENT, W. S. (1880–1882): A manual of the infusoria. Vols. I–III. London.

KUHLMANN, S., PATTERSON, D. J., und HAUSMANN, K. (1980): Untersuchungen zu Nahrungserwerb und Nahrungsaufnahme bei *Homalozoon vermiculare,* STOKES 1887. 1. Nahrungserwerb und Feinstruktur der Oralregion. Protistologica **16**: 39–55.

LYNN, D. H. (1981): The organization and evolution of microtubular organelles in ciliated protozoa. Biol. Rev. **56**: 243–292.

– (1985): Cortical ultrastructure of *Coleps bicuspis* NOLAND, 1925 and the phylogeny of the class Prostomatea (Ciliophora). BioSystems **18**: 387–397.

– and NICHOLLS, K. H. (1985): Cortical microtubular structures of the ciliate *Lepidotrachelophyllum fornicis* NICHOLLS and LYNN, 1984 and phylogeny of the litostomate ciliates. Can. J. Zool. **63**: 1835–1845.

PERTY, M. (1852): Zur Kenntnis kleinster Lebensformen nach Bau, Funktionen, Systematik, mit Specialverzeichnis der in der Schweiz beobachteten. Bern.

POCHE, F. (1913): Das System der Protozoa. Arch. Protistenkd. **30**: 125–321.

PUYTORAC, P. DE, et GRAIN, J. (1976): Ultrastructure du cortex buccal et évolution chez les ciliés. Protistologica **12**: 49–67.

– et KATTAR, M. R. (1969): Observations sur l'ultrastructure du cilié *Helicoprorodon multinucleatum* DRAGESCO 1960. Protistologica **5**: 549–560.

– et RODRIGUES DE SANTA ROSA, M. (1975): Observations cytologiques sur le cilié gymnostome *Loxophyllum meleagris* DUJ., 1841. Protistologica **11**: 379–390.

– BATISSE, A., BOHATIER, J., CORLISS, J. O., DEROUX, G., DIDIER, P., DRAGESCO, J., FRYD-VERSAVEL, G., GRAIN, J., GROLIÈRE, C.-A., HOVASSE, R., IFTODE, F., LAVAL, M., ROQUE, M., SAVOIE, A., et TUFFRAU, M. (1974): Proposition d'une classification du phylum Ciliophora DOFLEIN, 1901 (réunion de systématique, Clermont-Ferrand). C. r. hebd. Séanc. Acad. Sci., Paris **278**: 2799–2802.

RAIKOV, I. B., and KOVALEVA, V. G. (1980): Fine structure of the circumoral ciliature and pharyngeal apparatus of the marine ciliate *Helicoprorodon gigas* (Gymnostomata). Protistologica **16**: 177–198.

RODRIGUES DE SANTA ROSA, M., et DIDIER, P. (1975): Remarques sur l'ultrastructure du cilie gymnostome *Monodinium balbiani* (FABRE DOMERGUE, 1888). Protistologica **11**: 469–479.

SCHEWIAKOFF, W. (1896): Organization and classification of the Infusoria Aspirotricha (Holotricha auctorum). Zap. imp. Akad. Nauk SSSR (Ser. 8) **4**: 1–395 (in Russian).

SMALL, E. B., and LYNN, D. H. (1981): A new macrosystem for the phylum Ciliophora DOFLEIN, 1901. BioSystems **14**: 387–401.

– (1985): Phylum Ciliophora. In: LEE, J. J., HUTNER, S. H., and BOVEE, E. C. (eds.), An illustrated guide to the protozoa, pp. 393–575. Lawrence, Kansas.

TAYLOR, F. J. R., BLACKBOURN, D. J., and BLACKBOURN, J. (1971): The red-water ciliate *Mesodinium rubrum* and its "incomplete symbionts": a review including new ultrastructural observations. J. Fish. Res. Bd. Canada **28**: 391–407.

WESSENBERG, H., and ANTIPA, G. (1968): Studies on *Didinium nasutum* I. Structure and ultrastructure. Protistologica **4**: 427–447.

WILBERT, N. (1986): Beitrag zur Morphologie und Ökologie einiger planktischer Ciliaten aus dem Poppelsdorfer Weiher in Bonn (BRD). Arch. Protistenkd. **131**: 59–69.

WILLIAMS, D. B., WILLIAMS, B. D., and HOGAN, B. K. (1981): Ultrastructure of the somatic cortex of the gymnostome ciliate *Spathidium spathula* (O. F. M.). J. Protozool. **28**: 90–99.

Authors' addresses: Univ.-Prof. Dr. WILHELM FOISSNER, Universität Salzburg, Institut für Zoologie, Hellbrunnerstraße 34, A - 5020 Salzburg, Austria, and Dr. ILSE FOISSNER, Universität Salzburg, Institut für Pflanzenphysiologie, Hellbrunnerstraße 34, A - 5020 Salzburg, Austria.