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# CILIATES

## Cells as Organisms

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# Ontogenesis in ciliated Protozoa, with Emphasis on Stomatogenesis

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## 1 Introduction

The literature on morphogenesis of ciliates has been frequently reviewed, but almost exclusively from the viewpoint of the mechanisms involved (283). It was also usually a main topic at the international meetings of the Society of Protozoologists (326, 371, 408, 438, 719, 773); however, only Corliss (112, 118) collected extensive phenomenological data, but not at species level, and his last review (118) is now rather outdated. The present overview was therefore prepared in order to update the matter and to provide workers in various fields, especially alpha-taxonomists and evolutionary protozoologists with detailed background information, and even experimental morphogeneticists may profit from this collection, because the mechanisms of morphogenesis are still poorly understood. The pessimistic statement by Frankel (283), «my own view is that the true mechanisms of morphogenesis are not yet understood, not even in principle, and that answers will be found by scientists who are willing to think and work unconventionally», concurs with the view held by beta-taxonomists (179, 266) and indicates not only the need for intensified research with refined methods but also for a contemporary review of the ontogenetic data.

## 2 Scope of the review and benchmark literature on morphogenesis of ciliated protozoa

This review focuses on the phenomenology of stomatogenesis in ciliated protozoa. I have tried to collate all data relevant to this field, but have usually excluded material published only in abstracts. Likewise, general and other aspects of morphogenesis (e.g., nuclear division, experimental and excystment morphogenesis, sexual reproduction, life cycles, very old papers of purely historic interest) have been excluded, simply because of space restrictions. For these, the following literature guide might be of help.

Books: Several books on morphogenesis of ciliates are available (283, 511) but, as already mentioned, only that of Corliss (118) contains a fairly comprehensive compilation of the phenomenological data. Lwoff's (511) book is still highly useful and summarizes a lot of the French literature and especially Lwoff's view on the continuity of basal bodies (see also [512, 513]). Frankel (283) reviewed mainly experimental data and morphogenetic mechanisms. There are also some species monographs, viz. on *Stentor* (741), *Blepharisma* (311), *Paramecium* (423, 443, 452, 809) and colpodids (266), which review morphogenetic data in some detail. The

following textbooks also contain useful information: (164, 328, 380, 493, 602, 634, 645).

Ordinary reviews: The following papers treat morphogenesis mainly from a phenomenological viewpoint: (66, 113–115, 214, 258, 301, 308, 467, 518, 569, 700, 719, 720, 734, 739, 742, 744, 757, 800, 801).

Reviews on experimental morphogenesis and morphogenetic mechanisms: This subject has fascinated many workers, and most pertinent literature was extensively reviewed by Frankel (283) in his book on «pattern formation». Further readings: (14, 21, 64, 177, 206, 208, 212, 214, 258, 280–285, 291, 326, 336, 337, 361, 437–439, 467, 527, 569, 575, 576, 682, 683, 697, 727, 734, 739, 741, 744, 800, 801).

Reviews on ultrastructural morphogenesis: Few data are available on this subject. Most of the data known have been reviewed in the following references (24, 159, 178, 283, 341, 408, 443).

Morphogenetic laws: Gelei (307) and Poljansky and Raikov (613) showed that many of the morphogenetic principles known from the macroevolution of the metazoa are applicable to the protozoa.

Life cycles: A comprehensive review is not available. Valuable readings are found in the following references: (75, 118, 266, 511, 575, 634).

### 3 Terminology

The definitions set down by Corliss (118), which are widely accepted, are used in this review. See Kormos and Kormos (482) for further terms.

### 4 Fission types

Three basic types of cell division can be distinguished in ciliates, viz. homothetogenic (homopolar), enantiotropic, and parallel fission (Figs. 1e, 8, 11, 25, 39–43). Furthermore, division can be monotomic or polytomic. The monotomic mode is typical of most ciliates and results in two filial pro-

ducts, the proter (anterior daughter) and the opisthe (posterior daughter) (Figs. 2, 5, 7, 8, 33, 37, 39–43), called promer and opimer in experimentally treated cells (regenerates). Polytomic fission by palintomy, strobilation, or budding is common in specialized groups like apostomes, astomes, and suctorians (Figs. 23, 28, 32, 50).

Most ciliates divide homothetogenically, i.e. the axes of proter and opisthe have the same orientation or, in other words, the posterior end of the proter is in contact with the anterior end of the opisthe. This results in a transverse or slightly oblique (most cyrtophorids s.l.) division furrow and a perkinetal (transverse) division of the somatic kineties (Figs. 2–8, 14–18, 26, 27, 33, 37–43).

One large group of ciliates, the oligotrichs, divide enantiotropically, i.e. have an inverse homothety and slightly shifting body axes via pronounced morphogenetic movements during stomatogenesis (118, 211, 611). This causes a marked opposition of the axes of the proter and opisthe, at least 90° in middle dividers, and the filial products adhere posteriorly (Fig. 11). Petz and Foissner (611) suggested that enantiotropic cell division in oligotrichs is caused by the early completion of the opisthe's oral structures during stomatogenesis and their restriction to a small region at or below mid-body which later becomes the apical pole of the cell. Such a conclusion seems justified considering other ciliates with a polar oral apparatus, where the newly formed oral structures encircle the perimeter of the cell in mid-body and the division plane is thus transverse (Fig. 8).

Enantiotropic cell division is not restricted to oligotrichs but occurs also in the prostomatid *Pseudobalanion* and, in a modified form, in peritrichs and licnophorean heterotrichs. The last mentioned taxa divide longitudinally, i.e. the axes of the filial products are parallel (Figs. 1e, 25); however, late dividers adhere by their posterior regions, as in oligotrichs, and the pellicular annuli and somatic kineties, respectively, divide perkinetally (transversely). Longitudinal division, i.e. fission along the oral – aboral axis in peritrichs and licnophoreans is thus very probably an adaptation to their sessile mode of life.

## 5 Division modes

I distinguish two basic modes of division, viz. in active and cystic condition (Tab. 2). Division in active condition (as opposed to cystic, where the cell rounds up, secretes a special membrane, and ceases swimming and feeding) is the usual mode in ciliates. Binary or multiple division in reproductive cysts occurs in certain species of most main groups and usually causes a rapid increase in population density, indicating that such species are more *r* than *k*-selected ([266], Figs. 23, 28, 50). Thus, they are often parasites (e.g. apotomes, histophagous tetrahymenids and ophryoglenids, suctorians) or inhabitants of extreme biotopes such as astatic (ephemeral) puddles and soils (e.g. colpodids, some hypotrichs).

## 6 Stomatogenic modes

The value of ontogenetic and especially of stomatogenic data in reconstructing the phylogeny of ciliates has been emphasized by many authors (e.g. 84, 87, 113–118, 301, 304, 420). There is no need to repeat the well-known arguments. It should, however, be mentioned that Bardele's group opened a new dimension by studying stomatogenesis by electron microscopy (24). From their impressive results it became obvious that many important details are too small to be seen with the light microscope. Although probably being the best way to reconstruct ciliate phylogeny, such data will remain rare because it is extremely difficult and time consuming to investigate stomatogenesis with the transmission electron microscope. Many workers will continue to work with the classical methods, especially with the Spanish silver carbonate technique, which is extremely useful in studying fine details of the ciliary pattern (infraciliature). A first attempt to classify the stomatogenic modes («new-mouth-formation», taken in its broadest sense) was undertaken by Corliss (Table 1). He distinguished five types: de novo kinetosomal (e.g. *Diplodinium*, *Strombidium*, *Stentor*, *Euplotes*), de novo cytoplasmic (e.g. *Didinium*), somatic-meridional (e.g. *Colpoda*, *Tetrahymena*), autonomous

(e.g. *Paramecium*), and semi-autonomous (e.g. *Pseudomicrothorax*, *Pseudocohnilembus*). A few years later, Hanson (370) suggested another classification without, however, providing any details: paraflagellar stomatogenesis of the opisthe (e.g. *Dileptus*), preflagellar stomatogenesis of the proter and the opisthe (e.g. *Nassula*), and preflagellar stomatogenesis of the opisthe (e.g. *Paramecium*). In 1973, Corliss (116) proposed a refined classification which quickly became widely accepted and is still used (Table 1): apokinetal, parakinetal, buccokinetal, and telokinetal stomatogenesis. Recently, some subtypes were distinguished in the telokinetal mode (24, 501). Such a differentiation seems warrantable because there is an increasing amount of evidence that the main stomatogenic modes include several non-homologous subtypes. Furthermore, a sophisticated classification more appropriately reflects the greatly increased amount of data and might stimulate detailed studies. I thus introduce some additional subtypes which are detailed in the following paragraphs.

### 6.1 Apokinetal stomatogenesis (AK)

The oral anlage has no apparent preassociation with either somatic kineties or the parental buccal apparatus; it was formerly known as «de novo kinetosomal mode of stomatogenesis» (113). At least two subtypes can be distinguished.

#### 6.1.1 Epiapokinetal (EAK)

The oral anlage develops on the cell surface. Found, e.g., in some (many?) hypotrichs and in halteriids (Figs. 1d, 10, 14, 15).

#### 6.1.2 Hypoapokinetal (HAK)

The oral anlage develops in a subsurface pouch or in an intracellular tube (possibly a type of its own). Found in pseudohypotrichs (e.g. *Euplotes*), strombidiids and strobilidiids (Figs. 12, 13, 18, 19).

**Table 1:** Classification of stomatogenic patterns in ciliated protozoa

Corliss (113)	Corliss (116, 118)	New classification	
		main types	subtypes
de novo kinetosomal	→ apokinetal	→ apokinetal (AK)	epiapokinetal (EAK) hypoapokinetal (HAK)
de novo cytoplasmic	<hr/>		
somatic-meridional	→ parakinetal	→ parakinetal (PK)	monoparakinetal (MPK) polyparakinetal (PPK) amphiparakinetal (APK) teloparakinetal (TPK) biparakinetal (BPK)
autonomous	→ buccokinetal	→ buccokinetal (BK)	ophryobuccokinetal (OBK) scuticobuccokinetal (SBK)
semi-autonomous			
	→ telokinetal	→ telokinetal (TK)	holotelokinetal (HTK) merotelokinetal (MTK) pleurotelokinetal (PTK) monotelokinetal (MOTK) intertelokinetal (ITK) cryptotelokinetal (CTK)
<hr/>			
		→ mixokinetal (MK)	

## 6.2 Parakinetal stomatogenesis (PK)

The oral anlage is derived directly from (or appears alongside) one or more of the parental postoral somatic kineties at a level destined to be slightly posterior to the eventual fission furrow; the primordial field (anlage) for the opisthe's oral apparatus thus appears subequatorially on the ventral surface at a location (far) removed from the parental mouthparts; it was formerly known as «somatic-meridional stomatogenesis» (113). Several subtypes can be distinguished.

### 6.2.1 Monoparakinetal (MPK)

Only one postoral kinety («director meridian») is involved in the formation of the oral anlage. Proliferation is lateral. Found for example in many tetrahymenids but also in some small spirotrichs like *Blepharisma bimicronucleata* (Figs. 1a, 22).

### 6.2.2 Polyparakinetal (PPK)

Two or more postoral kineties are involved in the formation of the oral anlage. Proliferation of basal

bodies is oblique and/or longitudinal. Found in many heterotrichs, e.g. *Condylostoma* and *Blepharisma* (Figs. 1b, 2–4).

### 6.2.3 Amphiparakinetal (APK)

The curved oral primordium intersects many postoral kineties at two sites and thus encloses few to many short, nonproliferating parental kinety fragments. Found in some heterotrichs, e.g. *Fabrea* and *Stentor* (Figs. 1c, 8).

### 6.2.4 Teloparakinetal (TPK)

The oral anlage originates by proliferation of basal bodies at the anterior ends of postoral intercalary kineties and at the broken ends of bipolar kineties. By lateral proliferation of basal bodies, many short «kinetofragments» originate which later align to adoral membranelles and a paroral membrane. Typically found in ophryoglenids s. l. (Fig. 23). This mode is very similar to the pleurotelokinetal stomatogenesis found in colpodids and several heterotrichs. The main difference by light-microscopy is the site of the primordium formation: lateral in colpodids and heterotrichs, postoral in ophryoglenids.

### 6.2.5 Biparakinetal (BPK)

Two oral primordia are formed independently and amphiparakinetically. Found in folliculinids (Fig. 9).

## 6.3 Buccokinetal stomatogenesis (BK)

Parental oral basal bodies are directly involved in the generation of the opisthe's oral infraciliature; it was formerly known as «autonomous and/or semi-autonomous mode(s) of stomatogenesis» (113). At least two subtypes can be distinguished.

### 6.3.1 Ophryobuccokinetal (OBK)

The opisthe's oral infraciliature derives from one to several ophryo (germinal) kineties and the paroral membrane (e.g. peritrichs, *Frontonia*) or from a homologous anarchic field of basal bodies and the paroral membrane (e.g. *Paramecium*). This definition is based mainly on (still unpublished) results of Beran (34). I include in this group also the peritrichs, whose germinal (ophryo) kinety is – like the anarchic field of the peniculines – disordered and nonciliated (Figs. 24, 25).

### 6.3.2 Scuticobuccokinetal (SBK)

The opisthe's oral infraciliature derives either from the paroral membrane and a separate set of basal bodies («scutica») located posterior or parallel to the paroral membrane or solely from the paroral membrane (Figs. 26, 27). Several «minitypes» can be distinguished according to the exact origin of the oral primordia and the extent of parental membranellar dedifferentiation (166, 714).

The scutica is a transient «compound» kinetosomal structure or organelle identifiable by its shape, location, and presence during the developmental process of stomatogenesis, thus appearing in a late ontogenetic stage in the binary fission of the group of ciliates possessing it; quite conspicuous but generally nonciliated at the time of its (fleeting) existence, the scutica represents the remainder of an often much larger stomatogenic field of basal bodies (buccal anlage, in effect) located near (and slightly to the right of) the posterior termination of the presumptive infraciliary base of the paroral membrane

in both the proter and opisthe; typically, it manifests a hook-like or whiplash configuration (giving it its name), recurving back to the right; presumably its basal bodies arise from parts of the buccal infraciliature of the parental organism; its typical ultimate fate, if it does not disappear altogether or become entirely incorporated into the haplokinetal base of the paroral membrane, is to persist as a ciliiferous or nonciliiferous vestige of varying size and shape, next to the base of the trophont's paroral membrane and/or at the anterior end of the director-meridian. The scutica is thought to be limited to members of its namesake, the Scuticociliatida, but its homologue may be present in species of other orders; the term has been erroneously spelled «scuticus» in the recent literature – but it is a perfectly good Latin word of feminine gender requiring the terminal «a» in the nominative singular (118).

## 6.4 Telokinetal stomatogenesis (TK)

The formation of the new oral infraciliature occurs by direct involvement either of basal bodies at the anterior extremities of all or some of the encircling somatic kineties or of basal bodies comprising the short kinetofragments available in the vicinity (118). Several subtypes have been distinguished (24, 501) and some more are suggested here.

### 6.4.1 Holotelokinetal (HTK)

All somatic kineties proliferate kinetofragments. The oral ciliature is either a circumoral kinety, i.e. is clearly separate from the somatic kineties in the interphase cell, or it is simply composed of the anteriormost (oralized [270]) basal bodies of the somatic kineties. The dikinetids of the brush (one or several somatic ciliary rows with specialized, i.e. paired and/or shortened cilia at the anterior end; Fig. 37a) originate from the anteriormost monokinetids of the opisthe's brush kineties. Typically found in haptorids (Figs. 37, 39–43).

### 6.4.2 Merotelokinetal (MTK)

Only a limited number of somatic kineties are involved in the formation of the oral ciliature, i.e.



produce kinetofragments. If adoral membranelles are present, they arise from the leftmost stomatogenic somatic kineties whereas the circumoral kinety (paroral membrane) originates from the rightmost stomatogenic kineties. Found in colpodids s. str., cyrtophorids, and prorodontids (Figs. 31, 36, 50–52).

#### 6.4.3 Pleurotelokinetal (PTK)

The opisthe's oral structures originate as kinetofragments subequatorially within several right lateral kineties (Fig. 49). Found in cyrtolophosidid colpodids (e.g. *Platyophrya*) and, possibly, in some heterotrichs (e.g. *Nyctotherus*).

#### 6.4.4 Monotelokinetal (MOTK)

The kinetofragments are produced in the somatic portion of oral kineties. The dikinetids of the brush originate from the anteriormost monokinetids of the opisthe's brush kinety (Figs. 44, 45). This type, found only in pleurostomatid haptorids, was originally classified as buccokinetal (289); however, as only the posterior somatic portion, which lacks nematodesmata and transverse microtubular lamellae, of the perioral kineties is involved in the formation of the buccal kineties of the opisthe, it represents telokinetal rather than buccokinetal stomatogenesis (501).

#### 6.4.5 Intertelokinetal (ITK)

Similar to the holotelokinetal mode but additional kinetofragments are produced, possibly by lateral proliferation of basal bodies, and intercalated between the kinetofragments at the anterior end of the somatic kineties. This reinforces the circumoral ciliature (Fig. 38). Found in *Alloiozonia*, *Didesmis*, and possibly many other buetschliids (but apparently not in *Polymorpha*, which has a «normal» holotelokinetal stomatogenesis). *Balantidium* also belongs to this mode because the supernumerary kineties at the left side of the oral opening are produced by «elineation» (215). This confirms the classification of the Balantidiidae within the haptorids (504).

#### 6.4.6 Cryptotelokinetal (CTK)

The opisthe's oral structures originate as kinetofragments subequatorially from subcortical, non-ciliated, somatic basal bodies. The kinetofragments develop in two or three pouches, which do not seem to open exteriorly until an advanced stage of stomatogenesis has been reached, i.e. at least two of the anlagen have fused and are ciliated. Found in entodiniomorphids (Figs. 47, 48).

### 6.5 Mixokinetal stomatogenesis (MK)

This new main mode is introduced to describe stomatogenic patterns where the somatic kineties and the parental oral apparatus simultaneously participate in the formation of the oral infraciliature of the opisthe (Fig. 33). A mixokinetal stomatogenesis is found in nassulids, microthoracids, *Protocruzia*, and, possibly, in apostomes. Unfortunately, the exact origin of the paroral membrane and the oigival ciliary field (adoral membranelle 3?) is still unclear in apostomatid ciliates (59). However, other details (see below) are highly reminiscent of those found, e.g., in the nassulid *Furgasonia*. Thus, the apostomate stomatogenesis is provisionally classified as mixokinetal.

Typically, the paroral membrane is inconspicuous or recognizable only during stomatogenesis and is of buccal origin, often showing a distinct migration, i.e. the entire organelle or a part of it moves posteriorly (Figs. 29, 30, 33). In apostomes, for instance, the paroral migrates from the ventral surface near the apex of the organism to the posterior dorsal third of the body (59). In *Furgasonia* the posterior third of the parental paroral membrane migrates to mid-body and becomes the anlage of the paroral membrane of the opisthe. The adoral membranelles (falciform ciliary fields in apostomes) are well developed and of somatic origin, i.e. are formed merotelokinetally (59, 184). In *Protocruzia* a migrating basal body pair, generated by the proter's paroral membrane, produces the opisthe's adoral membranelles; the opisthe's paroral membrane originates by lateral proliferation of basal bodies from kinety 1 (352).

Corliss (116) postulated the following evolutionary sequence of the stomatogenic modes: the telokinetal mode gave rise to the buccokinetal mode on the

one hand, and to the parakinetal mode on the other; subsequently, the parakinetal mode gave rise to the apokinetal mode. Unfortunately, no data are available to prove or disprove this hypothesis a priori (84). Recent ultrastructural (519) and molecular (670) data, however, indicate that karyorelictids and heterotrichs are the most ancient ciliates, which would disprove Corliss's suggestion because most heterotrichs have a parakinetal stomatogenesis.

Corliss and Roque (120) proposed two hypotheses about how stomatogenic modes could be used for supra-generic classification of ciliates: (i) The general pattern of new mouth formation and the types of ciliature (really infraciliature) involved in the various stages of stomatogenesis allow separation of groups of organisms into suborders. (ii) The details of stomatogenesis allow recognition of taxonomic boundaries at family level. These suggestions have been widely accepted but little used, i.e. most recent supra-generic classifications are still based mainly on interphase morphology and ultrastructural data of the somatic cortex; however, the number of orders and families which have been morphogenetically defined is rapidly increasing. To mention only a few: the scuticociliates (701), most colpodids (266), and hypotrichs (241). Several authors demand that genera and even species should be defined morphogenetically (e.g. 383, 603). I agree with Corliss and Roque (120) that morphogenetic differences among the species of a genus are often very slight and can thus hardly be used to define species. If a certain species within a genus has a different stomatogenic mode, then it is likely misclassified, i.e. belongs to another genus or family. Examples are likely to be found in many hypotrich families.

Another aspect of stomatogenesis which has phylogenetic implications is the fate of the parental oral apparatus, viz. whether it remains intact or is partially or completely reorganized during cell division. This character was first used by Small (703) as one of several features distinguishing rhabdophoran (parental oral structures retained) form cyrtophoran ciliates (parental oral structures partially or completely reorganized); however, all gradations occur, e.g., in hypotrichs (Table 2), indicating that this character must be used with care and might be of significance for distinguishing lower categories only. Furthermore, it is often difficult, at least by light microscopy, to establish whether or not there is some reorganization because, possibly, it is frequently cryptic («internal»), i.e. occurs without forming special anlagen.

The characteristics discussed in this chapter can be summarized in a «stomatogenic fingerprint» which should include (597): (i) the stomatogenic mode; (ii) the site(s) of origin of the oral primordium; (iii) the number of basal body fields in the early primordium; (iv) the shape of primordia at different stages of stomatogenesis (principally, kinetal versus non-kinetal organization and existence of visible differentiation gradients); (v) the patterns of movement the primordia undergo at different stages of stomatogenesis, and (vi) the extent of dedifferentiation in the parental oral apparatus during opisthe stomatogenesis.

## 7 Phenomenology and phylogenetic implications of cortical morphogenesis in ciliated protozoa

In the following paragraphs, I have tried to briefly review the available data on cortical morphogenesis in certain ciliate groups. The data base, i.e. the species studied and the literature involved, is contained in Table 2. I have used simple vernacular names for the higher categories because the supra-familial classification of ciliates is still controversial.

### 7.1 Postciliodesmatophorea

#### 7.1.1 Heterotrichs

The heterotrichs typically have a conspicuous ad-oral zone of membranelles, either at the anterior end or extending from there to mid-body. Some of them, e.g. *Stentor* and the «bottle animal» *Folliculina*, are common and widely known. One large family, the Folliculinidae, is loricate; most lichenophorids are attached to marine invertebrates. Many heterotrichs live anaerobically in the sapropelic mud of freshwaters, e.g. metopids, caenomorphids, and odontostomatids.

**Table 2:** A collection of morphogenetic data on ciliated protozoa. Systematic groups are mainly according to Corliss (118); otherwise species are ordered alphabetically. No attempts have been made to correct taxonomic or nomenclatural mistakes. See footnotes for explanation of abbreviations.

Species <sup>1</sup>	Methods <sup>2</sup>	Evaluation <sup>3</sup>	Fission type <sup>4</sup>	Division mode <sup>5</sup>	Stomatogenic mode <sup>6</sup>	Parental oral infraciliature <sup>7</sup>	Macronucleus type <sup>8</sup>	References
<b>Postciliodesmatophorea</b>								
<b>Heterotrichs</b> (important general and/or monographic literature [8, 311, 723, 741, 784])								
<i>Blepharisma bimicronucleata</i>	L	+	H	AC	MPK	PCR	HOM	784
<i>Blepharisma japonicum</i>	L	+	H	AC	PPK	PPR	HOM	735
<i>Blepharisma japonicum</i>	L, P, TEM	+++	H	AC	PPK	PCR?	HOM	669
<i>Blepharisma lateritia</i>	L	+	H	AC	PK	?	HOM	723
<i>Blepharisma undulans</i>	L	++	H	AC	PPK	PPR	HOM	176
<i>Caenomorphia medusula</i>	SC	++	H?	AC	TK?	PR	HOM	530
<i>Chattonidium setense</i>	CL	+	H	AC	MPK	PR	HOM	784
<i>Climacostomum virens</i>	L	+	H	AC	PPK	PPR	HOM	723
<i>Climacostomum virens</i>	P	++	H	AC	PPK	PPR	HOM	174, 201
<i>Condylostoma arenarium</i>	CL	++	H	AC	PPK	PCR	HOM	784
<i>Condylostoma magnum</i>	L, P, TEM	*	—	—	—	—	—	48, 50, 743
<i>Condylostoma patens</i>	L, P, TEM	*	—	—	—	—	—	753
<i>Condylostoma spatiosum</i>	CL	+	H	AC	PPK	?	HOM	728, 729
<i>Eufolliculina uhligi</i>	L, P, SEM TEM	+++	H	AC	BPK	PCR	HOM	557–564
<i>Fabrea salina</i>	L	+	H	AC	?	PCR	HOM	185
<i>Fabrea salina</i>	CL	++	H	AC	APK	PCR	HOM	784
<i>Folliculinids</i>	L	+	H	AC	?	?	HOM	363
<i>Folliculina</i> sp.	L	*	—	—	—	—	—	3
<i>Folliculina ampulla</i>	L	+	H	AC	?	PCR	HOM	665
<i>Folliculina ampulla</i>	L, CL	+	H	AC	?	PCR	HOM	204
<i>Folliculina boltoni</i>	L	+	H	AC	?	PCR	HOM	600
<i>Folliculina boltoni</i>	L	*	—	—	—	—	—	367
<i>Folliculina simplex</i>	L?	+	H	AC	?	?	HOM	208
<i>Folliculinopsis producta</i>	CL	+	H	AC	BPK?	PCR	HOM	784
<i>Licnophora</i> spp.	L	+	PA	AC	?	?	HOM	725
<i>Licnophora</i> spp.	CL	++	PA	AC	EAK	PPR	HOM	783, 784
<i>Licnophora auerbachii</i>	L	+	PA	AC	EAK	?	HOM	792
<i>Licnophora macfarlandi</i>	L	+	PA	AC	EAK?	PPR	HOM	22
<i>Magnifolliculina binalata</i>	L	*	—	—	—	—	—	779
<i>Metafolliculina andrewsi</i>	L	*	—	—	—	—	—	4, 5

<sup>1</sup> Names usually given as written in original literature, i.e. no attempts have been made to correct taxonomic and nomenclatural mistakes. However, widely accepted new combinations, e.g. *Chilodonella* / *Trithigmostoma*, have been used if appropriate.

<sup>2</sup> CL = Chatton and Lwoff's wet silver nitrate method (and modifications), I = immunocytochemistry, K = Klein's dry silver nitrate method (and modifications), L = from life and/or conventional histological techniques (e.g., hematoxylin), P = protargol, SC = Fernandez-Galiano's silver carbonate method (and modifications), SEM = scanning electron microscopy, TEM = transmission electron microscopy.

<sup>3</sup> + = insufficient, e.g. based on live observations or data documented by micrographs only; ++ = good quality, sufficient for conventional purposes, data documented by reliable line drawings; +++ = excellent, usually containing electron microscopic observations, micrographs, and reliable drawings; \* = special aspects treated only, e.g. morphogenesis of fibrillar system, lorica, or microstome-macrotope transformation; A = only abstract available.

<sup>4</sup> Determined according to the data provided. E = enantiotropic, EVB = evaginative budding, EXB = external budding, H = homothetogenic, INB = internal budding, PA = parallel.

<sup>5</sup> Determined according to the data provided. AC = in active condition, i.e. not in reproductive cysts, C = reproductive cysts or budding within cysts.

<sup>6</sup> Determined according to the data provided (often difficult!). See chapter 6 for detailed explanation of modes. AK = apokinetal, APK = amphiparakinetal, BK = buccokinetal, BPK = biparakinetal, CTK = cryptotelokinetal, EAK = epiapokinetal, HAK = hypoapokinetal, HTK = holotelokinetal, ITK = intertelokinetal, MK = mixokinetal, MPK = monoparakinetal, MTK = merotelokinetal, MOTK = monotelokinetal, OBK = ophryobuccokinetal, PK = parakinetal, PPK = polyparakinetal, PTK = pleurotelokinetal, SBK = scuticobuccokinetal, TK = telokinetal, TPK = teloparakinetal.

<sup>7</sup> Determined according to the data provided (often insufficient and/or difficult to interpret!). PR = parental oral structures retained, PCR = parental oral structures completely reorganized, PPR = parental oral structures partially reorganized.

<sup>8</sup> Determined according to the data provided and from (217, 645). HEM = heteromeric, HOM homomeric, ND = non-dividing, RB = replication band.



(Table 2 continued)

Species <sup>1</sup>	Methods <sup>2</sup>	Evaluation <sup>3</sup>	Fission type <sup>4</sup>	Division mode <sup>5</sup>	Stomatogenic mode <sup>6</sup>	Parental oral infraciliature <sup>7</sup>	Macronucleus type <sup>8</sup>	References
<i>Metafolliculina andrewsi</i>	L	+	H	AC	?	PCR	HOM	777, 780
<i>Nyctotheroides njinei</i>	P?	+	H	AC	PTK	?	HOM	8
<i>Nyctotheroides lescurei</i>	P?	+	H	AC	PTK	PPR	HOM	8
<i>Nyctotherus cordiformis</i>	L	+	H	AC	?	?	HOM	723
<i>Nyctotherus cordiformis</i>	L	+	H	AC	PTK?	PPR	HOM	808
<i>Nyctotherus cordiformis</i>	CL	+	H	AC	PPK	?	HOM	784
<i>Nyctotherus cordiformis</i>	L	*	–	–	–	–	–	315
<i>Nyctotherus macropharyngeus</i>	L	+	H	AC	?	?	HOM	359
<i>Nyctotherus ovalis</i>	P?	++	H	AC	PTK	PPR	HOM	8
<i>Nyctotherus ovalis</i>	SC	+	H	AC	PTK?	PCR?	HOM	667
<i>Nyctotherus ovalis</i>	L	+	H	AC	?	?	HOM	846
<i>Pronyctotherus dragescoi</i>	P?	+	H	AC	PTK	?	HOM	8
<i>Protocruzia tuzeti</i>	P	++	H	AC	MK	PPR?	HOM	352, 680
<i>Spirostomum ambiguum</i>	L	+	H	AC	PPK?	?	HOM	723
<i>Spirostomum ambiguum</i>	L	+	H	AC	PPK?	PCR?	HOM	176
<i>Spirostomum intermedium</i>	L	+	H	AC	PPK?	PCR?	HOM	176
<i>Spirostomum teres</i>	L	+	H	AC	PPK?	?	HOM	723
<i>Spirostomum teres</i>	CL	+	H	AC	MPK	?	HOM	784
<i>Stentor coeruleus</i>	L	+	H	AC	APK?	?	HOM	723
<i>Stentor coeruleus</i>	L	+	H	AC	?	?	HOM	552
<i>Stentor coeruleus</i>	L	+	H	AC	APK	?	HOM	676
<i>Stentor coeruleus</i>	L	+	H	AC	APK	?	HOM	441
<i>Stentor coeruleus</i>	L	+	H	AC	APK	?	HOM	681
<i>Stentor coeruleus</i>	L	+	H	AC	APK	?	HOM	776
<i>Stentor coeruleus</i>	L	+	H	AC	APK	PPR	HOM	740–742, 752, 754
<i>Stentor coeruleus</i>	P	*	–	–	–	–	–	74
<i>Stentor coeruleus</i>	SEM, TEM	*	–	–	APK	–	–	152, 596
<i>Stentor coeruleus</i>	P	*	–	–	APK	–	–	598
<i>Stentor niger</i>	L	+	H	AC	APK?	?	HOM	723
<i>Stentor niger</i>	P	+	H	AC	APK?	?	HOM	168
<i>Stentor polymorphus</i>	L	+	H	AC	APK?	?	HOM	723
<i>Stentor polymorphus</i>	L	+	H	AC	?	?	HOM	566
<i>Stentor roeselii</i>	L	+	H	AC	APK?	?	HOM	723
<i>Transitella corbifera</i>	P	++	H	AC	PTK?	PPR	HOM	416
<b>Karyorelictids</b>								
<i>Loxodes</i> sp.	P	+	H	AC	MPK	?	ND	765
<i>Loxodes magnus</i>	P	+	H	AC	BK	?	ND	579, 624
<b>Spirotrichea</b>								
<b>Oligotrichs</b> (important general and/or monographic literature [211, 500, 610, 611])								
<i>Codonella cratera</i>	P	++	E	AC	HAK	PR	RB	611
<i>Cyrtarocyclus ehrenbergii</i>	L	+	E	AC	?	?	RB	684
<i>Favella ehrenbergii</i>	L	*	E	AC	–	–	–	499, 500
<i>Favella serrata</i>	L	+	E	AC	?	?	RB	80
<i>Halteria geleiana</i>	L	+	E	AC	?	?	?	737
<i>Halteria grandinella</i>	L	+	E	AC	?	?	?	16
<i>Halteria grandinella</i>	CL	++	E	AC	EAK	PR	?	211
<i>Halteria grandinella</i>	SC	+	E	AC	?	?	?	233
<i>Halteria grandinella</i>	L	+	E	AC	?	?	?	91
<i>Halteria grandinella</i>	SEM	++	E	AC	EAK	PR	?	610
<i>Halteria grandinella</i>	P	++	E	AC	EAK	PR	RB	715
<i>Meseres corlissi</i>	P, SEM	+++	E	AC	EAK	PR	RB	610
<i>Stenosemella ventricosa</i>	L	+	E	AC	?	?	RB	400
<i>Strobilidium caudatum</i>	L	+	E	AC	?	?	RB	482
<i>Strobilidium caudatum</i>	P	++	E	AC	HAK	?	RB	138
<i>Strobilidium caudatum</i>	P, SEM	++	E	AC	HAK	PR	RB	610
<i>Strombidium</i> spp.	L	+	?	AC	?	?	?	482
<i>Strombidium kryalis</i>	P	++	E	AC	EAK	PR	RB	851

(Table 2 continued)

Species <sup>1</sup>	Methods <sup>2</sup>	Evaluation <sup>3</sup>	Fission type <sup>4</sup>	Division mode <sup>5</sup>	Stomatogenic mode <sup>6</sup>	Parental oral infraciliature <sup>7</sup>	Macronucleus type <sup>8</sup>	References
<i>Strombidium mirabile</i>	L	+	?	AC	?	?	RB	599
<i>Strombidium oculatum</i>	L, CL	+	E	AC	?	PR	?	211
<i>Strombidium sulcatum</i>	L	+	E	AC	?	PR	?	211
<i>Strombidium sulcatum</i>	P	+	E	AC	?	?	RB	138
<i>Strombidium testaceum</i>	L	+	E	AC	?	?	RB	11
<i>Tintinnids</i> div. spec.	L	+	?	AC	HAK?	?	RB	187
<i>Tintinnidium fluviatile</i>	L	+	?	AC	?	?	RB	186
<i>Tintinnidium inquilinum</i>	L	+	E	AC	HAK	?	RB	203
<i>Tintinnidium pusillum</i>	L	*	—	—	—	—	—	647
<i>Tintinnidium pusillum</i>	P	++	E	AC	HAK	PR	RB	611
<i>Tintinnidium semiciliatum</i>	P, SEM	++	E	AC	HAK	PR	RB	611
<i>Tintinnopsis beroidea</i>	L	+	E	AC	?	?	RB	400
<i>Tintinnopsis campanula</i>	L	+	?	AC	?	?	RB	494
<i>Tintinnopsis cylindrata</i>	P	++	E	AC	HAK	PR	RB	611
<i>Tintinnopsis nucula</i>	L	+	E	AC	?	PR	RB	79
<i>Tintinnopsis subacuta</i>	L	+	E?	AC	?	?	RB	42, 43
<b>Hypotrichs</b> (important general and/or monographic literature [52, 55, 103, 241, 247, 248, 383, 722, 764, 771, 796])								
<i>Amphisiella australis</i>	P	++	H	AC	PK?	PPR	RB	265, 789
<i>Amphisiella marioni</i>	P	++	H	AC	PK?	PPR	RB	812
<i>Amphisiella terricola</i>	P	+	H	AC	PK?	?	RB	383
<i>Amphisiellides illuvialis</i>	P	++	H	AC	PK?	PPR	RB	848
<i>Aspidisca</i> spp.	P	++	H	AC	HAK	PR	RB	767
<i>Aspidisca cicada</i>	L, P	+	H	AC	HAK	PR	RB	156
<i>Aspidisca cicada</i>	L, P	++	H	AC	HAK	PR	RB	390
<i>Aspidisca lyncaster</i>	P	+	H	AC	?	?	RB	143
<i>Aspidisca lynceus</i>	L	+	H	AC	?	?	RB	722
<i>Aspidisca orthopogon</i>	P	++	H	AC	HAK	PR	RB	143
<i>Bakuella edaphoni</i>	P	++	H	AC	PK?	PPR	RB	718
<i>Bakuella pampinaria</i>	P	++	H	AC	PK?	PPR	RB	179
<i>Bakuella polycirrata</i>	CL	+	H	AC	?	?	RB	9
<i>Bakuella salinarum</i>	P	++	H	AC	PK?	PPR	RB	546, 718
<i>Certesias quadrinucleata</i>	P	++	H	AC	HAK	PPR	RB	813
<i>Cladotricha koltzowii</i>	P	++	H	AC	EAK	PPR	RB	54
<i>Cladotricha variabilis</i>	P	++	H	AC	PK?	PPR	RB	54
<i>Coniculostomum monilata</i>	P	++	H	AC	PK?	PPR	RB	453
<i>Cyrtohymena muscorum</i>	P	++	H	AC	EAK	PPR	RB	787
<i>Diophrys</i> spp.	P	++	H	AC	HAK	PPR	RB	392
<i>Diophrys appendiculata</i>	L	+	H	AC	?	PPR	RB	732
<i>Diophrys oligothrix</i>	P	++	H	AC	HAK	PCR?	RB	129
<i>Diophrys scutum</i>	P	++	H	AC	HAK	PPR	RB	717
<i>Discocephalus ehrenbergi</i>	P, SEM	++	H	AC	EAK	PPR	RB	812
<i>Engelmanniella mobilis</i>	P	++	H	AC	EAK	PPR	RB	824, 829
<i>Epiclintes ambiguus</i>	P	++	H	AC	PK?	PCR	RB	816
<i>Euplotes</i> sp.	CL	*	—	—	—	—	—	277, 303
<i>Euplotes</i> sp.	P, SEM	++	H	AC	HAK	PCR	RB	290, 291
<i>Euplotes</i> sp.	P	+	H	AC	HAK	?	RB	525
<i>Euplotes aediculatus</i>	SEM	*	—	—	—	—	—	469
<i>Euplotes aediculatus</i>	CL	++	H	AC	HAK	PR	RB	798
<i>Euplotes aediculatus</i>	P, SC	++	H	AC	HAK	PR	RB	786
<i>Euplotes aediculatus</i>	CL, SEM	A	H	AC	HAK	?	RB	679
<i>Euplotes aediculatus</i>	CL, P, TEM, IF	+++	H	AC	HAK	PR	RB	242, 243
<i>Euplotes affinis</i>	P	++	H	AC	HAK	PR	RB	592
<i>Euplotes albus</i>	SC	*	—	—	—	—	—	232
<i>Euplotes charon</i>	L	+	H	AC	?	?	RB	722
<i>Euplotes charon</i>	L	+	H	AC	?	?	RB	502
<i>Euplotes charon</i>	P, SC	++	H	AC	HAK	PR	RB	786

(Table 2 continued)

Species <sup>1</sup>	Methods <sup>2</sup>	Evaluation <sup>3</sup>	Fission type <sup>4</sup>	Division mode <sup>5</sup>	Stomatogenic mode <sup>6</sup>	Parental oral infraciliature <sup>7</sup>	Macronucleus type <sup>8</sup>	References
<i>Euplotes crassus</i>	L, CL	++	H	AC	HAK	PR	RB	92, 103
<i>Euplotes crassus</i>	P, SC	++	H	AC	HAK	PR	RB	786
<i>Euplotes daidaleos</i>	L	++	H	AC	HAK	PR	RB	154, 155, 157
<i>Euplotes daidaleos</i>	P, SC	++	H	AC	HAK	PR	RB	786
<i>Euplotes encysticus</i>	CL	*	—	—	—	—	—	536
<i>Euplotes eurytomus</i>	CL	+	H	AC	HAK	?	RB	51
<i>Euplotes eurytomus</i>	L, CL	*	—	—	—	—	—	389
<i>Euplotes eurytomus</i>	CL	++	H	AC	HAK	PR	RB	830
<i>Euplotes eurytomus</i>	P, TEM, SEM	+++	H	AC	HAK	?	RB	663
<i>Euplotes eurytomus</i>	P, SC	++	H	AC	HAK	PR	RB	786
<i>Euplotes eurytomus</i>	L, CL	+	H	AC	HAK	?	RB	692
<i>Euplotes finki</i>	P, SC	++	H	AC	HAK	PR	RB	786
<i>Euplotes harpa</i>	L	++	H	AC	HAK?	PCR?	RB	796
<i>Euplotes mediterraneus</i>	SC	+	H	AC	HAK	?	RB	235
<i>Euplotes minuta</i>	P, SC	++	H	AC	HAK	PR	RB	786
<i>Euplotes minuta</i>	CL	*	—	—	—	—	—	382
<i>Euplotes moebiusi</i>	K	++	H	AC	HAK	PCR?	RB	464, 465, 467
<i>Euplotes octocarinatus</i>	P, SC	++	H	AC	HAK	PR	RB	786
<i>Euplotes patella</i>	L	+	H	AC	HAK	?	RB	677, 678
<i>Euplotes patella</i>	L	++	H	AC	HAK	PR	RB	840
<i>Euplotes patella</i>	L	*	—	—	—	—	—	775
<i>Euplotes patella</i>	L, K, CL	++	H	AC	HAK	PR	RB	368, 369
<i>Euplotes patella</i>	L, CL	++	H	AC	HAK	PR	RB	103
<i>Euplotes patella</i>	P, SC	++	H	AC	HAK	PR	RB	786
<i>Euplotes plumipes</i>	L, CL, P	++	H	AC	HAK	PR	RB	409
<i>Euplotes raikovi</i>	L, CL	++	H	AC	HAK	PR?	RB	797
<i>Euplotes raikovi</i>	P, SC	++	H	AC	HAK	PR	RB	786
<i>Euplotes rariseta</i>	P, SC	++	H	AC	HAK	PR	RB	786
<i>Euplotes vannus</i>	L	+	H	AC	?	PR	RB	550
<i>Euplotes vannus</i>	L, CL, P	*	—	—	—	—	—	244, 409, 774
<i>Euplotes vannus</i>	P, SC	++	H	AC	HAK	PR	RB	785, 786
<i>Euplotes worcesteri</i>	L	++	H	AC	HAK	PR	RB	331
<i>Euplotes woodruffi</i>	P, SC	++	H	AC	HAK	PR	RB	786
<i>Gastrostyla steinii</i>	P	++	H	AC	PK?	PPR	RB	383
<i>Gastrostyla steinii</i>	P	++	H	AC	PK?	PPR	RB	790
<i>Gastrostyla steinii</i>	L, P	*	—	—	—	—	—	769, 802
<i>Gastrostyla sterkii</i>	L	+	H	AC	?	PPR	RB	796
<i>Gastrostyla vorax</i>	L	+	H	AC	?	?	RB	587
<i>Gonostomum affine</i>	P	++	H	AC	EAK	PPR	RB	383
<i>Gonostomum strenua</i>	P	++	H	AC	EAK	PPR	RB	712
<i>Hemiamphisiella terricola</i>	P	++	H	AC	PK?	PPR	RB	848
<i>Hemisincirra heterocirrata</i>	P	++	H	AC	PK?	PPR	RB	383
<i>Hemisincirra inquieta</i>	P	++	H	AC	PK?	PPR	RB	383
<i>Histiculus muscorum</i>	P, TEM	++	H	AC	PK?	PPR	RB	40, 535
<i>Histiculus similis</i>	P	+	H	AC	PK?	PPR	RB	77, 78, 578
<i>Histiculus similis</i>	L	+	H, INB	AC	?	?	RB	90
<i>Histiculus vorax</i>	L, CL	+	H, INB	AC	PK?	?	RB	124, 838
<i>Holosticha</i> spp.	?	A	—	—	—	—	—	391
<i>Holosticha diademata</i>	?	+	H	AC	?	?	RB	52
<i>Holosticha diademata</i>	P	++	H	AC	EAK	PPR	RB	383
<i>Holosticha geleii</i>	P	++	H	AC	EAK	PPR	RB	817
<i>Holosticha mancoidea</i>	P	+	H	AC	PK?	?	RB	383
<i>Holosticha multistilata</i>	P	++	H	AC	PK?	PCR	RB	383
<i>Holosticha musculus</i>	P	+	H	AC	PK?	PPR	RB	526

(Table 2 continued)

Species <sup>1</sup>	Methods <sup>2</sup>	Evaluation <sup>3</sup>	Fission type <sup>4</sup>	Division mode <sup>5</sup>	Stomatogenic mode <sup>6</sup>	Parental oral infraciliature <sup>7</sup>	Macro-nucleus type <sup>8</sup>	References
<i>Holosticha similis</i>	P	++	H	AC	PK?	PCR	RB	383
<i>Holostichides chardezi</i>	P	+	H	AC	PK?	?	RB	264
<i>Holostichides terricola</i>	P	+	H	AC	PK?	?	RB	265
<i>Hypotrichidium conicum</i>	P	++	H	AC	EAK	PPR	RB	246
<i>Hypotrichidium faurei</i>	P	+	H	AC	PK?	PPR	RB	769, 770
<i>Kahliella</i> sp.	P	+	H	AC	?	PPR	RB	245
<i>Kahliella acrobates</i>	P	++	H	AC	PK?	PPR	RB	768, 769
<i>Kahliella bacilliformis</i>	P	+	H	AC	PK?	PPR	RB	246
<i>Kahliella simplex</i>	L	++	H	AC	PK?	PCR	RB	407
<i>Kahliella franzi</i>	P	++	H	AC	EAK	PPR	RB	35
<i>Kahliella marina</i>	P	++	H	AC	PK?	PPR	RB	273
<i>Kerona polyporum</i>	L	*	—	—	—	—	—	88
<i>Kerona polyporum</i>	P	A	—	—	—	—	—	810
<i>Kerona polyporum</i>	P	++	H	AC	EAK	PPR	RB	383, 384
<i>Keronella gracilis</i>	P	++	H	AC	PK?	PPR	RB	804
<i>Keronopsis pulchra</i>	?	+	H	?	?	?	RB	52
<i>Keronopsis rubra</i>	P	+	H	AC	PK?	PCR	RB	440
<i>Keronopsis rubra</i>	P	+	H	AC	PK?	PCR	RB	843
<i>Laurentiella acuminata</i>	P	++	H	AC	PK?	PPR	RB	525, 527
<i>Laurentiella acuminata</i>	P	++	H	AC	PK?	PPR	RB	360
<i>Notohymena rubescens</i>	P	++	H	AC	PK?	PPR	RB	788
<i>Onychodromus acuminatus</i>	P	*	—	—	—	—	—	424
<i>Onychodromus grandis</i>	L	+	H	AC	?	?	RB	722
<i>Onychodromus indica</i>	P	++	H	AC	PK?	PPR	RB	850
<i>Onychodromus quadricornutus</i>	P, SEM	+++	H	AC	PK?	PPR	RB	274, 814
<i>Opisthotricha monspessulana</i>	CL	+	H	AC	EAK?	?	RB	103
<i>Opisthotricha monspessulana</i>	P	++	H	AC	PK?	PPR	RB	342, 343
<i>Orthoamphisiella grelli</i>	P	++	H	AC	EAK	PPR	RB	180
<i>Orthoamphisiella stramenticola</i>	P	++	H	AC	EAK	PPR	RB	180
<i>Oxytricha aeruginosa</i>	P	+	H	AC	PK?	PPR	RB	592
<i>Oxytricha agilis</i>	P	++	H	AC	EAK	PPR	RB	71
<i>Oxytricha bifaria</i>	L	*	—	—	—	—	—	648
<i>Oxytricha crassistilata</i>	P	++	H	AC	PK?	PPR	RB	383
<i>Oxytricha fallax</i>	L	*	—	—	—	—	—	377, 747
<i>Oxytricha fallax</i>	P, SEM, TEM	+++	H	AC	PK?	PPR	RB	334, 335, 338
<i>Oxytricha fennica</i>	P	++	H	AC	PK?	PPR	RB	383
<i>Oxytricha fusiformis</i>	P	+	H	AC	PK?	?	RB	383
<i>Oxytricha gigantea</i>	P	++	H	AC	EAK	PPR	RB	35
<i>Oxytricha granulifera</i>	P	++	H	AC	EAK	PPR	RB	267
<i>Oxytricha longa</i>	P	++	H	AC	PK?	PPR	RB	383
<i>Oxytricha pseudosimilis</i>	P	++	H	AC	PK?	PPR	RB	383
<i>Oxytricha selvatica</i>	P	+	H	AC	EAK	?	RB	383
<i>Oxytricha similis</i>	P	+	H	AC	EAK	?	RB	383
<i>Oxytricha terrestris</i>	P	++	H	AC	PK?	PPR	RB	383
<i>Parabakuella typica</i>	P	++	H	AC	PK?	PPR	RB	716
<i>Paragastrostyla lanceolata</i>	P	++	H	AC	PK?	PPR	RB	383
<i>Paraholosticha muscicola</i>	P	+	H	C	EAK	PCR	RB	772
<i>Paraholosticha muscicola</i>	P	++	H	C	EAK	PCR	RB	151
<i>Paraholosticha sterkii</i>	P	++	H	C	EAK	PCR	RB	150
<i>Parakahliella haideri</i>	P	++	H	AC	PK?	PPR	RB	37
<i>Parakahliella macrostoma</i>	P	++	H	AC	PK?	PPR	RB	40
<i>Paramphisiella caudata</i>	P	++	H	AC	PK?	PPR	RB	848
<i>Parastrongylidium martini</i>	P	++	H	AC	PK?	PPR	RB	246
<i>Parastrongylidium oswaldi</i>	P	++	H	AC	PK?	PPR	HOM	2

(Table 2 continued)

Species <sup>1</sup>	Methods <sup>2</sup>	Evaluation <sup>3</sup>	Fission type <sup>4</sup>	Division mode <sup>5</sup>	Stomatogenic mode <sup>6</sup>	Parental oral infraciliature <sup>7</sup>	Macronucleus type <sup>8</sup>	References
<i>Paraurostyla hymenophora</i>	P, SEM	+++	H	AC	PK?	PPR	RB	339
<i>Paraurostyla weissei</i>	K, P, TEM	+++	H	AC	PK?	PPR	RB	18, 19, 173, 428, 431, 433–436
<i>Paraurostyla weissei</i>	P	++	H	AC	PK?	PPR	RB	826
<i>Paruroleptus musculus</i>	P	+	H	AC	PK?	PPR	RB	526
<i>Pattersoniella vitiphila</i>	P	++	H	AC	PK?	PPR	RB	264
<i>Periholosticha lanceolata</i>	P	++	H	AC	PK?	PPR	RB	383
<i>Periholosticha wilberti</i>	P	++	H	AC	PK?	PPR	RB	713
<i>Plagiotoma lumbrici</i>	L	+	H	AC	?	?	?	723
<i>Plagiotoma lumbrici</i>	L	*	–	–	–	–	RB	175
<i>Plagiotoma lumbrici</i>	CL, P	++	H	AC	PK?	PCR?	?	7, 8
<i>Plagiotoma lumbrici</i>	P	++	H	AC	PK?	PR?	RB	246
<i>Pleurotricha lanceolata</i>	L	+	H	AC	?	?	RB	524
<i>Pleurotricha lanceolata</i>	P, SEM	*	–	–	–	–	–	340
<i>Pleurotricha tihanyiensis</i>	P	+	H	AC	?	PPR	RB	383
<i>Psammocephalus borrori</i>	P	+	H	AC	?	?	RB	812
<i>Psammocephalus faurei</i>	P	+	H	AC	PK?	PPR	RB	812
<i>Pseudokeronopsis</i> spp.	P	++	H	AC	PK?	PCR	RB	823
<i>Pseudokeronopsis ignea</i>	P	++	H	AC	PK?	PCR	RB	546
<i>Pseudokeronopsis rubra</i>	L	+	H	AC	?	PCR	RB	796
<i>Pseudouroleptus caudatus</i>	P	++	H	AC	PK?	PPR	RB	383
<i>Pseudourostyla nova</i>	P	+	H	AC	PK?	PCR	RB	805
<i>Psilotricha succisa</i>	P	++	H	AC	EAK	PR	RB	260
<i>Spiretella plancticola</i>	P	+	H	AC	EAK	?	RB	247
<i>Steinia platystoma</i>	P	+	H	AC	PK?	?	RB	342
<i>Stylonychia histrio</i>	L	+	H	AC	?	?	RB	587
<i>Stylonychia histrio</i>	L	+	H	AC	?	?	RB	376
<i>Stylonychia grandis</i>	P	++	H	AC	PK?	PPR	RB	383
<i>Stylonychia lemnae</i>	P	+	H	AC	PK?	PPR	RB	828
<i>Stylonychia mytilus</i>	L	+	H	AC	?	?	RB	722
<i>Stylonychia mytilus</i>	L	+	H	AC	?	PPR	RB	724
<i>Stylonychia mytilus</i>	P	*	–	–	–	–	–	696, 769
<i>Stylonychia mytilus</i>	P	+	H	AC	?	?	RB	525
<i>Stylonychia mytilus</i>	P	++	H	AC	PK?	PPR	RB	383
<i>Stylonychia mytilus</i>	P	++	H	AC	PK?	PPR	RB	799
<i>Stylonychia mytilus</i>	P	++	H	AC	PK?	PPR	RB	828
<i>Stylonychia mytilus</i>	P	+	H	AC	PK?	PPR	RB	695
<i>Stylonychia mytilus</i>	CL	+	H	AC	PK?	PCR	RB	749
<i>Stylonychia mytilus</i>	L	+	H	AC	?	PCR?	RB	796
<i>Stylonychia notophora</i>	CL	++	H	AC	EAK	PPR	RB	668
<i>Stylonychia pustulata</i>	L, SEM	*	–	–	–	–	–	338, 374
<i>Stylonychia pustulata</i>	P	++	H	AC	EAK	PPR	RB	825
<i>Stylonychia putrina</i>	P	+	H	AC	PK?	?	RB	342
<i>Stylonychia vorax</i>	P	++	H	AC	PK?	PPR	RB	825
<i>Styloplotes appendiculatus</i>	L	+	H	AC	?	?	RB	722
<i>Tachysoma longa</i>	P	+	H	AC	?	PPR	RB	383
<i>Tachysoma pellionellum</i>	L	+	H	AC	?	?	RB	722
<i>Tachysoma pellionellum</i>	P	++	H	AC	PK?	PPR	RB	383
<i>Tachysoma pellionellum</i>	P	++	H	AC	PK?	PPR	RB	751
<i>Tachysoma pellionellum</i>	SC	+	H	AC	?	?	RB	234
<i>Tachysoma perisincirra</i>	P	+	H	AC	?	PPR	RB	383
<i>Tachysoma perisincirra</i>	P	++	H	AC	PK?	PPR	RB	39
<i>Tachysoma terricola</i>	P	++	H	AC	PK?	PPR	RB	383

(Table 2 continued)

Species <sup>1</sup>	Methods <sup>2</sup>	Evaluation <sup>3</sup>	Fission type <sup>4</sup>	Division mode <sup>5</sup>	Stomatogenic mode <sup>6</sup>	Parental oral infraciliature <sup>7</sup>	Macronucleus type <sup>8</sup>	References
<i>Territricha stramenticola</i>	P	*	—	—	—	—	—	36
<i>Thigmokeronopsis jahodai</i>	P, SEM	+++	H	AC	PK?	PCR	RB	811
<i>Trachelochaeta gonostomoida</i>	P	+	H	AC	?	PPR	RB	383
<i>Trachelostyla pediculliformis</i>	L	A	H	AC	?	PCR	RB	471
<i>Tricoronella pulchra</i>	P	*	—	—	—	—	—	45
<i>Uroleptooides atypica</i>	P	+	H	AC	?	PPR	RB	383
<i>Uroleptooides binucleata</i>	P	+	H	AC	PK?	?	RB	383
<i>Uroleptooides caudata</i>	P	++	H	AC	PK?	PPR	RB	383
<i>Uroleptus</i> sp.	P	+	H	AC	EAK	PPR	RB	526
<i>Uroleptus</i> sp.	?	A	H	AC	?	PR	RB	585
<i>Uroleptus caudatus</i>	?	+	H	AC	?	?	RB	52
<i>Uronychia uncinata</i>	L	+	H	AC	?	?	RB	745
<i>Uronychia setigera</i>	L	+	H	AC	?	?	RB	841
<i>Uronychia transfuga</i>	L	++	H	AC	HAK	PPR	RB	796
<i>Uronychia transfuga</i>	L	+	H	AC	?	PR	RB	76
<i>Uronychia transfuga</i>	P	++	H	AC	HAK	PPR	RB	818
<i>Uronychia transfuga</i>	CL, P, SEM	+++	H	AC	HAK	PPR	RB	393
<i>Urosoma macrostyla</i>	P	++	H	AC	PK?	PPR	RB	259
<i>Urosomoida agilliformis</i>	P	++	H	AC	PK?	PPR	RB	268
<i>Urosomoida agilliformis</i>	P	++	H	AC	PK?	PPR	RB	296
<i>Urosomoida minima</i>	P	+	H	AC	PK?	?	RB	383
<i>Urostyla cristata</i>	L, P	++	H	AC	PK?	PCR	RB	179, 427, 429, 430
<i>Urostyla cristata</i>	P, SEM	++	H	AC	PK?	PCR	RB	750
<i>Urostyla grandis</i>	L	+	H	AC	?	?	RB	722
<i>Urostyla grandis</i>	L	+	H	AC	?	?	RB	756
<i>Urostyla grandis</i>	P	++	H	AC	PK?	PCR	RB	430
<i>Urostyla grandis</i>	P	*	—	—	—	—	—	803
<i>Urostyla grandis</i>	L	+	H	AC	?	PR	RB	426
<i>Urostyla marina</i>	L	++	H	AC	PK?	PCR	RB	53
<i>Urostyla thompsoni</i>	P	+	H	AC	PK?	PCR?	RB	807
<b>Oligohymenophorea</b>								
<b>Hymenostomes</b> (important general and/or monographic literature [87, 117, 146, 423, 443, 452, 555, 597, 658, 809])								
<i>Bursostoma bursaria</i>	P	+	H	AC	TPK?	PCR	HOM	297
<i>Colpidium campylum</i>	K	*	—	—	—	—	—	466, 467
<i>Colpidium colpoda</i>	SC	+	H	AC	MPK	?	HOM	528
<i>Colpidium kleini</i>	K	++	H	AC	MPK	?	HOM	250–252
<i>Colpidium kleini</i>	P	++	H	AC	MPK	PPR	HOM	417
<i>Colpidium truncatum</i>	K	+	H	AC	MPK	?	HOM	271
<i>Deltopylum rhabdoides</i>	L, CL	++	H	AC	TPK	PCR	HOM	555, 556
<i>Disematostoma buetschlii</i>	SC	++	H	AC	OBK	PPR	HOM	531
<i>Disematostoma colpidioides</i>	SC	++	H	AC	OBK	PPR	HOM	691
<i>Disematostoma tetraedrica</i>	CL	++	H	AC	OBK	PPR	HOM	657–659
<i>Espejoia culex</i>	P	+	H	AC	MPK?	PCR?	HOM	288
<i>Espejoia mucicola</i>	CL, P	++	H	AC	MPK	PCR?	HOM	288
<i>Frontonia atra</i>	CL	++	H	AC	OBK	PPR	HOM	658
<i>Frontonia atra</i>	SC	++	H	AC	OBK	PPR	HOM	34
<i>Frontonia depressa</i>	CL	A	H	AC	OBK	PPR	HOM	299
<i>Frontonia leucas</i>	CL	A	H	AC	OBK	PCR	HOM	707
<i>Frontonia leucas</i>	CL	++	H	AC	OBK	PPR	HOM	658
<i>Glaucoma chattoni</i>	CL	++	H	AC	MPK	PR	HOM	278
<i>Glaucoma dragescui</i>	SC, P	++	H	AC	MPK	PPR	HOM	523
<i>Glaucoma ferox</i>	CL	+	H	AC	MPK	?	HOM	659

(Table 2 continued)

Species <sup>1</sup>	Methods <sup>2</sup>	Evaluation <sup>3</sup>	Fission type <sup>4</sup>	Division mode <sup>5</sup>	Stomatogenic mode <sup>6</sup>	Parental oral infraciliature <sup>7</sup>	Macronucleus type <sup>8</sup>	References
<i>Glaucoma scintillans</i>	K	*	H	AC	MPK	?	HOM	462
<i>Glaucoma scintillans</i>	CL	++	H	AC	MPK	?	HOM	104
<i>Glaucoma scintillans</i>	K	+	H	AC	MPK	?	HOM	304
<i>Glaucoma scintillans</i>	P	++	H	AC	MPK	PPR	HOM	597
<i>Glaucoma scintillans</i>	CL, P	++	H	AC	MPK	?	HOM	731
<i>Histiobalantium natans</i>	P	++	H	AC	OBK?	PPR	HOM	169
<i>Ichthyophthirioides browni</i>	CL	+	H	C	TPK	PCR	HOM	660
<i>Ichthyophthirius multifiliis</i>	L, SEM	*	—	—	—	—	—	65, 362, 542
<i>Ichthyophthirius multifiliis</i>	L, K, CL	+	H	C	TPK	PCR	HOM	522
<i>Ichthyophthirius multifiliis</i>	L, CL	+	H	C	TPK	PCR	HOM	554, 555
<i>Ichthyophthirius multifiliis</i>	CL	++	H	C	TPK	PCR	HOM	662
<i>Ichthyophthirius multifiliis</i>	L, K, CL	++	H	C	TPK	PCR	HOM	87
<i>Lambornella clarki</i>	CL	+	H	AC	MPK?	?	HOM	119
<i>Lembadion bullinum</i>	SC	++	H	AC	OBK	PPR	HOM	358
<i>Lembadion bullinum</i>	CL	++	H	AC	OBK	PPR	HOM	766
<i>Lembadion luceus</i>	SC	++	H	AC	OBK	PPR	HOM	358
<i>Lembadion magnum</i>	P	+	H	AC	OBK	PPR	HOM	592
<i>Neobursaridium gigas</i>	P	+	H	AC	OBK	PCR	HOM	170
<i>Ophryoglena</i> spp.	L, K, CL	++	H	C	TPK	PCR	HOM	86, 87, 653
<i>Ophryoglena bacterocaryon</i>	CL	++	H	C	TPK	PCR	HOM	661
<i>Ophryoglena mucifera</i>	SC, TEM	++	H	C	TPK	PCR	HOM	632
<i>Ophryoglena pectans</i>	L, CL	++	H	C	TPK	PCR	HOM	553, 555, 556
<i>Paraglaucoma rostrata</i>	CL	+	H	AC	MPK	?	HOM	555
<i>Paramecium</i> sp.	CL	+	H	AC	OBK	PPR	HOM	302
<i>Paramecium</i> spp.	L, CL	++	H	AC	OBK	PPR	HOM	842
<i>Paramecium</i> spp.	L, CL	*	—	—	—	—	—	155
<i>Paramecium</i> spp.	CL	++	H	AC	OBK	PPR	HOM	694
<i>Paramecium aurelia</i>	L	+	H	AC	OBK	PPR	HOM	388
<i>Paramecium aurelia</i>	CL	+	H	AC	OBK	PPR	HOM	655, 656, 658
<i>Paramecium aurelia</i>	CL	+	H	AC	?	?	HOM	748
<i>Paramecium aurelia</i>	CL	++	H	AC	OBK	PPR	HOM	616
<i>Paramecium aurelia</i>	L, CL, TEM	*	—	—	—	—	—	33, 158, 372, 459, 698
<i>Paramecium bursaria</i>	L, TEM	+	H	AC	OBK?	PR?	HOM	178
<i>Paramecium bursaria</i>	L	*	—	—	—	—	—	486, 698, 699
<i>Paramecium caudatum</i>	CL, SC	*	—	—	—	—	—	228, 305, 455, 588
<i>Paramecium multimicronucleatum</i>	IF, TEM	*	—	—	—	—	—	10, 381
<i>Paramecium polycaryum</i>	SC, TEM	+++	H	AC	OBK	PPR	HOM	34
<i>Paramecium tetraurelia</i>	CL, P	++	H	AC	OBK	PPR	HOM	442
<i>Paramecium tetraurelia</i>	SC	++	H	AC	OBK	PPR	HOM	606
<i>Paramecium tetraurelia</i>	P, SC, IF	+++	H	AC	OBK	?	HOM	413
<i>Paramecium tetraurelia</i>	CL, SEM, IF	*	—	—	—	—	—	109, 418
<i>Paramecium trichium</i>	L, CL	+	H	AC	OBK	?	HOM	312
<i>Paramecium trichium</i>	CL	*	—	—	—	—	—	730
<i>Stockesia vernalis</i>	CL	+	H	AC	OBK?	PPR	HOM	658
<i>Tetrahymena bergeri</i>	CL	+	H	AC	MPK	?	HOM	659
<i>Tetrahymena corlissi</i>	CL	++	H	AC, C	MPK	?	HOM	659
<i>Tetrahymena dimorpha</i>	L, CL, SEM	+	H	AC	MPK?	?	HOM	30
<i>Tetrahymena paravorax</i>	P	++	H	AC	MPK	PCR	HOM	545, 580
<i>Tetrahymena patula</i>	L, CL	+	H	AC, C	MPK?	?	HOM	117
<i>Tetrahymena pyriformis</i>	CL	+	H	AC	MPK	?	HOM	555
<i>Tetrahymena pyriformis</i>	CL, P	++	H	AC	MPK	?	HOM	821

(Table 2 continued)

Species <sup>1</sup>	Methods <sup>2</sup>	Evaluation <sup>3</sup>	Fission type <sup>4</sup>	Division mode <sup>5</sup>	Stomatogenic mode <sup>6</sup>	Parental oral infraciliature <sup>7</sup>	Macronucleus type <sup>8</sup>	References
<i>Tetrahymena pyriformis</i>	CL, P, TEM	*	—	—	—	—	—	279, 820
<i>Tetrahymena pyriformis</i>	SEM	++	H	AC	MPK	?	HOM	70
<i>Tetrahymena pyriformis</i>	L, CL, P, TEM, IF	*	—	—	—	—	—	6, 399, 570, 822, 839
<i>Tetrahymena setifera</i>	P	++	H	AC	MPK	PR	HOM	345
<i>Tetrahymena thermophila</i>	L, CL, P, SEM, TEM, IF	+++	H	AC	MPK	PPR	HOM	20, 286, 287, 496, 571–574
<i>Tetrahymena thermophila</i>	L, P, SEM, TEM, IF	*	—	—	—	—	—	432, 446, 758, 831
<i>Tetrahymena vorax</i>	CL, SEM	*	—	AC, C	MPK	PCR	HOM	68, 69, 405
<i>Turaniella vitrea</i>	CL, P	++	H	AC	MPK	PCR?	HOM	414, 415
<i>Urocentrum turbo</i>	CL	+	H	AC	OBK	?	HOM	213
<i>Urocentrum turbo</i>	CL	++	H	AC	OBK	PPR	HOM	658
<i>Urocentrum turbo</i>	CL, SC	A	H	AC	OBK	PPR	HOM	666
<i>Urocentrum turbo</i>	SC	++	H	AC	OBK	PCR?	HOM	529
<b>Scuticociliates</b> (important general and/or monographic literature [85, 166, 194, 345, 555, 597, 701])								
<i>Anophryoides salmacida</i>	P	++	H	AC	SBK	PPR	HOM	622
<i>Anophrys sacrophaga</i>	CL	++	H	AC	SBK	PPR	HOM	555, 701
<i>Cinetochilum margaritaceum</i>	CL	+	H	AC	SBK	?	HOM	300
<i>Cinetochilum margaritaceum</i>	P	++	H	AC	SBK	PPR	HOM	627
<i>Cohnilembus</i> sp.	P	+	H	AC	SBK	PCR	HOM	701
<i>Cohnilembus verminus</i>	P	++	H	AC	SBK	PCR	HOM	147
<i>Conchophthirus</i> spp.	K	+	H	AC	?	?	HOM	638
<i>Conchophthirus curtus</i>	P, SEM	++	H	AC	SBK	PPR	HOM	13
<i>Conchophthirus mytili</i>	L	+	H	AC	?	PCR	HOM	458
<i>Cryptochilum echini</i>	L	+	H	AC	?	?	HOM	664
<i>Cyclidium</i> sp.	CL	++	H	AC	SBK	PCR	HOM	701
<i>Cyclidium</i> sp.	P	A	H	AC	SBK	?	HOM	44
<i>Cyclidium bonneti</i>	P	++	H	AC	SBK	PPR	HOM	349
<i>Cyclidium citrullus</i>	K	+	H	AC	SBK	PCR	HOM	127
<i>Cyclidium glaucoma</i>	K	*	H	AC	?	?	HOM	462
<i>Dexiotricha colpidiopsis</i>	?	++	H	AC	SBK	PCR	HOM	701
<i>Dexiotricha media</i>	P, TEM	+++	H	AC	SBK	PPR	HOM	597
<i>Homalogastra setosa</i>	P	++	H	AC	SBK	PPR	HOM	614
<i>Loxocephalus luridus</i>	CL	+	H	AC	?	?	HOM	222
<i>Metanophrys durchoni</i>	CL, P	+++	H	AC	SBK	PPR	HOM	628
<i>Mytilophilus pacificae</i>	P	++	H	AC	SBK	PCR	HOM	166
<i>Paralembus rostrata</i>	P	++	H	AC	SBK	PPR	HOM	345
<i>Paranophrys carcini</i>	P	++	H	AC	SBK	PPR	HOM	351
<i>Paranophrys carnivora</i>	CL, P	++	H	AC	SBK	PCR	HOM	131
<i>Paranophrys thompsoni</i>	CL, P	++	H	AC	SBK	PPR	HOM	148
<i>Parauronema virginianum</i>	P	++	H	AC	SBK	PPR	HOM	345
<i>Peniculistoma mytili</i>	P	++	H	AC	SBK	PCR	HOM	166
<i>Philaster</i> sp.	CL	++	H	AC	SBK	PCR	HOM	701
<i>Philaster digitiformis</i>	CL	++	H	AC	SBK	PCR	HOM	555
<i>Philaster digitiformis</i>	P	++	H	AC	SBK	PPR	HOM	345
<i>Philaster digitiformis</i>	CL, P	+	H	AC	SBK	PPR	HOM	626
<i>Philaster hiatti</i>	CL, P	++	H	AC	SBK	PPR	HOM	108
<i>Philasterides armata</i>	CL	+	H	AC	SBK	?	HOM	555
<i>Philasterides armata</i>	P	++	H	AC	SBK	PPR	HOM	349
<i>Plagiopyliella pacifica</i>	L, CL, P	+	H	AC	SBK	?	HOM	516
<i>Pleurocoptes furgasoni</i>	CL, SEM	+	H	AC	SBK	?	HOM	704
<i>Pleuronema</i> sp.	CL, P	++	H	AC	SBK	PCR	HOM	701
<i>Pleuronema puytoraci</i>	P	++	H	AC	SBK	PCR	HOM	350



(Table 2 continued)

Species <sup>1</sup>	Methods <sup>2</sup>	Evaluation <sup>3</sup>	Fission type <sup>4</sup>	Division mode <sup>5</sup>	Stomatogenic mode <sup>6</sup>	Parental oral infraciliature <sup>7</sup>	Macronucleus type <sup>8</sup>	References
<i>Porpostoma notatum</i>	L, CL	++	H	C	SBK	PPR	HOM	555
<i>Potomacus pottsii</i>	P	++	H	AC	SBK	PPR	HOM	646
<i>Pseudocohnilembus</i> sp.	CL	+	H	AC	SBK	PCR	HOM	555
<i>Pseudocohnilembus persalinus</i>	CL, P	++	H	AC	SBK	PPR	HOM	196
<i>Pseudocohnilembus persalinus</i>	P	++	H	AC	SBK	PPR	HOM	614
<i>Sathrophilus vernalis</i>	CL, P	++	H	AC	SBK	PCR	HOM	344, 347
<i>Thigmocoma acuminata</i>	L, K	+	H	AC	SBK	PCR	HOM	456
<i>Thigmophyra saxicavae</i>	CL	+	H	AC	SBK	PPR	HOM	223
<i>Thyrophylax vorax</i>	P	+	H	AC	SBK	PPR	HOM	517
<i>Uronema marinum</i>	CL	+	H	AC	SBK	PCR	HOM	555
<i>Uronema marinum</i>	CL	++	H	AC	SBK	PCR	HOM	701
<i>Uronema marinum</i>	K	+	H	AC	SBK	PCR	HOM	128
<i>Uronema nigricans</i>	P	A	H	AC	SBK	PPR	HOM	195
<i>Uronema nigricans</i>	CL	+	H	AC	SBK	PPR	HOM	628
<i>Uronema nigricans</i>	P	++	H	AC	SBK	PPR	HOM	714
<i>Uronema parduczi</i>	K	*	H	AC	–	–	HOM	253
<i>Urozona buetschli</i>	P	++	H	AC	SBK	PPR	HOM	347
<b>Peritrichs</b> (important general and/or monographic literature [188, 505])								
<i>Astylozoon pyriforme</i>	SC	++	PA	AC	OBK	PPR	HOM	357
<i>Ballodora dimorpha</i>	L	+	PA	AC	?	?	HOM	537
<i>Carchesium polypinum</i>	L	*	–	–	–	–	–	615
<i>Carchesium polypinum</i>	SC	++	PA	AC	OBK	PPR	HOM	192
<i>Cothurnia variabilis</i>	L	+	PA	AC	?	?	HOM	366
<i>Cylochaeta astropectinis</i>	CL	++	PA	AC	OBK	PPR	HOM	99
<i>Ellobiophrya donacis</i>	L	+	PA	AC	?	?	HOM	94
<i>Epistylis anastatica</i>	L	+	PA	AC	?	?	HOM	782
<i>Epistylis epistyliformis</i>	L	+	PA	AC	?	?	HOM	537
<i>Heteropolaria colisarum</i>	P	+	PA	AC	?	?	HOM	272
<i>Lagenophrys</i> spp.	L, P	*	–	–	–	–	–	106
<i>Lagenophrys callinectes</i>	P	A	–	–	–	–	–	121
<i>Leiotrocha serpularum</i>	L	+	PA	AC	?	?	HOM	197
<i>Opercularia coarctata</i>	SC	++	PA	AC	OBK	PPR	HOM	231
<i>Opisthonecta henneguyi</i>	SC	+	PA	AC	OBK	PPR	HOM	709
<i>Platycola truncata</i>	L	+	PA	AC	?	?	HOM	489, 505
<i>Pyxicola nolandi</i>	L	+	PA	AC	?	PR?	HOM	240
<i>Telotrochidium</i> sp.	P	++	PA	AC	OBK	PPR	HOM	505
<i>Thuricola folliculata</i>	P, TEM	+++	PA	AC	OBK	PPR	HOM	188–191, 320
<i>Trichodina</i> spp.	L	+	PA	AC	?	PPR	HOM	132, 153
<i>Trichodina</i> sp.	L, P	+	PA	AC	?	?	HOM	89
<i>Trichodina mitra</i>	L	+	PA	AC	?	PR	HOM	794, 795
<i>Trichodina mitra</i>	L	+	PA	AC	?	PCR	HOM	608
<i>Trichodina nobilis</i>	L, K	++	PA	AC	OBK	PPR	HOM	226
<i>Trichodina pediculus</i>	L	+	PA	AC	?	PR	HOM	794, 795
<i>Trichodina pediculus</i>	L	+	PA	AC	?	?	HOM	292
<i>Trichodina spheroidesi</i>	L, K, CL	+	PA	AC	?	PPR	HOM	589
<i>Trichodina steinii</i>	L	+	PA	AC	?	PCR	HOM	608
<i>Trichodina truttae</i>	?	*	–	–	–	–	HOM	46
<i>Trichodina urechi</i>	L	+	PA	AC	?	PCR	HOM	584
<i>Urceolaria korschelii</i>	L	+	PA	AC	?	PCR	HOM	844
<i>Urceolaria paradoxa</i>	L	+	PA	AC	?	?	HOM	32
<i>Urceolaria synaptae</i>	L	+	PA	AC	?	PPR	HOM	411
<i>Vorticella</i> sp.	K	*	–	–	–	–	–	462
<i>Vorticella convallaria</i>	L	+	PA	AC	?	?	HOM	782

(Table 2 continued)

Species <sup>1</sup>	Methods <sup>2</sup>	Evaluation <sup>3</sup>	Fission type <sup>4</sup>	Division mode <sup>5</sup>	Stomatogenic mode <sup>6</sup>	Parental oral infraciliature <sup>7</sup>	Macronucleus type <sup>8</sup>	References
<i>Vorticella nebulifera</i>	L	+	PA	AC	?	?	HOM	593
<i>Vorticella nebulifera</i>	L	+	PA	AC	?	?	HOM	295
<i>Vorticella striata</i>	L, CL	+	PA	AC	?	PCR	HOM	375
<i>Zoothamnium</i> sp.	SEM	+	PA	AC	?	?	—	568
<b>Thigmotrichs</b> (important general and/or monographic literature [101, 379, 639])								
<i>Ancistrum japonica</i>	L	+	H	AC	?	PCR	HOM	781
<i>Ancistrum mytili</i>	CL, P	++	H	AC	SBK	PCR	HOM	379
<i>Boveria subcylindrica</i>	L	+	H	AC	?	PCR	HOM	725
<i>Hysterozineta cheissini</i>	L	+	H	AC	?	?	HOM	637
<i>Hysterozineta paludinarum</i>	L, K	+	H	AC	SBK?	?	HOM	637
<i>Hysterozineta paludinarum</i>	L, K	*	—	—	—	—	—	445
<i>Plagiospira crinita</i>	CL	+	H	AC	SBK?	?	HOM	101
<i>Proboveria loripedis</i>	CL	++	H	AC	SBK	PCR	HOM	97, 101
<i>Protoptychostomum simplex</i>	L, K	+	H	AC	?	PCR	HOM	444
<i>Ptychostomum saenurides</i>	K	*	—	—	—	—	—	637
<b>Apostomes</b> (important general and/or monographic literature [59, 96, 98])								
<i>Ascophrys rodor</i>	L, P	++	H	C	MK?	PR	HOM	82, 145
<i>Chromidina elegans</i>	L, CL	++	H	AC?	MK?	PCR	HOM	96
<i>Collinia</i> sp.	CL, P, SC	A	?	AC	?	?	HOM	702
<i>Collinia branchiarum</i>	CL	++	H	AC	MK?	PCR	HOM	623
<i>Collinia circulans</i>	CL	++	H	AC	MK?	PCR	HOM	623
<i>Collinia orchestiae</i>	CL, P	++	H	AC	MK?	PCR	HOM	621
<i>Conidophrys pilisuctor</i>	L, CL	++	H	C	MK?	PR	HOM	95, 98
<i>Conidophrys pitelkae</i>	L, P	++	H	C	MK?	PR	HOM	58, 62
	SEM, TEM							
<i>Foettingeria actiniarum</i>	L, CL	++	H	C	MK?	PCR	HOM	96
<i>Gymnodinioides inkystans</i>	L, CL	+++	H	C	MK?	PCR	HOM	96
<i>Hyalophysa chattoni</i>	L, CL, P	+++	H	C	MK?	PCR	HOM	56, 57, 59, 61, 495, 651, 652
	TEM							
<i>Phoretophrya nebaliae</i>	L, CL	++	H	C	MK?	PCR	HOM	96
<i>Phtorophrya insidiosa</i>	L, CL	++	H	C	MK?	PCR	HOM	96
<i>Polyspira delagei</i>	L, CL	++	H	AC	MK?	PCR	HOM	96
<i>Spirophrya subparasitica</i>	L, CL	++	H	C	MK?	PCR	HOM	96
<i>Synophrya hypertrophica</i>	L, CL	++	H	C	MK?	PCR	HOM	96
<i>Terebrospira chattoni</i>	L, CL, P	++	H	C	MK?	PCR	HOM	63
<i>Vampyrophrya pelagica</i>	L, CL,	*	H	C	—	—	HOM	333
	TEM							
<b>Cyrtophorea</b>								
<b>Cyrtophorids</b> (important general and/or monographic literature [139, 209, 402, 403])								
<i>Alinostoma plurivacuolata</i>	P	+	H	AC	MTK	?	HEM	142
<i>Allosphaerium paraconvexa</i>	L, K	++	H	AC	MTK	?	HEM	162
<i>Atelepithites misellum</i>	P	++	H	AC	MTK	?	HEM	139
<i>Atopochilodon distichum</i>	P	+	H	AC	?	?	HEM	140
<i>Brooklynella hostilis</i>	P	++	H	AC	MTK	PPR	HEM	506
<i>Chilodonella crassa</i>	CL	++	H	AC	AK	?	HEM	209
<i>Chilodonella cyprini</i>	CL, SEM	+++	H	AC	MTK	?	HEM	402
	TEM							
<i>Chilodonella uncinata</i>	K	++	H	AC	MTK	?	HEM	462
<i>Chilodonella uncinata</i>	L, K	++	H	AC	MTK	PCR?	HEM	162
<i>Chilodonella uncinata</i>	P	++	H	AC	MTK	?	HEM	139
<i>Chilodonella uncinata</i>	K, SC	++	H	AC	MTK	PPR	HEM	236

(Table 2 continued)

Species <sup>1</sup>	Methods <sup>2</sup>	Evaluation <sup>3</sup>	Fission type <sup>4</sup>	Division mode <sup>5</sup>	Stomatogenic mode <sup>6</sup>	Parental oral infraciliature <sup>7</sup>	Macro-nucleus type <sup>8</sup>	References
<i>Chlamyodon mnemosyne</i>	CL	+	H	AC	MTK?	PPR	HEM	209
<i>Chlamyodon pedarius</i>	L, CL	+	H	AC	MTK	PPR	HEM	454
<i>Chlamydonella galeata</i>	P	+	H	AC	MTK	?	HEM	140
<i>Chlamydonella pseudochilodon</i>	P	++	H	AC	MTK	PPR	HEM	136
<i>Chlamydonyx paucidentatus</i>	P	+	H	AC	MTK	?	HEM	141
<i>Cyrtophoron isagogicum</i>	CL	+	H	C	?	?	HEM	137
<i>Dysteria monostyla</i>	P	++	H	AC	MTK	PR	HEM	135
<i>Gastronauta membranaceus</i>	P	+	H	AC	MTK	PR?	HEM	142
<i>Hartmannula acrobates</i>	P	+	H	AC	MTK	PPR	HEM	142
<i>Hartmannula oliva</i>	P	+	H	AC	MTK	?	HEM	142
<i>Hartmannulopsis dysteriana</i>	P	++	H	AC	MTK	PPR	HEM	142
<i>Lynchella dirempta</i>	P	+	H	AC	MTK	?	HEM	136
<i>Lynchella nordica</i>	P	+	H	AC	MTK	?	HEM	136, 137
<i>Lynchella tentaculata</i>	P	+	H	AC	MTK	PPR	HEM	136
<i>Microxysma acutum</i>	P	++	H	AC	MTK	PPR	HEM	141
<i>Orthotrochilia agamalievi</i>	P	+	H	AC	MTK	?	HEM	141
<i>Orthotrochilia pilula</i>	P	++	H	AC	MTK	PPR	HEM	141
<i>Phascolodon vorticella</i>	P	+	H	AC	MTK	?	HEM	255
<i>Pithites vorax</i>	P	+	H	AC	MTK	PCR?	HEM	142
<i>Scaphiodon navicula</i>	L	+	H	AC	?	?	HEM	722
<i>Schedotrochilia disjoncta</i>	P	+	H	AC	MTK	?	HEM	141
<i>Thigmogaster pardus</i>	P	+	H	AC	MTK	?	HEM	140
<i>Trochilia minuta</i>	P	++	H	AC	MTK	PCR	HEM	592
<i>Trochilioides sp.</i>	P	++	H	AC	MTK	?	HEM	592
<i>Trochilioides bathybius</i>	P	+	H	AC	MTK	?	HEM	141
<i>Trochilioides recta</i>	P	+	H	AC	MTK	?	HEM	141
<i>Trochilioides tenuis</i>	P	++	H	AC	MTK	PPR?	HEM	141
<i>Trichopodiella lachmanni</i>	CL	+	H	AC	?	?	HEM	216
<i>Trichopodiella lachmanni</i>	P	++	H	AC	MTK	PPR	HEM	142
<i>Trichopodiella pulex</i>	P	+	H	AC	MTK	?	HEM	141
<i>Trochochilodon flavum</i>	P	++	H	AC	MTK	?	HEM	139
<i>Trithigmostoma cucullulus</i>	L	+	H	AC	?	?	HEM	502
<i>Trithigmostoma cucullulus</i>	CL	++	H	AC	MTK	PPR	HEM	209
<i>Trithigmostoma cucullulus</i>	K	+	H	AC	MTK	?	HEM	644
<i>Trithigmostoma cucullulus</i>	CL	++	H	AC	MTK	PR	HEM	447–449
<i>Trithigmostoma cucullulus</i>	P	+	H	AC	MTK	?	HEM	140
<i>Trithigmostoma steini</i>	CL, TEM	++	H	AC	MTK	PR	HEM	450, 451
<i>Trithigmostoma steini</i>	CL, TEM	+++	H	AC	MTK	?	HEM	403
<i>Trithigmostoma steini</i>	L	*	–	–	–	–	–	492
<b>Chonotrichs</b> (important general and/or monographic literature [356, 421, 551])								
<i>Chilodochona quennerstedti</i>	L	+	EXB	AC	–	–	HEM	793
<i>Chilodochona quennerstedti</i>	CL	++	EXB	AC	–	–	HEM	325, 355, 356
<i>Heliochona scheutenii</i>	L	+	EXB	AC	–	–	HEM	793
<i>Heliochona scheutenii</i>	L	+	EXB	AC	–	–	HEM	162
<i>Kentrochona nebaliae</i>	L	+	INB	AC	–	–	HEM	163
<i>Lobochona porates</i>	L, P, TEM	++	EXB	AC	–	PR	HEM	533, 534
<i>Spirochona elegans</i>	L	+	EXB	AC	–	–	HEM	736
<i>Spirochona gemmipara</i>	L	+	EXB	AC	–	–	HEM	67
<i>Spirochona gemmipara</i>	L	++	EXB	AC	–	PPR	HEM	387
<i>Spirochona gemmipara</i>	L, P, SEM	A, *	EXB	AC	–	PPR	HEM	198–200

(Table 2 continued)

Species <sup>1</sup>	Methods <sup>2</sup>	Evaluation <sup>3</sup>	Fission type <sup>4</sup>	Division mode <sup>5</sup>	Stomatogenic mode <sup>6</sup>	Parental oral infra-ciliature <sup>7</sup>	Macronucleus type <sup>8</sup>	References
<b>Suctorians</b> (important general and/or monographic literature [27, 28, 83, 111, 355, 476, 484, 721])								
<i>Acineta papillifera</i>	L	+	INB	AC	–	–	HOM	475, 483
<i>Acineta tuberosa</i>	L, K, TEM	++	INB	AC	–	–	HOM	476, 477
<i>Acineta tuberosa</i>	L, TEM	+++	INB	AC	–	–	HOM	23
<i>Acinetopsis rara</i>	TEM	*	INB	AC	–	–	–	330
<i>Catharina florae</i>	L	+	EVB	AC	–	–	HOM	475, 483
<i>Choanophrya infundibulifera</i>	L	+	INB	AC	–	–	HOM	111
<i>Choanophrya infundibulifera</i>	TEM	*	–	–	–	–	–	398
<i>Choanophrya subsessilis</i>	L	+	INB	AC	–	–	HOM	601
<i>Cyathodinium</i> spp.	L, CL, P	++	EVB	AC	–	–	HOM	118, 509, 577, 594, 595
<i>Cyathodinium chagasi</i>	L	+	EVB	AC	–	–	HOM	122, 123
<i>Cyathodinium pyriformis</i>	L, P	++	EVB	AC	–	–	HOM	122, 123, 577
<i>Cyclophrya magna</i>	L, K	++	EVB	AC	–	–	HOM	474, 475, 483
<i>Cyclophrya magna</i>	L	+	EVB	AC	–	–	HOM	649
<i>Dendrocometes paradoxus</i>	L	+	EVB	AC	–	–	HOM	67
<i>Dendrocometes paradoxus</i>	L	++	EVB	AC	–	–	HOM	612
<i>Dendrocometes paradoxus</i>	L	++	EVB	AC	–	–	HOM	497
<i>Dendrocometes paradoxus</i>	L	+	EVB	AC	–	–	HOM	601
<i>Dendrocometes paradoxus</i>	L	++	EVB	AC	–	–	HOM	609
<i>Dendrocometes paradoxus</i>	L, SC, SEM	++	EVB	AC	–	–	HOM	791
<i>Dendrosoma radians</i>	L	+	INB	AC	–	–	HOM	601
<i>Dendrosomoides grassei</i>	L	+	EXB	AC	–	–	HOM	29
<i>Discophrya</i> sp.	TEM	*	–	–	–	–	–	125
<i>Discophrya astaci</i>	L	++	EVB	AC	–	–	HOM	474, 475, 477, 483
<i>Discophrya brachystyla</i>	L	++	EVB	AC	–	–	HOM	473
<i>Discophrya buckei</i>	L	+	EVB	AC	–	–	HOM	481
<i>Discophrya pyriformis</i>	CL	++	EVB	AC	–	–	HOM	355, 356
<i>Discophrya steinii</i>	L	+	EVB	AC	–	–	HOM	110
<i>Endosphaera engelmanni</i>	L	+	INB	AC	–	–	HOM	514
<i>Endosphaera engelmanni</i>	L	+	INB	AC	–	–	HOM	590
<i>Endosphaera terebrans</i>	L, SC	++	INB	AC	–	–	HOM	193
<i>Ephelota</i> spp.	TEM	*	–	–	–	–	–	329
<i>Ephelota gemmipara</i>	L	++	EXB	AC	–	–	HOM	386
<i>Ephelota gemmipara</i>	L	++	EXB	AC	–	–	HOM	111
<i>Ephelota gemmipara</i>	CL	++	EXB	AC	–	–	HOM	354–356
<i>Ephelota gigantea</i>	L	+	EXB	AC	–	–	HOM	582
<i>Ephelota minima</i>	L	+	EXB	AC	–	–	HOM	582
<i>Heliophrya riederi</i>	L	+	INB	AC	–	–	HOM	649
<i>Heliophrya rotunda</i>	L	+	INB	AC	–	–	HOM	649
<i>Lernaeophrya capitata</i>	L, TEM	++	INB	AC	–	–	HOM	475, 476, 483
<i>Metacineta mystacina</i>	L	+	EXB	AC	–	–	HOM	483
<i>Ophryodendron reversum</i>	L	+	EXB	AC	–	–	HOM	111
<i>Paracineta lauterborni</i>	P	++	EXB	AC	–	–	HOM	849
<i>Paracineta patula</i>	L	++	EXB	AC	–	–	HOM	111
<i>Periacineta gammari</i>	L	+	INB	AC	–	–	HOM	601
<i>Peridiscophrya linguifera</i>	L	++	EVB	AC	–	–	HOM	472, 477
<i>Phalacrocleptes verruciformis</i>	L, CL, P, TEM	++	?	AC	–	–	HOM	488, 507
<i>Physaliella collini</i>	L	+	INB	AC	–	–	HOM	601
<i>Podophrya fixa</i>	L	+	EXB	AC	–	–	HOM	541
<i>Podophrya fixa</i>	L	++	EXB	AC	–	–	HOM	111
<i>Podophrya fixa</i>	L	+	EXB	AC	–	–	HOM	601
<i>Podophrya fixa</i>	L	++	EXB	AC	–	–	HOM	473

(Table 2 continued)

Species <sup>1</sup>	Methods <sup>2</sup>	Evaluation <sup>3</sup>	Fission type <sup>4</sup>	Division mode <sup>5</sup>	Stomatogenic mode <sup>6</sup>	Parental oral infraciliature <sup>7</sup>	Macronucleus type <sup>8</sup>	References
<i>Podophrya fixa</i>	CL	++	EXB	AC	–	–	HOM	512, 513
<i>Podophrya grelli</i>	L	+++	EXB	AC, C	–	–	HOM	149
<i>Podophrya halophila</i>	L, P	+	EXB	AC	–	–	HOM	45
<i>Podophrya parameciorum</i>	L	+	EXB	AC	–	–	HOM	419
<i>Podophrya parasitica</i>	L, CL	++	EXB	AC	–	–	HOM	205
<i>Podophrya parasitica</i>	CL	++	EXB	AC	–	–	HOM	355, 356
<i>Podophrya parasitica</i>	L	+	EXB	AC	–	–	HOM	477
<i>Podophrya stylonychia</i>	L, K	+	EXB	AC	–	–	HOM	256
<i>Podophrya urostylae</i>	L	+	EXB	AC	–	–	HOM	419
<i>Pottsiocles infusiorum</i>	L	+	INB	AC	–	–	HOM	93
<i>Prodiscophrya collini</i>	L	+	EVB	AC	–	–	HOM	654
<i>Prodiscophrya collini</i>	L, K	++	EVB	AC	–	–	HOM	473, 474, 477
<i>Prodiscophrya collini</i>	SEM	++	EVB	AC	–	–	HOM	385
<i>Prodiscophrya collini</i>	L, TEM	+++	EVB	AC	–	–	HOM	126
<i>Prodiscophrya collini</i>	L, P	+	EVB	AC	–	–	HOM	2
<i>Pseudogemma fraiponti</i>	L	+	INB	AC	–	–	HOM	111
<i>Pseudogemma pachystyla</i>	L	+	INB	AC	–	–	HOM	111
<i>Pseudogemmides globosa</i>	L	+	INB	AC	–	–	HOM	473
<i>Rhyncheta cyclosum</i>	L	+	INB	AC	–	–	HOM	397
<i>Solenophrya dubia</i>	L	+	INB	AC	–	–	HOM	601
<i>Solenophrya micraster</i>	L, CL	+	EXB?	AC	–	–	HOM	410
<i>Sphaerophrya canelli</i>	L, CL	++	EXB	AC	–	–	HOM	107
<i>Sphaerophrya insolita</i>	L	+	EXB	AC	–	–	HOM	422
<i>Sphaerophrya terricola</i>	L, P	+	EXB	AC	–	–	HOM	263
<i>Tachyblaston ephelotensis</i>	L	++	EXB	AC	–	–	HOM	327
<i>Thecacineta calix</i>	L	+	EXB	AC	–	–	HOM	538
<i>Tokophrya cyclosum</i>	L	++	INB	AC	–	–	HOM	110, 111
<i>Tokophrya cyclosum</i>	L	+	INB	AC	–	–	HOM	601
<i>Tokophrya cyclosum</i>	L	++	INB	AC	–	–	HOM	472
<i>Tokophrya cyclosum</i>	TEM	*	–	–	–	–	–	26
<i>Tokophrya infusionum</i>	CL	++	INB	AC	–	–	HOM	355, 356
<i>Tokophrya infusionum</i>	CL, P, TEM	+++	INB	AC	–	–	HOM	373, 547–549
<i>Tokophrya lemnarum</i>	L	+	INB	AC	–	–	HOM	601
<i>Tokophrya lemnarum</i>	L	++	INB?	AC	–	–	HOM	583
<i>Tokophrya multifasciculata</i>	L	+	INB	AC	–	–	HOM	473, 477, 479, 480
<i>Tokophrya quadripartita</i>	L	+	INB	AC	–	–	HOM	239
<i>Tokophrya quadripartita</i>	L	+	INB	AC	–	–	HOM	110
<i>Tokophrya quadripartita</i>	L	+	INB	AC	–	–	HOM	601
<i>Tokophrya quadripartita</i>	L, K	+	INB	AC	–	–	HOM	473, 474, 483
<i>Tokophrya quadripartita</i>	L	+	INB	AC	–	–	HOM	674
<i>Trichophrya epistylides</i>	L	+	INB	AC	–	–	HOM	479, 480
<i>Trichophrya myriophylli</i>	L	+	INB	AC	–	–	HOM	601
<i>Trichophrya salparum</i>	L	+	INB	AC	–	–	HOM	111
<i>Urnula epistylides</i>	L	+	INB	AC	–	–	HOM	479, 480
<i>Urnula turpissima</i>	L, K	++	INB	AC	–	–	HOM	485
<b>Rhynchodids</b> (important general and/or monographic literature [102, 641])								
<i>Ancistrocoma pelseneeri</i>	L	+	H	AC	–	–	HOM	635
<i>Anisocomides zyrphaeae</i>	CL	+	H	AC	–	–	HOM	102
<i>Gagarius gagarius</i>	CL	+	EXB?	AC	–	–	HOM	102
<i>Goniocoma macomae</i>	CL	+	H	AC	–	–	HOM	102
<i>Hypocoma acinetarum</i>	P	+	H	AC	MTK?	?	HOM	137

(Table 2 continued)

Species <sup>1</sup>	Methods <sup>2</sup>	Evaluation <sup>3</sup>	Fission type <sup>4</sup>	Division mode <sup>5</sup>	Stomatogenic mode <sup>6</sup>	Parental oral infra-ciliature <sup>7</sup>	Macronucleus type <sup>8</sup>	References
<i>Hypocoma parasitica</i>	P	+	H	AC	MTK?	?	HOM	137
<i>Hypocoma rostellum</i>	P	+	H	AC	?	?	HOM	140
<i>Hypocomella cardii</i>	L, CL	+	H	AC	—	—	HOM	100, 101, 102
<i>Hypocomella chattoni</i>	L, K	+	H	AC	—	—	HOM	425
<i>Hypocomidium fabius</i>	L	+	H	AC	—	—	HOM	635
<i>Lwoffia cilifera</i>	L, P	+	EXB?	AC	—	—	HOM	487
<i>Parachaenia myae</i>	L	+	H	AC	—	—	HOM	470
<i>Pelecypophrya tapetis</i>	L, CL	++	EXB?	AC	—	—	HOM	100, 101
<i>Sphenophrya dosinia</i>	L	++	EXB	AC	—	—	HOM	635, 636
<i>Sphenophrya dosinia</i>	CL	++	EXB	AC	—	—	HOM	102
<i>Sphenophrya dosinia</i>	CL, P	+	EXB	AC	—	—	HOM	224
<i>Sphenophrya dreissenae</i>	L, K	++	EXB	AC	—	—	HOM	160, 161
<i>Sphenophrya sphaerii</i>	L, K	++	EXB	AC	—	—	HOM	636
<b>Nassulids</b> (important general and/or monographic literature [183, 184, 597])								
<i>Drepanomonas revoluta</i>	P	+	H	AC	MK?	PCR	HOM	12
<i>Discotricha papillifera</i>	P	+	H	AC	MK?	PCR	HOM	815
<i>Furgasonia</i> spp.	CL	+	H	AC	MK?	?	HOM	220, 221
<i>Furgasonia blochmanni</i>	CL, TEM	+++	H	AC	MK	PPR	HOM	183, 184
<i>Furgasonia protectissima</i>	CL?	++	H	AC	MK	PPR	HOM	346
<i>Leptopharynx costatus</i>	L, K, CL	+	H	AC	MK	PCR	HOM	617
<i>Leptopharynx macrostoma</i>	P	++	H	AC	MK	PPR	HOM	581
<i>Nassula</i> sp.	CL, TEM	*	H	AC	—	—	HOM	759–761
<i>Nassula citrea</i>	CL	++	H	AC	MK	PPR	HOM	184
<i>Nassulopsis lagenula</i>	CL, P	+	H	AC	MK	?	HOM	144
<i>Paranassula brunnea</i>	CL	+	H	AC	MK?	?	HOM	219
<i>Pseudomicrothorax dubius</i>	CL	+	H	AC	MK?	PCR	HOM	755
<i>Pseudomicrothorax dubius</i>	P, TEM	+++	H	AC	MK	PPR	HOM	597
<i>Pseudomicrothorax dubius</i>	CL	++	H	AC	MK	PPR	HOM	693, 694
<b>Prostomatids</b> (important general and/or monographic literature [171, 395])								
<i>Bursellopsis spaniopogon</i>	SC, SEM	+++	H	AC	MTK	PPR	HOM	395
<i>Bursellopsis spumosa</i>	L	+	H	AC	?	PPR?	HOM	673
<i>Coleps amphacanthus</i>	SC, TEM	+++	H	AC	MTK	PPR	HOM	412
<i>Coleps hirtus</i>	SC	+	H	AC	?	?	HOM	688
<i>Lagynus elegans</i>	SC	+	H	AC	HTK	?	HOM	711
<i>Longifragma obliqua</i>	P	+	H	AC	?	?	HOM	261
<i>Prorodon aklitolophon</i>	L, K, CL	*	—	—	—	—	—	396
	P, SEM, TEM							
<i>Prorodon palustris</i>	L, CL, P	++	H	C	MTK	PCR?	HOM	625
<i>Prorodon teres</i>	SC	A	H	AC	MTK	PCR	HOM	394
<i>Pseudobalanion planctonicum</i>	P	++	E	AC	MTK	PR	HOM	275
<i>Trimyema compressum</i>	SC	++	H	AC	HTK	PPR	HOM	690
<i>Urotricha ondina</i>	SC	++	H	AC	MTK	PR	HOM	567
<i>Urotricha puytoraci</i>	CL	++	H?	AC	MTK	PR	HOM	171
<b>Litostomatea</b>								
<b>Haptorids</b> (important general and/or monographic literature [24, 270, 289, 501, 504])								
<i>Acropisthium mutabile</i>	SC	+	H	AC	HTK	?	HOM	687
<i>Amphileptus pleurosigma</i>	P	+	H	AC	MOTK	?	HOM	289
<i>Bryophyllum tegularum</i>	P	++	H	AC	HTK	?	HOM	289
<i>Didinium nasutum</i>	CL	*	—	—	—	—	—	306
<i>Didinium nasutum</i>	CL	+	H	AC	HTK	PR	HOM	167
<i>Didinium nasutum</i>	L, TEM	*	—	—	—	—	—	650

(Table 2 continued)

Species <sup>1</sup>	Methods <sup>2</sup>	Evaluation <sup>3</sup>	Fission type <sup>4</sup>	Division mode <sup>5</sup>	Stomatogenic mode <sup>6</sup>	Parental oral infra-ciliature <sup>7</sup>	Macronucleus type <sup>8</sup>	References
<i>Didinium nasutum</i>	TEM	A	–	–	–	–	–	406
<i>Didinium nasutum</i>	SEM	++	H	AC	HTK	PR	HOM	708
<i>Dileptus</i> spp.	L, P, TEM	*	H	AC	HTK	?	HOM	47, 49, 316–319, 461
<i>Fuscheria terricola</i>	P	++	H	AC	HTK	PR	HOM	38
<i>Homalozoon vermiculare</i>	CL	+	H	AC	?	PR	HOM	313
<i>Homalozoon vermiculare</i>	P	++	H	AC	HTK	?	HOM	289
<i>Homalozoon vermiculare</i>	P, TEM	+++	H	AC	HTK	PR	HOM	501
<i>Lacrymaria olor</i>	P, TEM	*	–	–	–	–	–	460
<i>Litonotus</i> sp.	P	+	H	AC	MOTK	?	HOM	289
<i>Loxophyllum</i> sp.	P	+	H	AC	MOTK	?	HOM	289
<i>Mesodinium acarus</i>	L	+	H	AC	?	?	HOM	738
<i>Mesodinium rubrum</i>	L	+	H	AC	?	?	HOM	503
<i>Paradileptus</i> spp.	CL, P	+	H	AC	HTK	?	HOM	289
<i>Protospathidium serpens</i>	P	++	H	AC	HTK	PR	HOM	39
<i>Spathidium</i> sp.	P	+	H	AC	HTK	?	HOM	289
<i>Spathidium amphoriforme</i>	P	+	H	AC	HTK	?	HOM	294
<i>Spathidium anguilla</i>	P	+	H	AC	HTK	?	HOM	15
<i>Spathidium muscicola</i>	P	+	H	AC	HTK	?	HOM	130
<i>Spathidium muscorum</i>	P	++	H	AC	HTK	PR	HOM	38
<i>Sphaerobactrum warduae</i>	L	+	H	AC	?	?	HOM	672
<i>Trachelius ovum</i>	L	+	H	AC	?	PR	HOM	365
<b>Archistomatids</b> (important general and/or monographic literature [322, 323])								
<i>Alloiozoon trizona</i>	CL	+	H	AC	ITK	PR	HOM	322, 323
<i>Didesmis ovalis</i>	P	++	H	AC	ITK	?	HOM	834
<i>Didesmis quadrata</i>	CL	++	H	AC	ITK	PR	HOM	322, 323
<i>Polymorpha ampulla</i>	CL	++	H	AC	HTK	PR	HOM	322, 323
<b>Vestibuliferids</b> (important general and/or monographic literature [322, 323, 833])								
<i>Balantidium</i> spp.	CL	+	H	AC	ITK	PR	HOM	215
<i>Balantidium caviae</i>	L, K	+	H	AC	TK	PR	HOM	491
<i>Balantidium coli</i>	L	+	H	AC	?	?	HOM	685
<i>Balantidium elongatum</i>	CL	+	H	AC	?	?	HOM	784
<i>Balantidium entozoon</i>	L	+	H	AC	?	?	HOM	723
<i>Dasytricha ruminantium</i>	CL	+	H	AC	MTK?	PR	HOM	322, 323
<i>Isotricha intestinalis</i>	CL	+	H	AC	MTK?	PR	HOM	321–323
<i>Isotricha prostoma</i>	L	+	H	AC	?	PCR?	HOM	81
<i>Isotricha prostoma</i>	CL	+	H	AC	MTK?	PR	HOM	322, 323
<i>Paraisotricha colpoidea</i>	SC	++	H	AC	ITK	PR	HOM	832, 833
<i>Paraisotricha colpoidea</i>	Cl	++	H	AC	ITK	PR	HOM	321–323
<i>Paraisotricha minuta</i>	SC	++	H	AC	ITK	PR	HOM	832, 833
<i>Paraisotricha minuta</i>	CL	+	H	AC	ITK	PR	HOM	322, 323
<i>Plagiopyla frontata</i>	L, TEM	*	–	–	–	–	–	225
<i>Plagiopyla marina</i>	CL	+	H	AC	?	?	HOM	210
<i>Plagiopyla nasuta</i>	P	++	H	AC	HTK	PR	HOM	852
<i>Rhizotricha beckeri</i>	SC	+	H	AC	ITK	?	HOM	832, 833
<b>Entodiniomorphids</b> (important general and/or monographic literature [293, 586, 837])								
<i>Anoplodinium costatum</i>	L	+	H	AC	?	?	HOM	105
<i>Blepharocorys bovis</i>	L	+	H	AC	CTK	?	HOM	165
<i>Blepharocorys jubata</i>	SC	+	H	AC	CTK	?	HOM	835
<i>Blepharocorys uncinata</i>	L	+	H	AC	?	?	HOM	73
<i>Charonina ventriculi</i>	SC	+	H	AC	CTK	?	HOM	836

(Table 2 continued)

Species <sup>1</sup>	Methods <sup>2</sup>	Evaluation <sup>3</sup>	Fission type <sup>4</sup>	Division mode <sup>5</sup>	Stomatogenic mode <sup>6</sup>	Parental oral infraciliature <sup>7</sup>	Macronucleus type <sup>8</sup>	References
<i>Cycloposthium bipalmatum</i>	L	+	H	AC	?	?	HOM	73
<i>Diplodinium</i> sp.	L	+	H	AC	CTK	?	HOM	677
<i>Diplodinium dentatum</i>	SC	++	H	AC	CTK	PR	HOM	586
<i>Entodinium</i> sp.	L	+	H	AC	CTK	?	HOM	677
<i>Entodinium</i> spp.	SC	++	H	AC	CTK	PR	HOM	227, 586, 689
<i>Entodinium caudatum</i>	SC	++	H	AC	CTK	PR	HOM	230
<i>Entodinium dubardi</i>	L	+	H	AC	CTK	?	HOM	845
<i>Entodinium longinucleatum</i>	SC	++	H	AC	CTK	PR	HOM	230, 586
<i>Epidinium ecaudatum</i>	SC	+	H	AC	?	?	HOM	586
<i>Eudiplodinium affine</i>	SC	+	H	AC	?	?	HOM	586
<i>Eudiplodinium maggi</i>	SC	+	H	AC	?	?	HOM	586
<i>Eudiplodinium maggi</i>	TEM	+++	H	AC	CTK	PR	HOM	293
<i>Eudiplodinium neglectum</i>	L	+	H	AC	CTK	PPR?	HOM	490
<i>Ophryoscolex</i> sp.	L	+	H	AC	CTK	?	HOM	677
<i>Ophryoscolex caudatus</i>	L	+	H	AC	?	?	HOM	353
<i>Ophryoscolex caudatus</i>	L	+	H	AC	?	?	HOM	586
<i>Ophryoscolex purkinjei</i>	SC	+	H	AC	?	?	HOM	586
<i>Ostracodinium gracile</i>	SC	+	H	AC	?	?	HOM	586
<i>Polyplastron multivesiculatum</i>	SC	++	H	AC	CTK	PR	HOM	227
<i>Polyplastron multivesiculatum</i>	L, SC	++	H	AC	CTK	PR	HOM	586
<i>Spirodinium equi</i>	L	+	H	AC	CTK	PR	HOM	133
<i>Tetratouxum unifasciculatum</i>	L	+	H	AC	?	PR	HOM	134
<b>Colpodea</b> (important general and/or monographic literature [266])								
<i>Bresslaia vorax</i>	CL	+	H	C	?	?	HOM	726
<i>Bresslaia vorax</i>	SC	++	H	C	MTK	PCR	HOM	298
<i>Bryometopus atypicus</i>	SC	++	H	AC	PTK	PPR	HOM	827
<i>Bursaria</i> sp.	L	+	H	AC	?	PCR	HOM	510
<i>Bursaria truncatella</i>	L	+	H	AC	?	PCR	HOM	671
<i>Bursaria truncatella</i>	L	+	H	AC	?	PPR	HOM	607
<i>Bursaria truncatella</i>	SC, P	++	H	AC	PTK	PCR	HOM	266, 605
<i>Bursaria truncatella</i>	SEM	+	H	AC	?	PCR	HOM	686
<i>Colpoda cucullus</i>	P	++	H	C	MTK	PCR	HOM	763
<i>Colpoda cucullus</i>	L	*	-	C	-	-	-	276
<i>Colpoda cucullus</i>	CL	+	H	C	MTK	PCR	HOM	378
<i>Colpoda cucullus</i>	CL, SC	++	H	C	MTK	PCR	HOM	237
<i>Colpoda duodenaria</i>	CL	++	H	C	MTK	PCR	HOM	746
<i>Colpoda ellioti</i>	CL	++	H	C	MTK	PCR	HOM	60
<i>Colpoda inflata</i>	CL	+	H	C	MTK	PCR	HOM	378
<i>Colpoda inflata</i>	CL	++	H	C	MTK	PCR	HOM	238
<i>Colpoda inflata</i>	SC	++	H	C	MTK	PCR	HOM	532
<i>Colpoda maupasi</i>	L	*	H	C	-	-	-	591
<i>Colpoda maupasi</i>	CL	+	H	C	MTK	PCR	HOM	378
<i>Colpoda steinii</i>	K	++	H	C	MTK	PCR	HOM	463, 467
<i>Colpoda steinii</i>	CL	+	H	C	MTK	PCR	HOM	763
<i>Colpoda steinii</i>	CL	+	H	C	MTK	PCR	HOM	378
<i>Colpoda steinii</i>	SC, TEM	++	H	C	MTK	PCR	HOM	604
<i>Cyrtolophosis colpidiformis</i>	SC	+	H	AC	PTK	PPR	HOM	266
<i>Cyrtolophosis elongata</i>	P	++	H	AC	PTK	PPR	HOM	72
<i>Cyrtolophosis minor</i>	SC	+	H	AC	PTK	PPR	HOM	266
<i>Cyrtolophosis mucicola</i>	L, CL, P	+	H	AC	PTK	?	HOM	543, 544
<i>Cyrtolophosis mucicola</i>	K	*	H	AC	-	-	-	254
<i>Maryna galeata</i>	L	*	-	C	-	-	-	1



(Table 2 continued)

Species <sup>1</sup>	Methods <sup>2</sup>	Evaluation <sup>3</sup>	Fission type <sup>4</sup>	Division mode <sup>5</sup>	Stomatogenic mode <sup>6</sup>	Parental oral infraciliature <sup>7</sup>	Macronucleus type <sup>8</sup>	References
<i>Microdiaphanosoma arcuata</i>	SC	++	H	AC	PTK	?	HOM	257
<i>Platyophrya spumacola</i>	P	++	H	AC, C	PTK	PR	HOM	348
<i>Platyophrya spumacola</i>	P	++	H	AC	PTK	PR	HOM	172
<i>Pseudoplatyophrya nana</i>	SC	++	H	C	MTK	PCR	HOM	269
<i>Sorogena stoianovitchae</i>	L, CL, SC	++	H	AC	PTK	PR	HOM	25
<i>Tillina</i> sp.	SC	++	H	C	MTK	PCR	HOM	603
<i>Tillina magna</i>	CL, P	+	H	C	MTK	PCR	HOM	762, 763
<i>Tillina magna</i>	CL	+	H	C	MTK	PCR	HOM	378
<i>Woodruffia metabolica</i>	CL	+	H	C, C	?	PR	HOM	618
<i>Woodruffia metabolica</i>	SC	+	H	?	PTK?	PPR?	HOM	630

<sup>1</sup> Names usually given as written in original literature, i. e. no attempts have been made to correct taxonomic and nomenclatural mistakes. However, widely accepted new combinations, e.g. *Chilodonella* / *Trithigmostoma*, have been used if appropriate.

<sup>2</sup> CL = Chatton and Lwoff's wet silver nitrate method (and modifications), I = immunocytochemistry, K = Klein's dry silver nitrate method (and modifications), L = from life and/or conventional histological techniques (e.g., hematoxylin), P = protargol, SC = Fernandez-Galiano's silver carbonate method (and modifications), SEM = scanning electron microscopy, TEM = transmission electron microscopy.

<sup>3</sup> + = insufficient, e.g. based on live observations or data documented by micrographs only; ++ = good quality, sufficient for conventional purposes, data documented by reliable line drawings; +++ = excellent, usually containing electron microscopic observations, micrographs, and reliable drawings; \* = special aspects treated only, e.g. morphogenesis of fibrillar system, lorica, or microstome-macrostome transformation; A = only abstract available.

<sup>4</sup> Determined according to the data provided. E = enantiotropic, EVB = evaginative budding, EXB = external budding, H = homothetogenic, INB = internal budding, PA = parallel.

<sup>5</sup> Determined according to the data provided. AC = in active condition, i. e. not in reproductive cysts, C = reproductive cysts or budding within cysts.

<sup>6</sup> Determined according to the data provided (often difficult!). See chapter 6 for detailed explanation of modes. AK = apokinetal, APK = amphiparakinetal, BK = buccokinetal, BPK = biparakinetal, CTK = cryptotelokinetal, EAK = epiapokinetal, HAK = hypoapokinetal, HTK = holotelokinetal, ITK = intertelokinetal, MK = mixokinetal, MPK = monoparakinetal, MTK = merotelokinetal, MOTK = monotelokinetal, OBK = ophryobuccokinetal, PK = parakinetal, PPK = polyparakinetal, PTK = pleurotelokinetal, SBK = scuticobuccokinetal, TK = telokinetal, TPK = teloparakinetal.

<sup>7</sup> Determined according to the data provided (often insufficient and/or difficult to interpret!). PR = parental oral structures retained, PCR = parental oral structures completely reorganized, PPR = parental oral structures partially reorganized.

<sup>8</sup> Determined according to the data provided and from (217, 645). HEM = heteromeric, HOM homomeric, ND = non-dividing, RB = replication band.

Although these ciliates are conspicuous and common, detailed morphogenetic studies are rare, and there are, for instance, no data available on the metopids and the odontostomatids. Many studies are outdated and incomplete, which makes their evaluation difficult.

The heterotrichs have a homomeric macronucleus and divide in active condition. Usually fission is homothetogenic, but parallel in *Licnophora*, as in peritrichs, possibly as an adaptation to the sessile mode of life. The heterotrichs show a wide variety of stomatogenic modes; most of them belong, how-

ever, to the parakinetal pattern. *Licnophora* apparently has an apokinetal stomatogenesis although this must be re-studied with refined methods. *Caenomorpha*, a sapropelic species with a strongly reduced somatic ciliature, the endosymbiotic Nyctotheridae, and the edaphic *Transitella* possibly have some kind of telokinetal stomatogenesis. The stomatogenesis of *Nyctotherus* in fact appears so similar to that of the colpodid *Bursaria*, that it is hard to deny a close relationship; however, the ultrastructure of the somatic kinetids of *Nyctotherus* and *Bursaria* is very different, and the similarities

in stomatogenesis are thus very likely convergences.

*Fabrea*, *Stentor*, and *Folliculina*, which are now in different suborders, have an amphiparakinetal stomatogenesis and might thus be rather closely related (557). The morphogenesis of the folliculinids is highly complicated because of their complex life cycle. It was first correctly described by Sahrhage (665) and recently comprehensively re-studied by Uhlig (777–780) and Mulisch (557). The parental oral apparatus is retained (possibly only in caenomorphids) or partially or completely reorganized during cell division. Most data are, however, incomplete. Possibly, there is an internal (cryptic) reorganization as assumed in several hypotrichs (290, 291, 796).

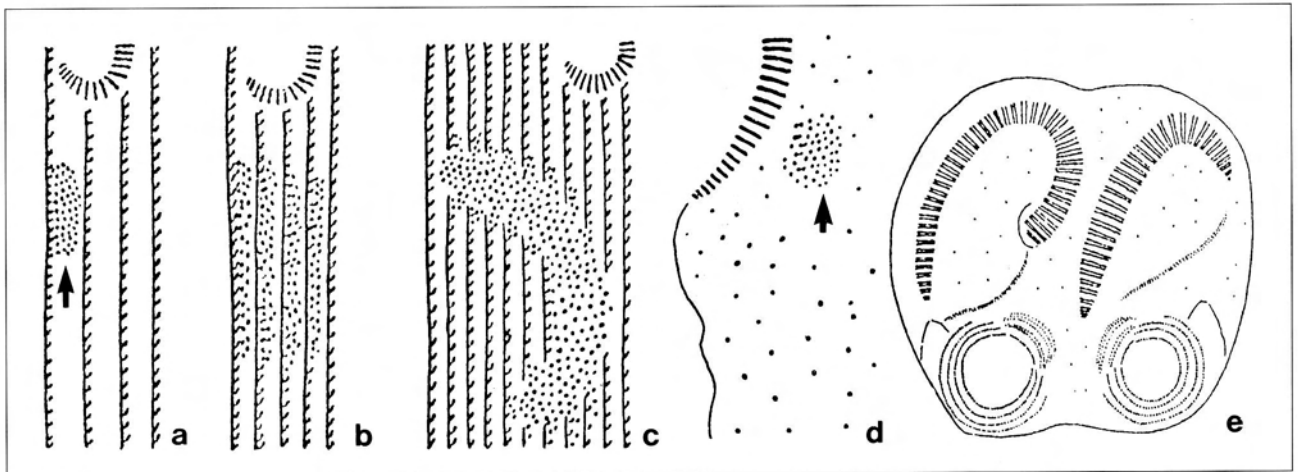
Lorica formation in folliculinids has been extensively studied (363, 367, 558, 559, 777). The lorica is produced from precursor material secreted by the mobile swarmer after settling and shaped by the action of the cilia and certain movements of the cell.

Probably heterotrichs are a melting pot of highly diverse ciliates having no more than a conspicuous adoral zone of membranelles in common. In fact, some of them were recently transferred to the colpodids (families Bursariidae and Bryometopidae,

[266]) or to the hypotrichs (families Plagiotomidae and Phacodinidae, [229, 241]). Considering the diverse stomatogenic modes, it is reasonable to assume that refined morphogenetic studies, especially by electron microscopy, will further «clean up» the heterotrichs. *Chattonidium*, for example, could be an oligotrich because the oral anlage originates in a subsurface pouch. *Protocruzia* has a mixed parakinetal and scuticokinetal stomatogenesis and, because of its nuclear apparatus, could belong to the karyorelictids.

### 7.1.2 Karyorelictids

The karyorelictids have a diploid, non-dividing macronucleus. Most live in marine sands; only *Loxodes* inhabits freshwater biotopes. The nuclear events during cell division have been well investigated (645). In contrast, almost nothing is known about stomatogenesis because most or all species are extremely difficult to impregnate with silver. I found only two reports describing the stomatogenesis of *Loxodes*. Unfortunately, they differ significantly. According to Tuffrau (765), the new oral apparatus originates parakinetally from a single somatic kinety. Njine (579), in contrast, observed



**Fig. 1 a–e:** Stomatogenic and fission modes in heterotrich ciliates (from [784]. – **a:** Monoparakinetal stomatogenesis in, e.g., *Spirostomum*. A single postoral (stomatogenic) ciliary row proliferates basal bodies laterally (arrow). – **b:** Polyparakinetal stomatogenesis in, e.g., *Condylostoma*. Several postoral (stomatogenic) ciliary rows proliferate basal bodies. – **c:** Amphiparakinetal stomatogenesis in, e.g., *Stentor* (cp. Fig. 8). The curved oral primordium intersects many postoral (stomatogenic) ciliary rows at two sites, and thus encloses many short, non-proliferating parental kinety fragments which become the ciliary rows on the peristomial field of the opisthe. – **d:** Apokinetal stomatogenesis in *Lichophora*. The oral primordium (arrow) originates near the proximal end of the parental adoral zone of membranelles without apparent participation of pre-existing basal bodies, as, e.g., in the hypotrich *Euplotes* (cp. Fig. 18, 19). – **e:** Longitudinal fission in *Lichophora*; all other heterotrichs divide transversely (homothetogenically).

that the oral apparatus of the opisthe differentiates from a single parental buccal kinety which spreads fan-like to produce the oral kineties. This is supported by very recent data (468). These enigmatic ciliates clearly represent a challenge to a patient master of silver impregnation.

## 7.2 Spirotrichea

### 7.2.1 Oligotrichs

The oligotrichs typically have a conspicuous oral apparatus with large adoral membranelles at the anterior end and an inconspicuous somatic ciliature. Many species, especially tintinnids, are loricate. Although oligotrichs are one of the largest ciliate groups (> 1000 species), it was only very recently that Petz and Foissner (610, 611) updated knowledge of their morphogenesis, using protargol impregnation and scanning electron microscopy. The main features of oligotrich morphogenesis were, however, recognized earlier by Fauré-Fremiet (211) and Kormos and Kormos (482). Laackmann (494) reviewed the older, very fragmentary literature.

The oligotrichs divide in active condition. Fission is enantiotropic, i.e. the axes of the proter and opisthe are more or less distinctly at right-angles to one another and the daughters thus adhere by their posterior portions. Stomatogenesis is apokinetal. The oral primordium develops epiapokinetally on the

cell surface in halteriids and most (?) strombidiids, hypoapokinetally in a subsurface pouch in tintinnids and strobilidiids, or in an intracellular tube in some strombidiids. The parental oral infraciliature is retained unchanged. The macronucleus has a replication band (324) which is sometimes difficult to recognize (610).

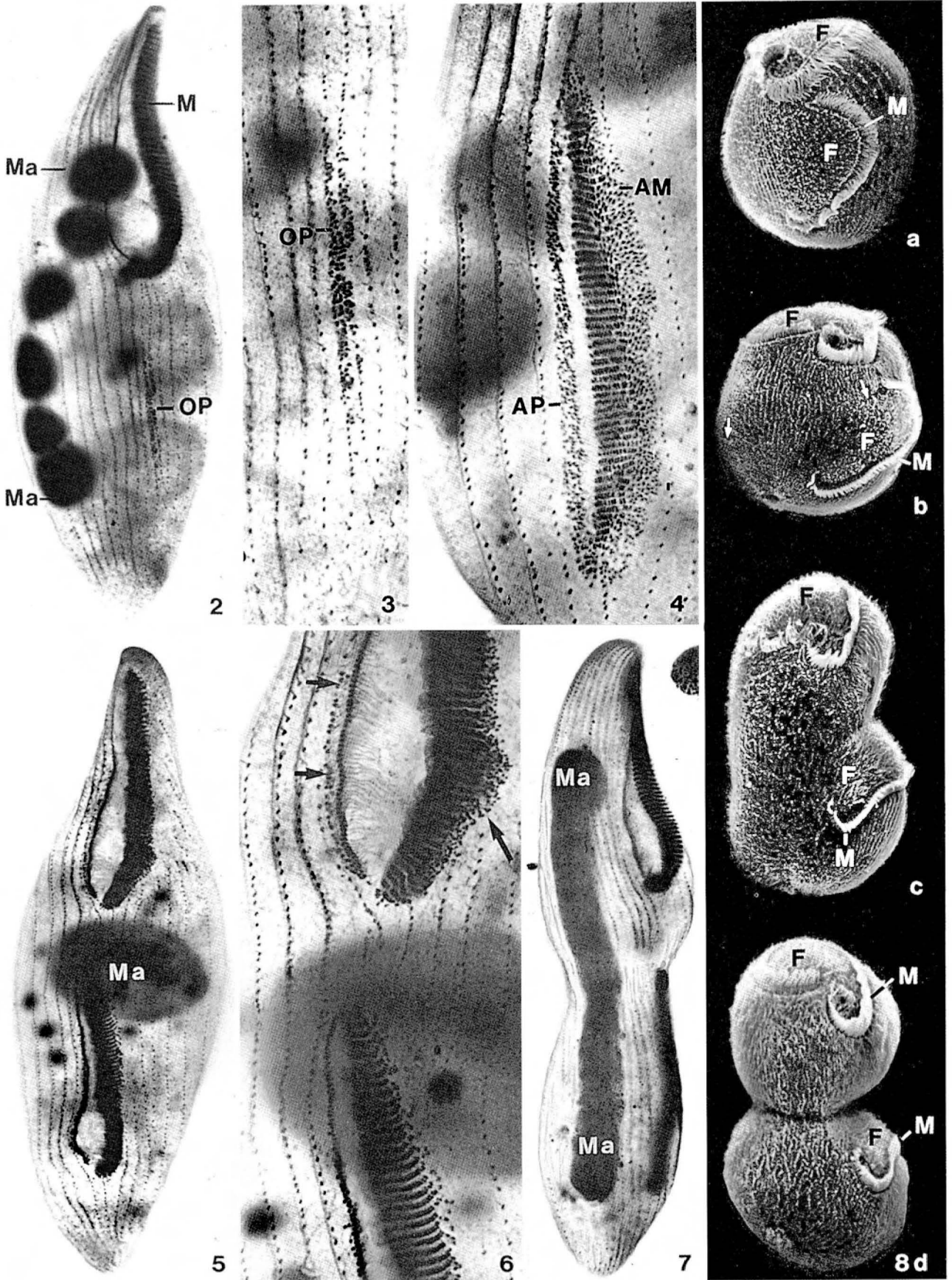
The main patterns of stomatogenesis and cell division are now well known in oligotrich ciliates; however, only few species have been studied in detail. Careful studies of more species will possibly show that the tintinnids and strombidiids are more diverse than hitherto recognized.

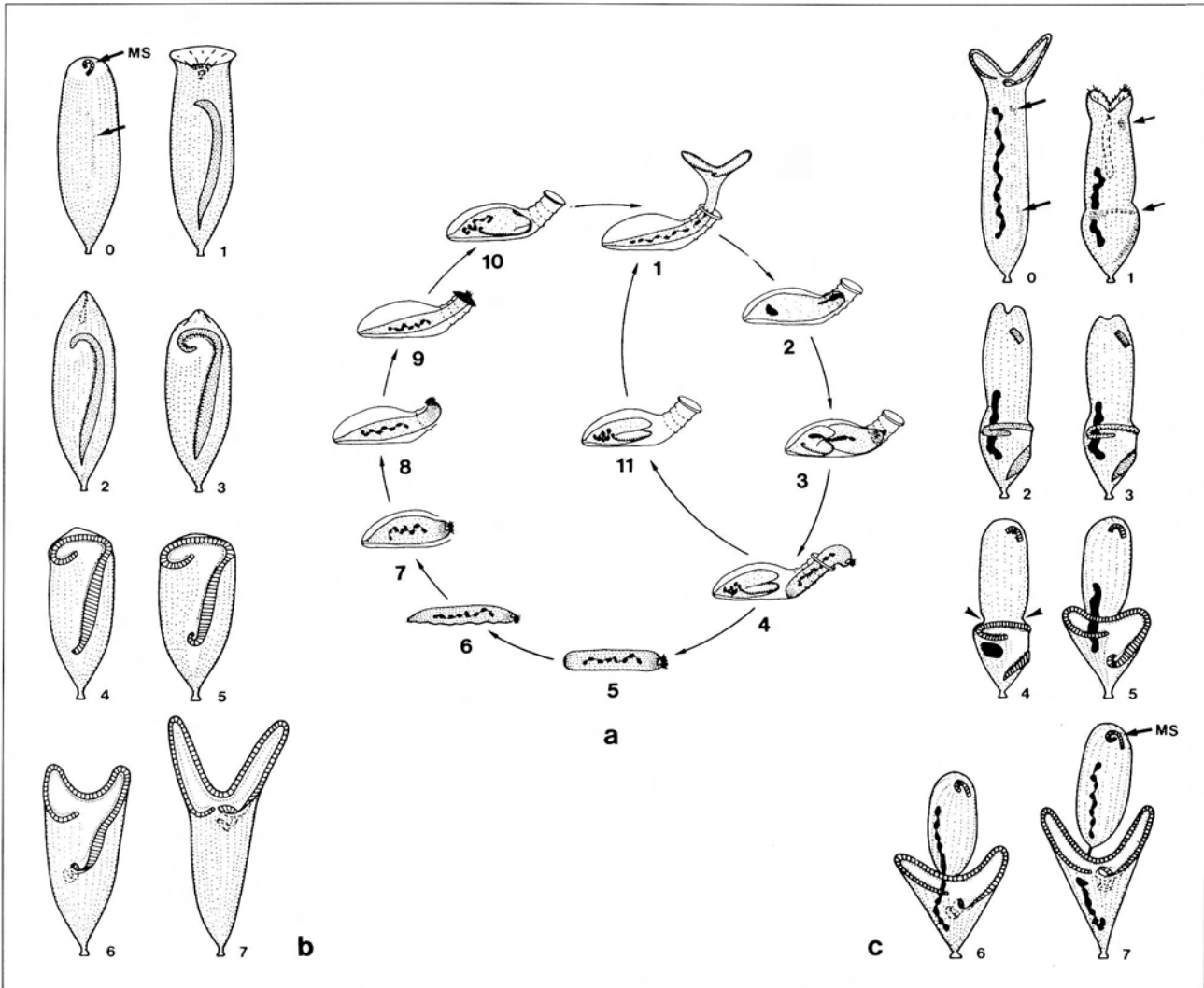
Lorica formation has been extensively studied in various tintinnids (43, 79, 80, 187, 314, 401, 499, 500). *Favella ehrenbergii* alternatively produces two differently shaped loricae (500). The somatic cilia assist in designing the lorica shape. The building material is produced by the cell or taken from the environment. Lorica splitting has been described in some freshwater tintinnids (647).

Petz and Foissner (611) could not discern a unique morphogenetic character defining oligotrichs as monophyletic group, because their enantiotropic cell division is possibly less pronounced in some tintinnids and also occurs in peritrichs and a few prostomatids (Table 2). They suggested, however, that enantiotropic cell division evolved convergently in these groups, and thus they consider this special mode of cell division as the most reliable apomorphy (derived character) for the oligotrichs. Furthermore, the character combination – polar oral apparatus and apokinetal origin of the oral primordium – is unique to the oligotrichs.

**Figs. 2–7:** Polyparakinetal stomatogenesis and homothetogenic (transverse) fission in the heterotrich ciliate *Blepharisma americana* (originals from a protargol – impregnated population collected in Costa Rica, Central America). – **2, 3:** Overview and detail of a very early stage. A few postoral (stomatogenic) ciliary rows proliferate basal bodies laterally, forming an anarchic field (OP). – **4:** Middle stage showing developing paroral membrane and adoral membranelles. – **5, 6:** Late stage with almost fully organized oral apparatus in the proter and opisthe and condensed macronucleus. The proximal portion of the parental paroral membrane (short arrows) and of the parental adoral zone of membranelles (long arrow) are reorganized. – **7:** Very late stage showing cytokinesis and elongation of macronucleus. AM = anlage for adoral zone of membranelles, AP = anlage for paroral membrane, M = adoral zone of membranelles, Ma = macronucleus, OP = oral primordium.

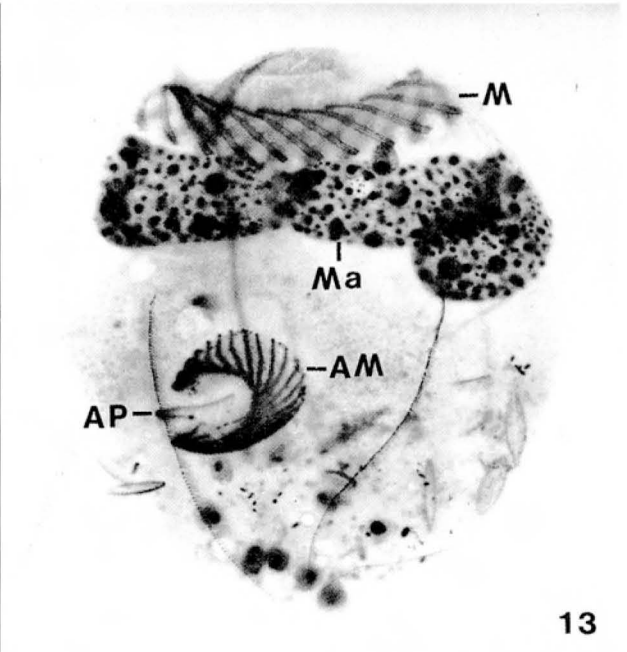
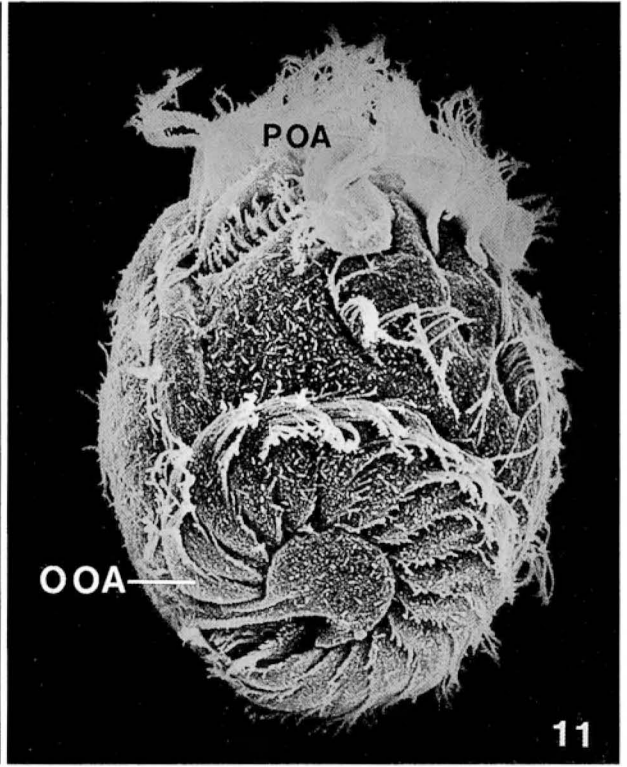
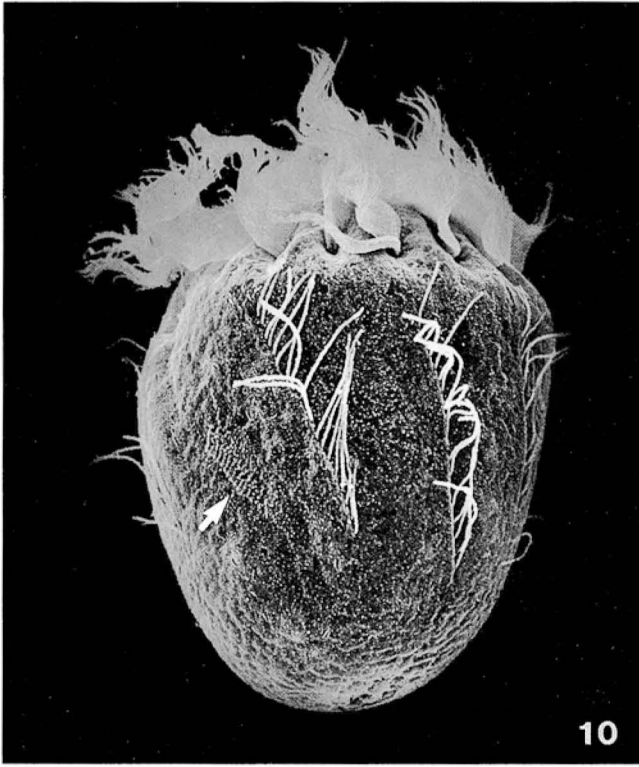
**Fig. 8 a–d:** Scanning electron micrographs of the amphiparakinetal stomatogenesis and homothetogenic (transverse) fission in the heterotrich ciliate *Stentor coeruleus* (from [152]). – **a:** Early stage showing developing membranelar band (oral primordium) intersecting many postoral ciliary rows which become peristomial ciliary rows on the frontal field of the opisthe (cp. Fig. 1 c). – **b:** Middle stage showing developing fission furrow (faintly visible at arrows). The anterior portion of the developing membranelar band begins to shift posteriorly and dorsally around the cell. – **c:** This movement continues so that by the late stage the new membranelar band is almost horizontal enabling transverse fission. – **d:** Very late stage showing deep division furrow and filial products arranged homothetogenically, i.e. the axes of the proter and opisthe have the same orientation. F = frontal field, M = adoral zone of membranelles.





**Fig. 9:** Schematic illustration of (a) the life-cycle of *Eufolliculina uhligi* and of the stages during (b) metamorphosis and (c) division (from [562]). – **a:** The sessile cell (1) divides (2–4) into a swarmer (5) and a trophic cell (11). The swarmer secretes a new lorica (6–9). Finally it transforms into the trophic form (10). – **b:** Metamorphosis. Stage 0 (0 min): Initial appearance of the primordium (arrow) during lorica construction. MS = membranellar spiral. Stage 1 (10 min): Short, disorganized cilia form a curved band. Stage 2 (20 min): The anterior portion of the primordium expands. Stage 3 (30 min): The paroral cilia appear. Stage 4 (45 min): Membranelles have formed and the buccal spiral develops. Stage 5 (60 min): The paroral membrane is organized. Stage 6 (90 min): The peristomial wings grow out. Stage 7 (120 min): The cystostome forms. – **c:** Division. Stage 0: Resorption of the peristomial wings. Arrows mark hypothetical initiation sites of basal body replication. Stage 1: The buccal cavity is resorbed. The hook-shaped oral primordium of the opisthe and the short oral primordium of the proter become visible (arrows). Stage 2: The anterior loop of the opisthe's oral primordium develops. Stage 3: Both primordia give rise to the right paroral ciliature and the left adoral primordium. Stage 4: Adoral membranelles form in both proter and opisthe. The paroral cilia of the proter disappear. The cleavage furrow (arrowheads) constricts. Stage 5: The paroral membrane and the buccal cavity are organized in the opisthe. Stage 6: The peristomial wings of the opisthe have developed. Stage 7: Proter and opisthe separate. MS = membranellar spiral of the proter.





**Figs. 10, 11:** Scanning electron micrographs of the epiapokinetal stomatogenesis and enantiotropic cell division in the oligotrich ciliate *Meseres corlissi* (from [610]). – **10:** Early stage showing oral primordium (arrow) developing on cell surface postorally between somatic ciliary rows. – **11:** Late stage showing proter's and opisthe's oral apparatus orientated enantiotropically, i. e. having axes opposed at 90°. OOA = opisthe's oral apparatus, POA = proter's oral apparatus.

**Figs. 12, 13:** Scanning electron micrograph and protargol impregnation of early dividers of the oligotrich ciliate *Strobilidium caudatum* (from [610]). The oral primordium develops hypoapokinetally in a subsurface pouch (arrow). Cell division is enantiotropic as in *Meseres* (Fig. 11). AM = anlage for the adoral membranelles, AP = anlage for the paroral membrane, M = proter's adoral membranelles, Ma = macronucleus.

## 7.2.2 Hypotrichs

The hypotrichs are easily distinguishable from practically all other ciliates by their cirri, which are compound organelles usually formed by many cilia. About 700 species are known which live in freshwater, terrestrial, and marine environments. With few exceptions, they are free-living, i.e. do not build cases or parasitize other organisms. The cirral pattern is highly diverse and has attracted many workers, because it is easily seen and stained. Thus, a vast amount of data on normal and experimental morphogenesis is available (Tab. 2, [283]). Although there are a lot of studies from the 19th century, e.g. Stein's (721–723) beautiful books, the benchmark was set by the careful investigation of Wallengren (796), whose cirral numbering system is still used. In recent times, Borror's (52) revision greatly stimulated research on hypotrichs although many of his synonyms later proved to be distinct species.

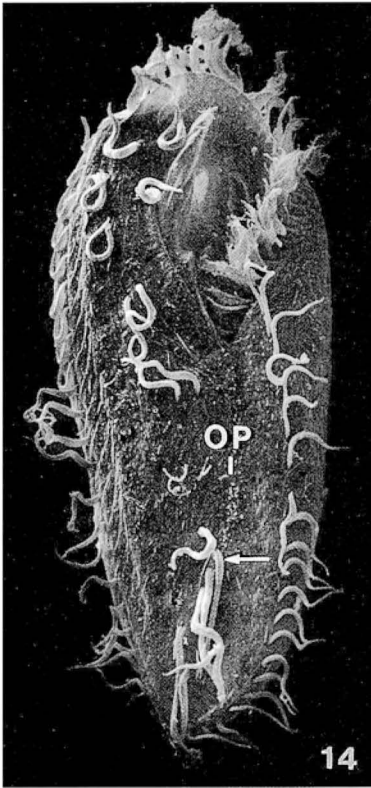
Most hypotrichs divide in active condition by homopolar fission; however, *Paraholosticha* spp. divide in reproductive cysts by a process which is rather similar to the excystment morphogenesis described in kinosome-resorbing cysts of, e.g., several oxytrichids (78, 360). Very likely, the paraholostichids developed reproductive cysts as an adaptation to their highly variable terrestrial and semi-terrestrial biotopes; they are, like many colpodids s. str., adversity strategists (151, 266). Endogenous bud formation was described in *Histiculus vorax* and *Histiculus similis* (90, 124); however, the data are not convincing, and I agree with Yanbin Pang and Zuoren Zhang (838) that the buds are ingested ciliates; suctorian parasites, which are widespread

in hypotrichs (149), also cannot be excluded. Three stomatogenic patterns occur: parakinetal (e.g., *Bakuella*, many oxytrichids and urostylids), epiapokinetal (e.g., *Cladotricha*, *Kabliella*, *Psilotricha*, some oxytrichids), and hypoapokinetal (typically in pseudohypotrichs like *Euplotes* and *Uronychia*). The occurrence of parakinetal and epiapokinetal stomatogenesis varies even in single (morpho) genera, e.g. in *Oxytricha* and *Kabliella*. This indicates that such differences cannot be used for suprageneric classification of hypotrichs. I suggest, however, that genera should contain at least only species with the same mode of stomatogenesis. Some large hypotrich genera, e.g. *Oxytricha*, are very likely polyphyletic and need to be split; however, the matter is complicated. Grimes (334) showed by protargol impregnation that *Oxytricha fallax* has a typical parakinetal stomatogenesis, i.e. basal bodies for the opisthe's oral primordium seemingly originate from the leftmost transverse cirrus. Transmission electron microscopy of such early dividers proved, however, that there is no donation of any cirral part to the oral primordium (334, 335). We thus must face the possibility that a parakinetal stomatogenesis is absent in hypotrichs; it is, possibly, always epi- or hypoapokinetal as in oligotrichs.

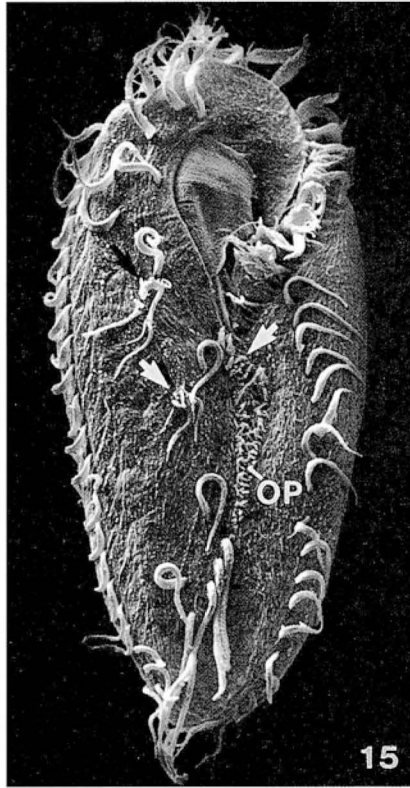
The parental oral infraciliature is retained unchanged (in many pseudohypotrichs like *Euplotes* and *Aspidisca*, but not in *Uronychia*; possibly only in *Psilotricha* within the euhypotrichs), partially reorganized (in most euhypotrichs, which usually renew only the undulating membranes), or completely renewed (in many urostylids) during cell division. There is some evidence that euplotine hypotrichs renew the whole parental oral apparatus dur-

**Figs. 14–17:** Apokinetal (parakinetal?) stomatogenesis, cirral development and migration, and homothetogenic (transverse) fission in the euhypotrich ciliate *Steinia sphagnicola* (originals from a population collected in a brook in Bavaria, Germany; 14–16 scanning electron micrographs, 17 protargol-impregnation). – **14:** Very early stage. The oral primordium consists of an anarchic field of basal bodies and develops close to the uppermost transverse cirrus (arrow), which appears unchanged in both the scanning electron microscope and protargol-impregnated specimens. – **15:** Early stage. The oral primordium elongates and some frontal and postoral cirri disaggregate to form cirral anlagen (arrows). – **16:** Middle stage. Adoral membranelles organize within the oral primordium which slightly invaginates. A set of fronto-ventral-transverse cirral anlagen (arrows) develops each in the proter and opisthe from disaggregated parental frontal and ventral cirri. – **17:** Late stage showing fully developed opisthe's adoral zone of membranelles, migration of newly formed cirri, developing marginal rows, and elongation of condensed macronucleus. All parental cirri (arrows) are gradually resorbed, whereas the proter's adoral zone of membranelles is retained. Ma = Macronucleus, MR = new marginal cirral rows, OP = oral primordium.

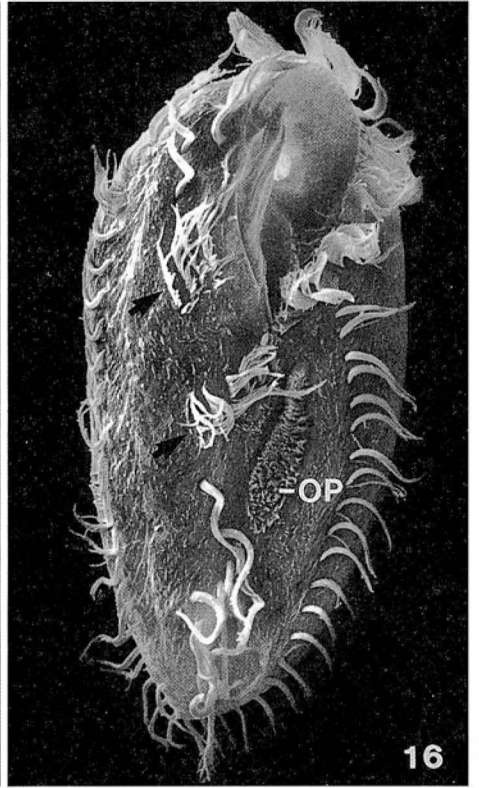
Fig. 18: Dry silver nitrate impregnation of an early divider of the pseudohypotrich ciliate *Euplotes moebiusi* (original). The oral primordium (OP) develops hypoapokinetically in a subsurface pouch close to the proximal end of the parental adoral zone of membranelles. Two new sets of fronto-ventral-transverse cirri originate de novo in discrete areas having a narrowly meshed silverline system (thick arrows). Thin arrows mark primordia for caudal cirri.



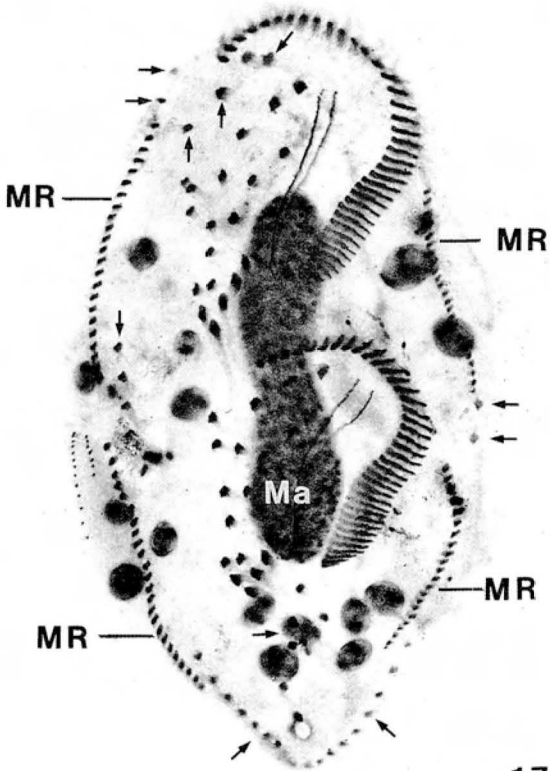
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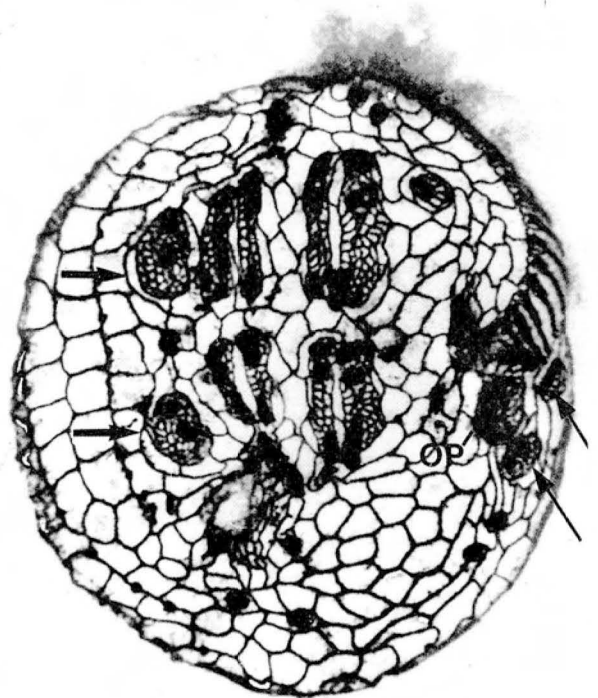
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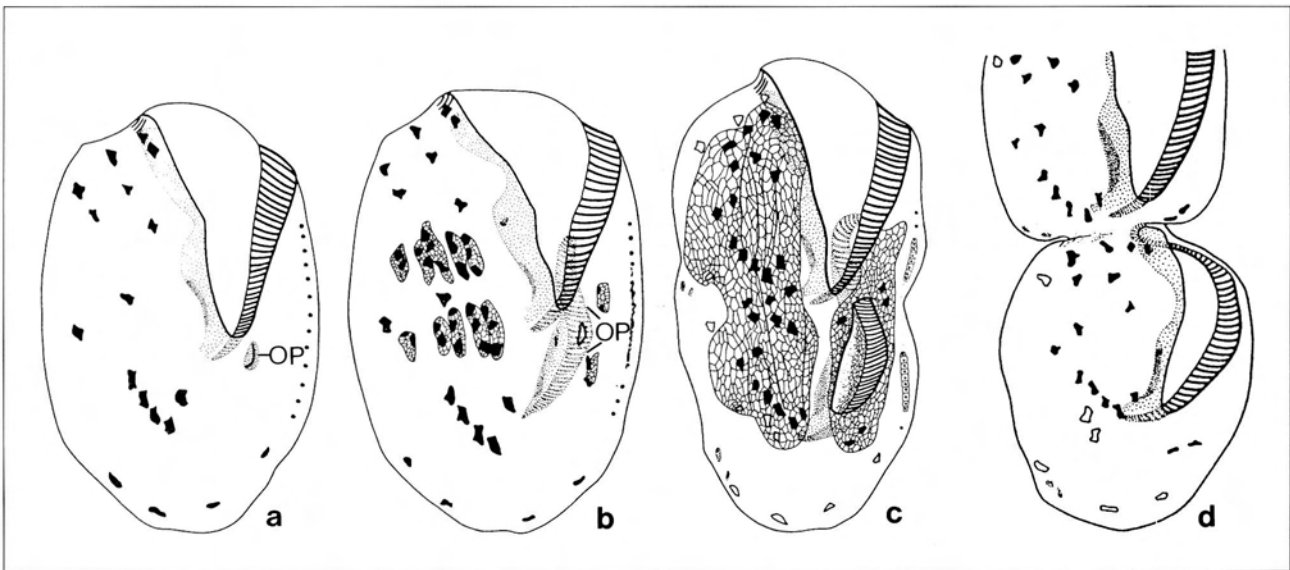
ing asexual reproduction by a process which may be termed internal reorganization, i.e. the resorption of the old and the formation of the new oral structures occur concomitantly without production of a special anlage (290, 291, 464, 775, 796). The data, however, are somewhat ambiguous, and Fleury (242, 243), using immunocytochemical methods, definitely states: «the parental peristomal area remains strictly unaffected during the whole morphogenesis.»

Practically all euhypotrichs are at least binucleate. Each macronuclear segment develops a replication band when fission commences (more detailed studies must confirm whether such bands are really absent in *Parastrongylidium* [246]). The segments fuse during the middle morphogenetic stages, and the rounded mass divides to the species-specific number of segments during cytokinesis; however, in *Pseudokeronopsis* spp., which have a rather normal looking holostichid infraciliature, each of the many macronuclear segments divides individually. It is not known, how these species regulate the macronuclear number (823).

The morphogenesis of some species has been investigated by electron microscopy (Table 2). These studies describe the origin of the ciliature from single basal bodies and their assemblage into pairs

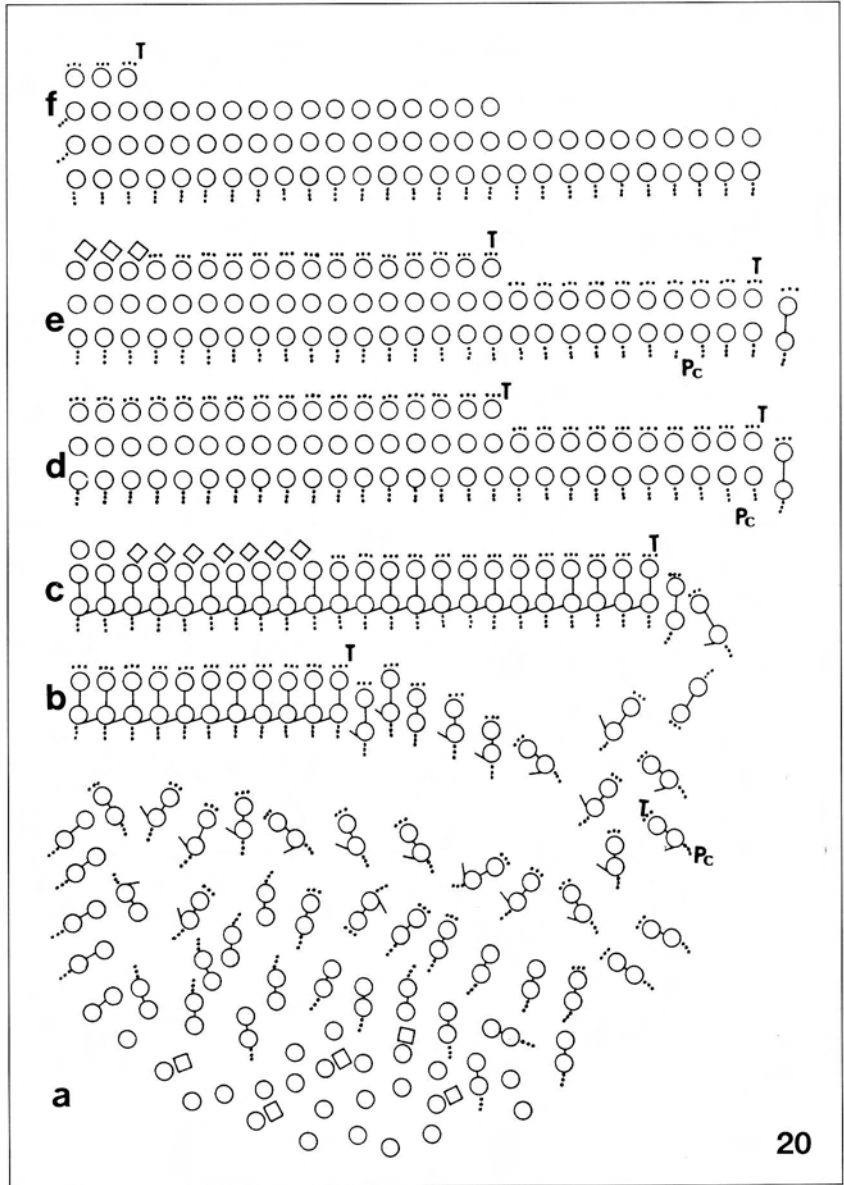
and compound cirral structures. The patterning of the individual organelles is a highly ordered process and supports a gross separation of the hypotrichs into two subtaxa (see below).

Two curious genera, which were moved repeatedly from the heterotrichs to the hypotrichs and vice versa, must be mentioned, i.e. *Plagiotoma*, which lives in the gut of oligochaete annelids, and *Phacodinium*, which lives in terrestrial biotopes. *Plagiotoma* has a distinctly differentiated dorso-ventral infraciliature (as is usual in hypotrichs), a parakinetal stomatogenesis (as in many hypotrichs and all heterotrichs), and a macronuclear reorganization band (as in hypotrichs and oligotrichs). I thus agree with Fleury (241) that it is an aberrant hypotrich. *Phacodinium* was recently also assigned to the hypotrichs, because its adoral and paroral infraciliature bears some resemblance to that of *Euplotes* (229). Unfortunately, morphogenetic data are lacking. I thus keep *Phacodinium* with the heterotrichs. Considering the huge amount of morphostatic, morphogenetic, and ultrastructural data, one would expect the main evolutionary lines within the hypotrichs to be uncontested. Unfortunately, they are still highly controversial, and many classifications have been suggested. Likewise, evolution within families is highly uncertain (179, 806).



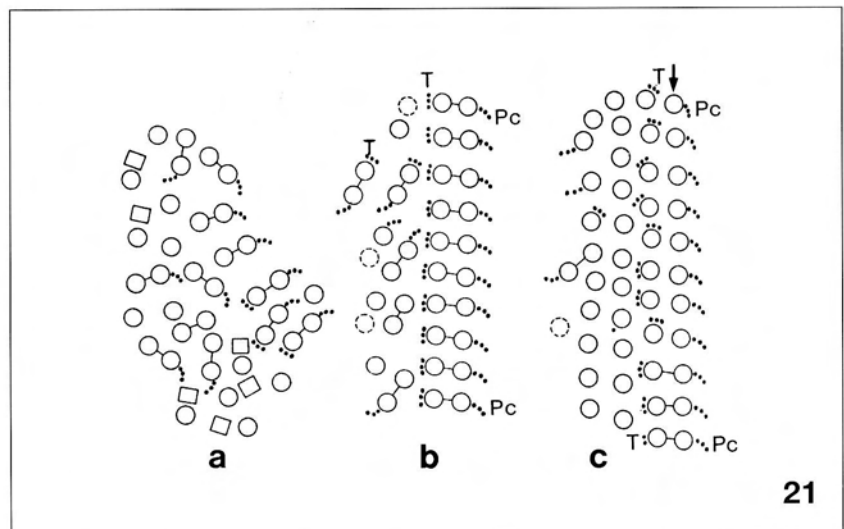
**Fig. 19 a–d:** Hypoapokinetal stomatogenesis and homothetogenic (transverse) fission in the pseudohypotrich ciliate *Euplotes eurystomus* (wet silver nitrate impregnation; parental silverline network omitted; from [830]). – **a:** Very early stage showing the oral primordium (OP) developing in a subsurface pouch close to the proximal end of the parental adoral zone of membranelles. – **b:** Middle stage showing the oral primordium (OP) still within a large, subsurface pouch having a small exterior opening. Two new sets of fronto-ventral-transverse cirri develop de novo in discrete areas having a narrowly meshed silverline system (cp. Fig. 18). – **c:** Late stage showing evagination of the oral primordium and migration of the newly formed cirri. – **d:** Very late stage showing the evaginated new adoral zone of membranelles and the deep, transverse division furrow. All parental cirri (shown in outline) are resorbed, whereas the parental oral apparatus is retained.

**Fig. 20 a–f:** Schematic illustration of the successive steps of adoral membranelle formation in a euhypotrich ciliate, *Paraurostyla weissei*, according to transmission electron microscopic investigations (from [433]). Open squares represent forming basal bodies; open circles, fully developed basal bodies; black dots, postciliary (Pc) and transverse (T) microtubular ribbons. Starting from (c) the connectives between the basal bodies are omitted. Note that the adoral zone of membranelles develops from anterior to posterior (f to a) in the oral primordium (cp. Figs. 15, 16), while the formation of the individual membranelles occurs from posterior to anterior (a to f). – **a:** The oral primordium is composed of an anarchic field of single and paired basal bodies. – **b:** The paired basal bodies align to a two-rowed promembranelle. – **c, d:** A third row of basal bodies is added to the promembranelle. – **e:** A fourth row of basal bodies is added to the promembranelle. – **f:** Fully developed adoral membranelle.



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**Fig. 21 a–c:** Schematic illustration of the successive steps of the formation of the undulating membranes (paroral and endoral membrane) in a euhypotrich ciliate, *Paraurostyla weissei* (from [434]). – **a:** The undulating membranes develop from an anarchic field of basal bodies. – **b:** Pairs of basal bodies align at the left side of the forming organelle; these become the endoral membrane. The pairs left of the ordered row later forms the paroral membrane. – **c:** The connectives between the basal body pairs dissociate and the transverse microtubular ribbons translocate. Later, the leftmost row (arrow) moves under a cytoplasmic fold and becomes the endoral membrane, while the other basal bodies organize to a multi-rowed paroral membrane.



21

For a long time most workers followed the classification proposed by Fauré-Fremiet (218), who divided the hypotrichs into two suborders, the Stichotrichina (e.g. Spirofilidae, Kahliellidae) and the Sporadotrichina (e.g. Oxytrichidae, Euplotidae). In 1985, Small and Lynn (706) made a radical change by transferring all euplotids to the Nassophorea. Recently, however, they returned to the classical view (519). Fleury (241, 248) divided the hypotrichs into two suborders too, the Pseudohypotrichina (euplotids s. l.) and the Euhypotrichina (others). Her system was criticized by Tuffrau (771), who suggested a refined Faurean classification. From the data available, Fleury's classification seems to reflect the state of knowledge most appropriately. I suggest, however, the following refined diagnoses.

**Euhypotrichina:** Hypotrichida with epiapokinetal or parakinetal stomatogenesis. Ventral and dorsal infraciliature completely reorganized during cell division. Kinetodesmal fiber of dorsal dikinetids transient, i.e. resorbed during late morphogenetic stages.

**Pseudohypotrichina:** Hypotrichida with hypoapokinetal stomatogenesis. Dorsal infraciliature retained during cell division. Kinetodesmal fiber of dorsal dikinetids permanent.

These diagnoses use entirely morphogenetic characters and show that ontogenetic studies greatly influenced our understanding of hypotrich evolution. It is reasonable to assume that more detailed studies will also help to elucidate the diversification at intra- and interfamilial level. The morphogenetic processes in hypotrichs are very similar to those found in oligotrichs. These groups are thus more closely related than, e.g., heterotrichs and oligotrichs. This is corroborated by a comparative analysis of the 16S-like r RNA (670).

## 7.3 Oligohymenophorea

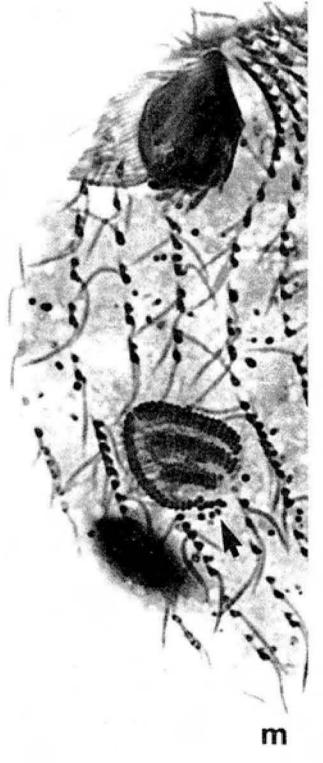
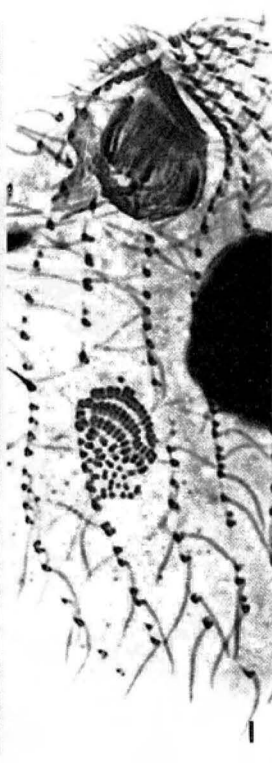
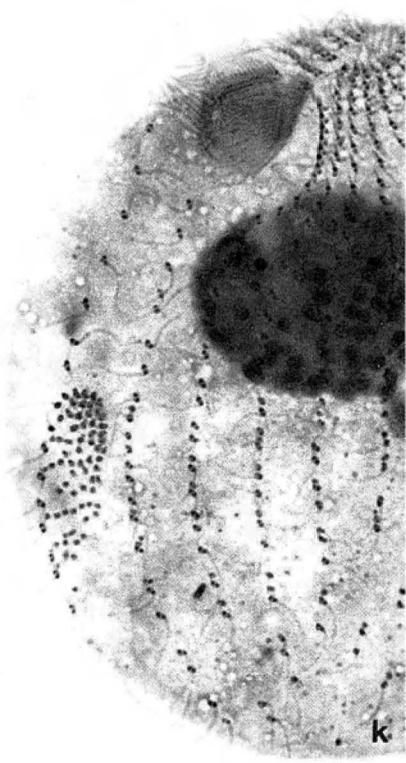
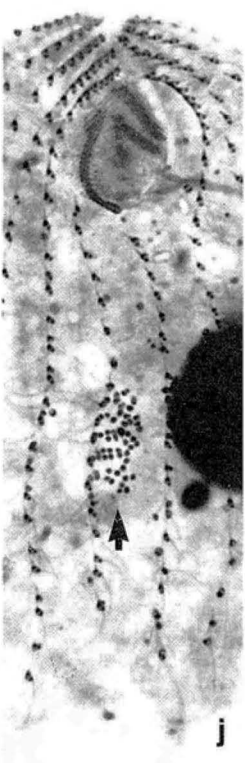
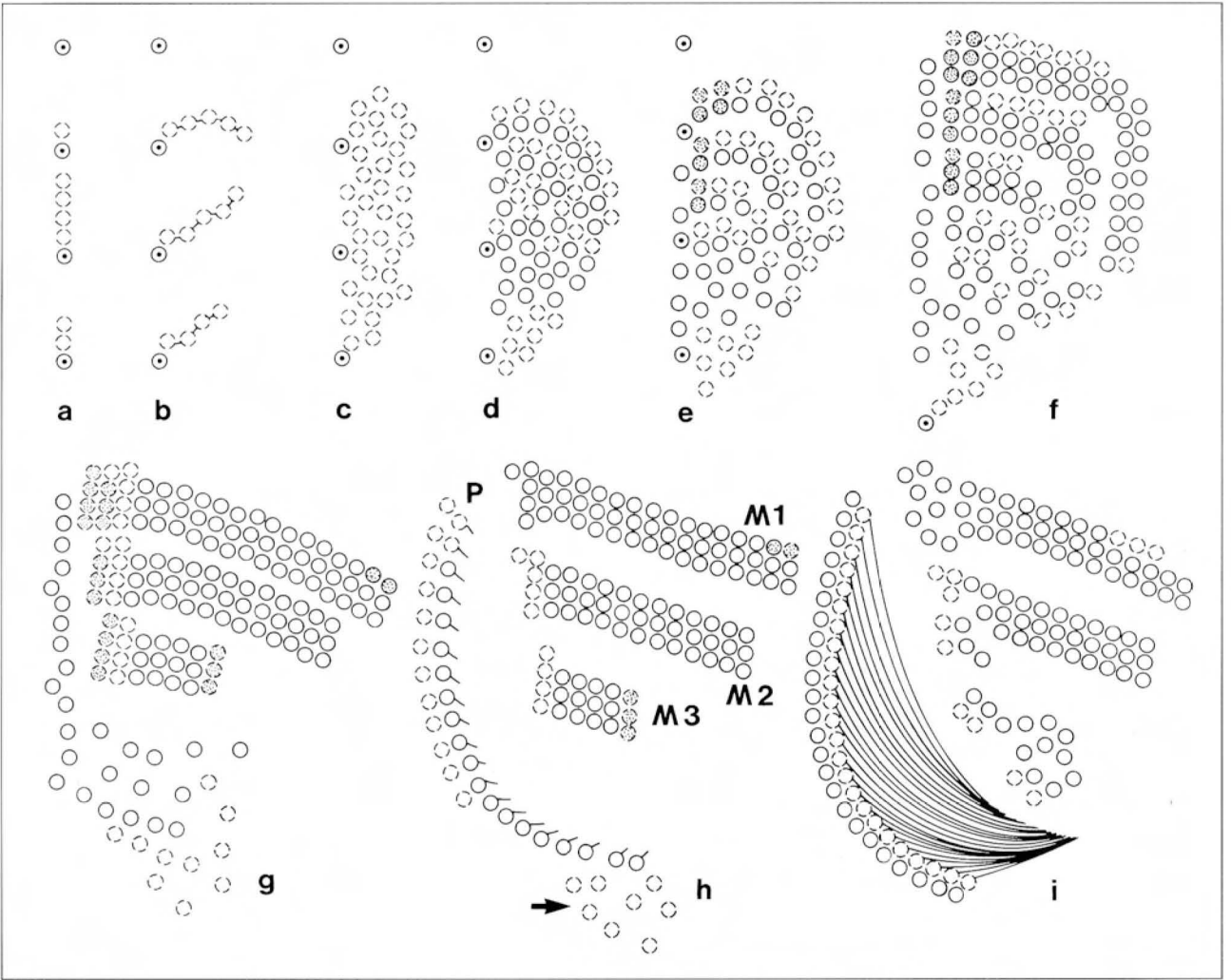
The Oligohymenophorea contain the pets of the ciliatologists, viz. *Tetrahymena* and *Paramecium*. Literature on morphogenesis is extensive, and stomatogenesis was studied by electron microscopy in a few species (Table 2). The classification of the peniculines, to which *Paramecium* belongs, has been queried recently. Some consider them as nassophoreans (519); other keep them separate as incertae sedis. There is now, however, convincing evidence available from a comparative light and electron microscopical study that the ophryokinetics of, for example, *Frontonia* are homologous with the anarchic stomatogenetic field of *Paramecium* and with the scutica of the scuticociliates (34). Beran (34) suggested that the peniculines are an ancestral group from which the scuticociliates and even the tetrahymenids originated and which are most strongly derived, showing a scuticus-like residue only during the last stages of stomatogenesis (345).

### 7.3.1 Hymenostomes

These are small (e.g., *Tetrahymena*) to large (e.g., *Ophryoglena*) ciliates with usually small, but often highly complicated oral structures, typically located in a narrow buccal cavity and organized into three prominent adoral membranelles and an inconspicuous paroral membrane. Most hymenostomes are bacteria feeders, but ophryoglenids are histophagous, and some (e.g., *Ichthyophthirius*) can cause severe fish diseases.

The hymenostomes have a homomerous macronucleus and divide homothetogenically in active condition or in reproductive cysts (most ophryoglenids and some *Tetrahymena* species), where a large number of offspring are produced by palintomy. Stomatogenesis is ophryobuccokinetal in peniculines, monoparakinetal in tetrahymenids, and telo-

**Fig. 22 a–m:** Monoparakinetal stomatogenesis in the hymenostome ciliate *Tetrahymena*. Figures **a–i** (from [20]) are a diagrammatic representation of pattern formation according to scanning electron microscopic investigations; figures **j–m** (originals) show the same events in protargol-impregnated specimens. Circles indicate locations of basal bodies. Those bounded by solid lines (⊙, ○, ⊕) indicate ciliated basal bodies: ⊙, basal body of stomatogenic kinety; ○, permanent basal body of stomatogenic field; ⊕, basal body of stomatogenic field that is destined for resorption. Circles bounded by dashed lines (⊖, ⊗) indicate unciliated basal bodies, with stippling having the same meaning as before. – **a, b, j:** The central portion of the right postoral ciliary row (stomatogenic kinety) proliferates new basal bodies laterally (arrow). – **c, d, k:** A large anarchic field of basal bodies is formed by continued proliferation. – **e, f, l:** Two-rowed promembranelles develop from anterior to posterior. – **g, h, i, m:** The adoral membranelles (M1–M3) become three-rowed and the paroral membrane (P) is assembled. Note a scuticus-like structure (arrows) at proximal end of paroral membrane. The parental oral structures are retained.





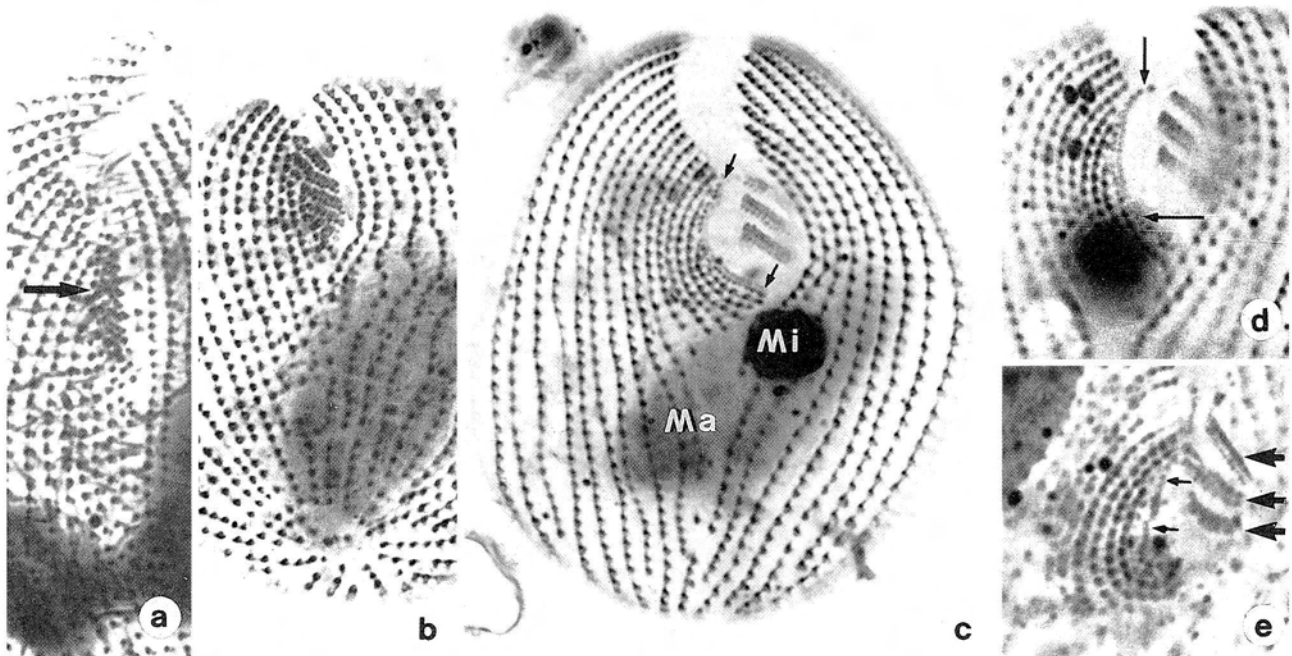
parakinetal in ophryoglenids, including *Ichthyophthirius*. Microstome-macrostome transformation occurs in some tetrahymenids and was comprehensively studied by Njine (580) and Metenier and Grolière (545). The parental oral structures are partially reorganized in most (very likely all) tetrahymenids and peniculines and completely resorbed in ophryoglenids and during microstome-macrostome transformation. As usual, these processes have not yet been studied in detail in most species. Roque et al. (661) and Roque and Puytorac (660) describe a unique stomatogenic mode in *Ophryoglena bacterocaryon*, *Ichthyophthirioides browni*, and *Ichthyophthirius multifiliis*. The paroral membrane is said to migrate out of the parental oral apparatus to act as a director meridian in producing the new oral infraciliature for both the proter and opisthe; however, this extraordinary behavior of the paroral membrane was not confirmed by Puytorac et al. (632) and Foissner (in preparation), who reinvestigated the stomatogenesis of *Ophryoglena* and *Ichthyophthirius*. In both genera the paroral membrane is resorbed during the last stages of stomatogenesis (Fig. 23). Ophryoglenids are

further united by a special structure, viz. the Lieberkühn organelle in the oral region [521].

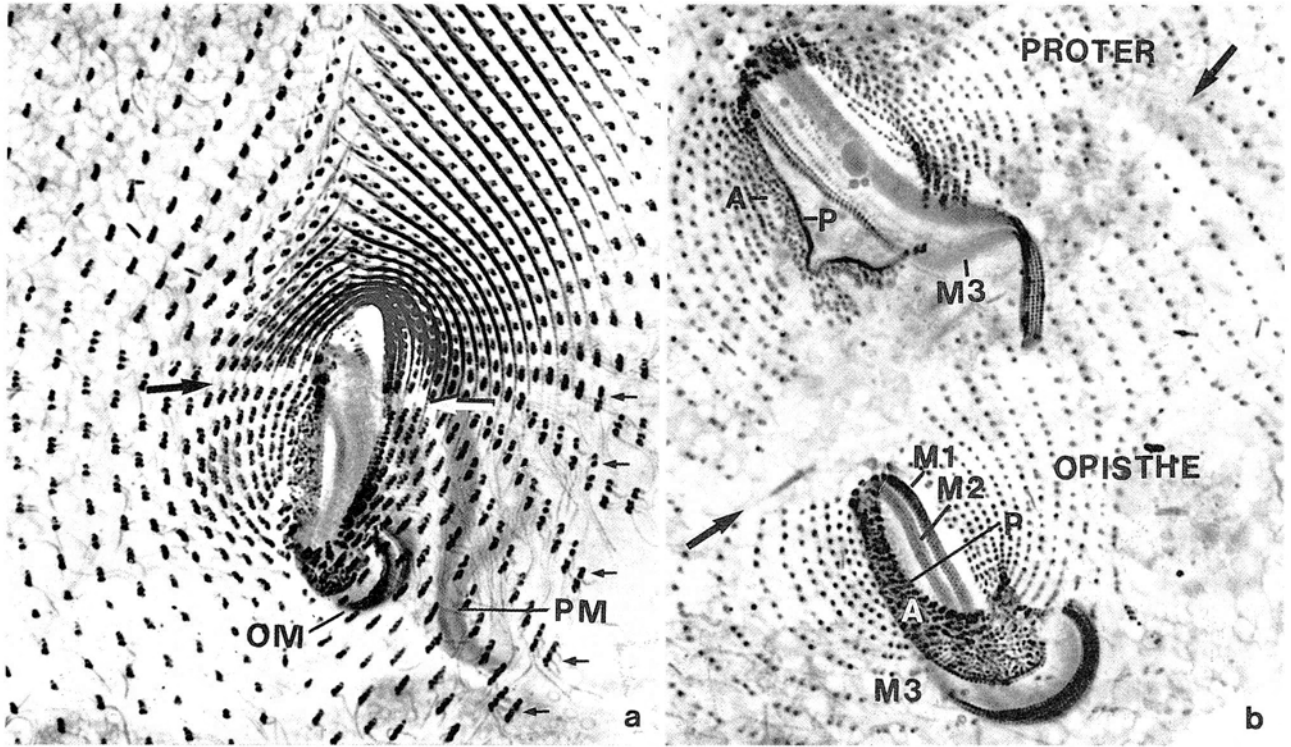
There are several genera whose classification is still under discussion. *Urocentrum*, for instance, was separated at ordinal level from *Paramecium* by a phenetic analysis (633, 634). This is, however, contradicted by morphogenetic data which show that the paroral membrane and the anarchic field of basal bodies accompanying it produce all new oral structures in both *Paramecium* and *Urocentrum*. Likewise, the position of *Turaniella* is questioned because it has peniculine adoral membranelles (146, 414) and a monoparakinetal stomatogenesis (415). *Histiobalantium*, classified by Corliss (118) and others as scuticociliate, is probably a highly aberrant peniculine (169).

### 7.3.2 Scuticociliates

The general morphology and ecology of this group are very similar to the hymenostomes. The main character uniting the scuticociliates is stomatogenesis. Originally, the scuticociliates were a rather



**Fig. 23 a–e:** Teloparakinetal stomatogenesis in the hymenostome ciliate *Ichthyophthirius multifiliis* (silver carbonate impregnation; originals). – **a:** Young tomite from last palintomic division. A small, disordered field of basal bodies is recognizable near the anterior end (arrow). – **b:** By further proliferation of basal bodies many short kinetofragments are produced. – **c, d:** Late tomites showing kinetofragments assembled to three adoral membranelles each composed of three rows of basal bodies. A faintly impregnating paroral membrane appears at the right slope of the forming buccal cavity (arrows). – **e:** Very late tomite showing resorption of paroral membrane (small arrows) and migration of adoral membranelles (thick arrows) into buccal cavity; during this process one basal body row is resorbed in each membranelle. Ma = macronucleus, Mi = micronucleus.



**Fig. 24 a, b:** Ophryobuccokinetal stomatogenesis and homothetogenic (transverse) fission in the hymenostome ciliate *Paramecium* (silver carbonate impregnation; originals). – **a:** Middle stage showing proter's (PM) and opisthe's (OM) adoral membranelles still close together in parental buccal cavity. Large arrows mark developing fission furrow extending across parental oral opening. Note replicating somatic kinetids (small arrows). – **b:** Late stage showing distinct division furrow (arrows) and proter's and opisthe's oral apparatus separated. The new adoral membranelles (M1–M3) originated from the paroral membrane and the attached anarchic field (A) of basal bodies which is very likely homologous to the ophryokineties of *Frontonia* and the germinal row of peritrichs.

small group; however, it soon became larger and is still growing because morphogenetic studies showed that many genera which were originally classified as, for example, thigmotrichs or peniculines, belong to the scuticiliates. A lot of excellent morphogenetic studies have been published since the pioneering paper by Small (701); however, transmission electron microscopic studies on stomatogenesis are still very fragmentary.

The scuticiliates have a homomerous macronucleus and divide homothetogenically in active condition, except for *Porpostoma notatus*, a marine histophagous ciliate which reproduces in cysts. Stomatogenesis is scutiobuccokinetal throughout, but several «minitypes» can be distinguished. Microstome-macrostome transformation occurs in some species, but has not yet been studied in detail. The parental oral structures are partially or completely reorganized.

There are few problems with classification. *Histiobalantium* has been discussed above. *Conchophthirus* has a unique stomatogenic pattern, and its scu-

tica, the «deep kinetosomal unit», bears considerable similarity to the «germinal row» of the peritrichs and the ophryokineties of the peniculines, suggesting a common ancestor.

### 7.3.3 Peritrichs

The peritrichs are easily distinguishable from practically all other ciliates. They have an oral field covering the entire apical end (ventral surface?) of the body, a greatly reduced somatic ciliature, and often a stalk or holdfast organelle plus a locomotor fringe of cilia near the aboral pole. Their unusual arrangement of prominent peristomial ciliature encircles the oral end of the organism counterclockwise to plunge deep into an infundibular cavity, at the bottom of which is found the cytostome. A further major character is the scopula which produces the stalk that attaches the organism to the substrate (118). The scopula is modified to a highly complicated adhesive apparatus in the mobiline peritrichs

which live on or in vertebrate and invertebrate hosts.

Literature on morphogenesis of peritrich ciliates is not extensive, but it indicates a great homogeneity within the group. The division plane is parallel to the major axis of the body, apparently caused by the sedentary life habit. The daughters adhere by their posterior portions like enantiotropically dividing oligotrichs. All peritrichs divide in active condition and have a ophryobuccokinetal stomatogenesis commencing from a special germinal kinety highly reminiscent of the ophryokineties found in *Frontonia* and the scutica of the scuticociliates. The parental oral ciliature is partially reorganized in the sessiline peritrichs and retained or completely resorbed in some mobiline peritrichs; data on this group are, however, ambiguous. The complicated adhesive disc of the mobiline peritrichs is also divided, the old denticles are then resorbed, and a new denticle ring is formed in each daughter cell (46, 226, 364, 457).

Stalk formation in colonial peritrichs has been extensively studied in various species, e.g., in *Carchesium* (207), *Epistylis* (540), and *Zoothamnium* (498, 565, 733). Likewise, numerous studies are available on the formation of the lorica in loricate peritrichs (17, 202, 240, 366, 367, 489, 505, 539, 602). The most detailed study is that by González (320) on *Thuricola folliculata*. The lorica material is produced in the cytoplasm and secreted by exocytosis in the scopula region. The shape of the lorica is determined by the shape of the cell and by special movements it performs during the secretion process.

Morphogenetic studies have significantly contributed to the classification of peritrich ciliates. There is now hardly any doubt that they evolved via pleuronematids from thigmotrichs (188).

### 7.3.4 Thigmotrichs

These are small ciliates living in marine and freshwater molluscs and annelids. The oral ciliature is often inconspicuous and located subequatorially. The anterior pole bears a strongly thigmotactic ciliature and/or a pronounced sucker or adhesive disc. Many of the genera recognized by Raabe (639–643), the latest reviser of the group, have since been transferred to other orders, mainly to the scuticociliates and the cyrtophorids. The boundaries between thigmotrichs and scuticociliates are indistinct.

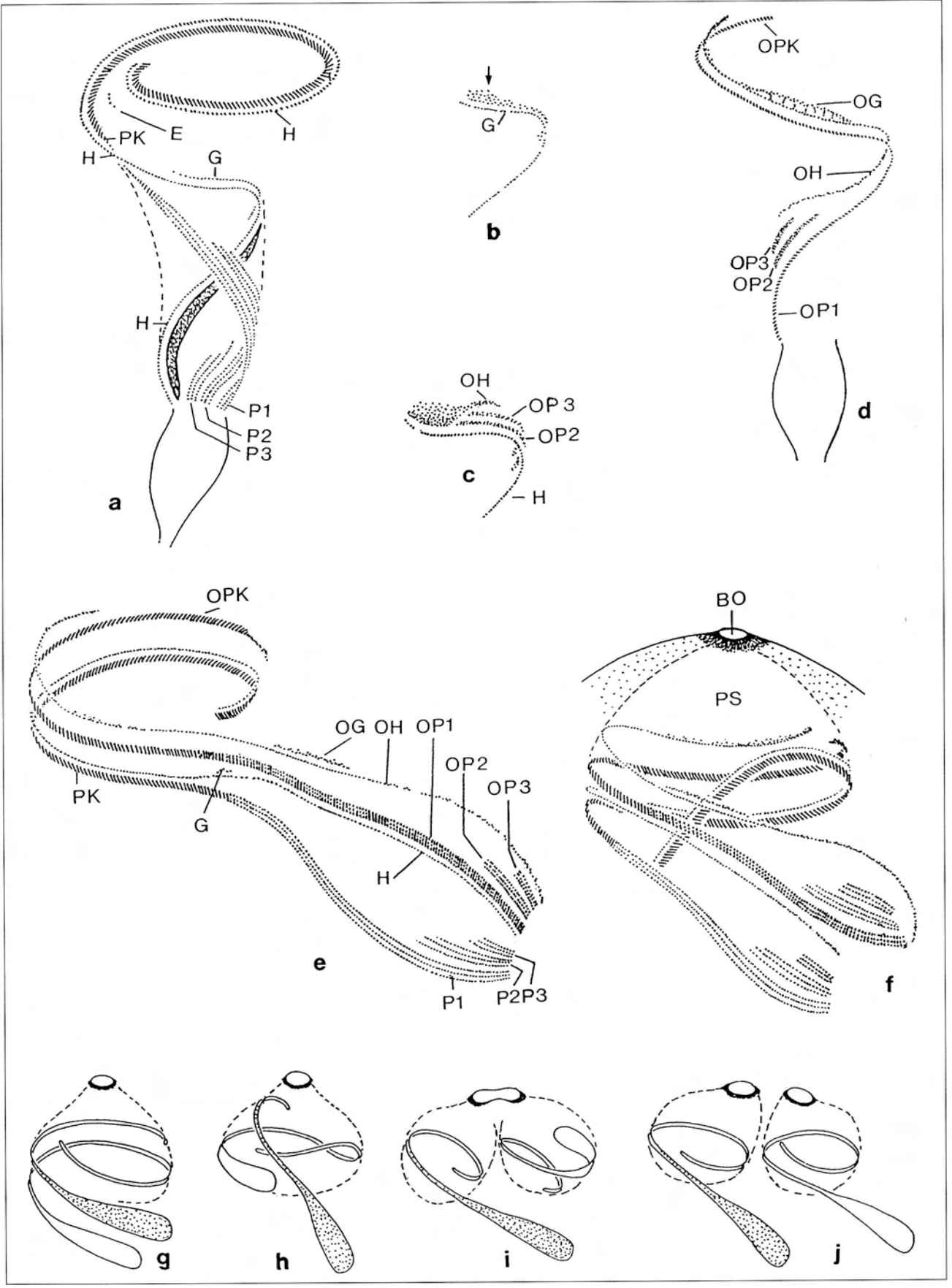
Knowledge of the morphogenesis of thigmotrichs is scanty and based mainly on comprehensive studies by Chatton and Lwoff (101) and Hatzidimitriou and Berger (379). It is not yet possible to establish whether thigmotrichine ciliates have special morphogenetic characteristics. Hatzidimitriou and Berger (379) suggested that the bipartite scutica, which extends parallel and posteriad to the paroral membrane, might be a special characteristic of thigmotrichine ciliates.

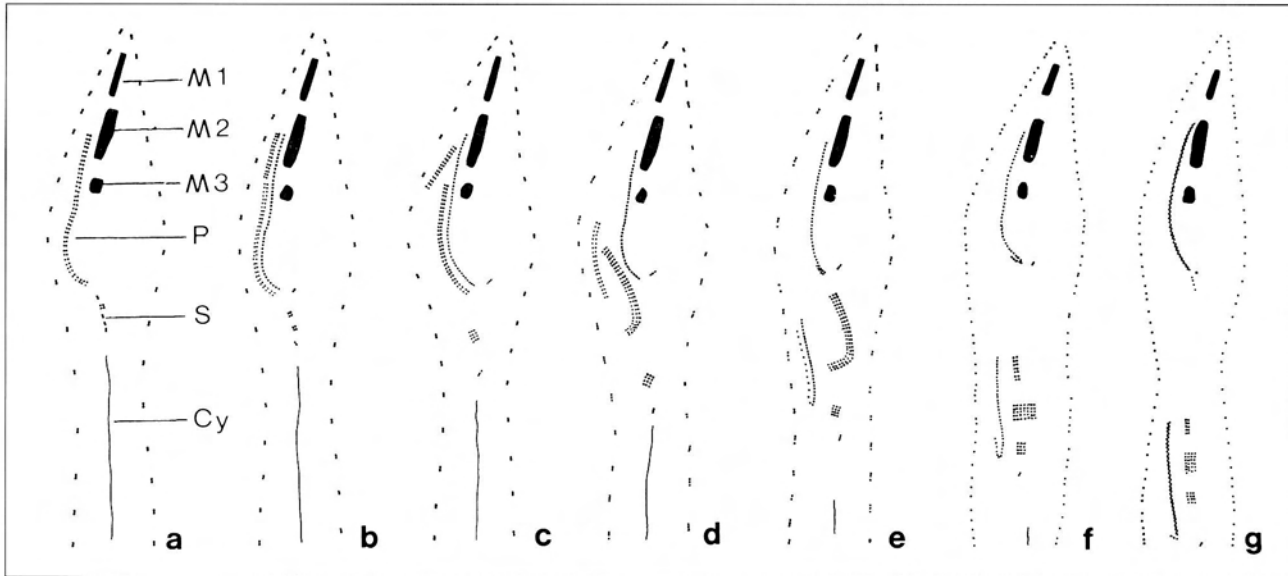
### 7.3.5 Apostomes

Apostome ciliates have complex infraciliatures and life cycles typically involving crustaceans and rarely other invertebrates; most are marine. The life cycle includes a non-feeding microstome tomite and a macrostomatous trophont, which rapidly ingests the crustacean exuvial fluid by pinocytosis. Most divide in reproductive cysts by palintomy or strobilation. The somatic infraciliature consists of meridional or spiraling kineties composed of monokinetids. The oral infraciliature of the apostomes was long misidentified, viz. three short midventral kine-

**Fig. 25 a–j:** Ophryobuccokinetal stomatogenesis and longitudinal fission in the peritrich ciliate *Opisthonecta* ▷ (protargol impregnation; from [505]). – **a:** Interphase oral apparatus. – **b:** Stomatogenesis commences with a proliferation of basal bodies (arrow) by the nonciliated germinal (ophryo) row. – **c:** By further proliferation of basal bodies evolve propeniculi (adoral membranelles) 2 and 3 and a new haplokinety (paroral membrane). – **d:** A new haplokinety and a new germinal row are recognizable. The parental haplokinety transforms into opisthe's peniculus (adoral membranelle) 1. – **e:** Two new sets of oral structures are recognizable and lie one above the other. – **f:** The new oral sets begin to separate. – **g–j:** Separation of new oral sets by longitudinal fission of cell (schematic): Dotted parts represent newly formed (opisthe's) oral structures, undotted parts are unchanged portions of the parental (proter's) oral apparatus, i.e. peniculi 1–3. Interrupted lines indicate space above retracted peristomial disc. BO = buccal opening, E = epistomial membrane, G = germinal row, H = haplokinety (paroral membrane), OG = opisthe's germinal row, OH = opisthe's haplokinety, OP1–OP3 = opisthe's peniculi 1–3, OPK = opisthe's polykinety (= outer portion of peniculus 1), PK = polykinety (= outer portion of peniculus 1), PS = peristomial space, P1–P3 = peniculi 1–3 (adoral membranelles).







**Fig. 26 a–g:** Scuticobuccokinetal stomatogenesis and homothetogenic (transverse) fission in the scuticociliate *Parauronema virginianum* (protargol impregnation; from [345]). The opisthe's oral structures originate from the scutica (S), which produces adoral membranelle 3 (M3), and the paroral membrane (P), which produces adoral membranelles 1, 2 (M1, M2) and the paroral membrane and scutica in both the proter and opisthe. The parental adoral membranelles are retained. Cy = cytopogye.

ties (x, y, z) and the rosette nearby were considered as part of the oral apparatus, and the whole group was thus thought to be related to the cyrtophorids (118). It was only recently that Bradbury (59) showed that there are three adoral membranelles (falciform fields 8, 9, and the ogival field) and a very inconspicuous, non-ciliated paroral membrane, identifiable as such only in the electron microscope. In some genera, especially those belonging to the Astomatophorina and Pilisuctorina, a functional oral infraciliature is possibly absent.

Most of what we know about apostome ciliates is contained in the monographs by Chatton and Lwoff (96, 98) and in the studies by Bradbury and her students. Bradbury (59) reviewed the available data and concluded convincingly that the apostomes are closely related to the hymenostomes, which is also indicated by their general morphology (compare, for instance, the scuticociliate *Pseudocohnilembus* and the apostome *Hyalophyssa*). Unfortunately, the origin of the paroral membrane and the ogival ciliary field (adoral membranelle 3) is still unknown. If they are produced buccokinetically then stomatogenesis would be mixokinetal, as in nassulids and microthoracids, because the falciform ciliary fields (adoral membranelles 1 and 2) are derived from somatic kineties.

### 7.3.6 Astomes

The astomatous ciliates lack an oral infraciliature and are thus not treated here. Most of what we know about this group, which lives principally in the digestive tract of oligochaete annelids, is contained in the monographs by Puytorac (619, 620). Division always occurs in active condition and is transverse or oblique to the main body axis (homothetogenic); the separation of the products is often incomplete, resulting in formation of catenoid colonies (31). Most of today's specialists agree that the astomatous ciliates belong to the oligohymenophorans; very probably they evolved from thigmotrichine scuticociliates (118, 629).

## 7.4 Cyrtophorea

### 7.4.1 Cyrtophorids

The cyrtophorids have a heteromeric macronucleus and a distinct pharyngeal basket (cyrtos) composed of complex microtubular lamellae. Typically, the ventral side is completely or partially ciliated whereas the dorsal side is barren or bears only few kineties. The reduction of the somatic ciliature is

apparently related to the mode of life; most cyrtophorids are Aufwuchs inhabitants. A few are ecto- or endocommensals of freshwater and marine invertebrates and vertebrates.

Literature on morphogenesis in cyrtophorid ciliates is rather extensive and a few species (*Chilodonella* spp., *Trithigmotoma* spp.) have been studied in great detail, especially by Hofmann (402) and Hofmann and Bardele (403). Almost all cyrtophorids divide homothetogenically in active condition (except *Cyrtophoron isagogicum*, which divides in a reproductive cyst) and have a merotelokinetal stomatogenesis (except, possibly, *Chilodonella crassa*). The parental oral structures are partially reorganized; data on this subject are, however, incomplete.

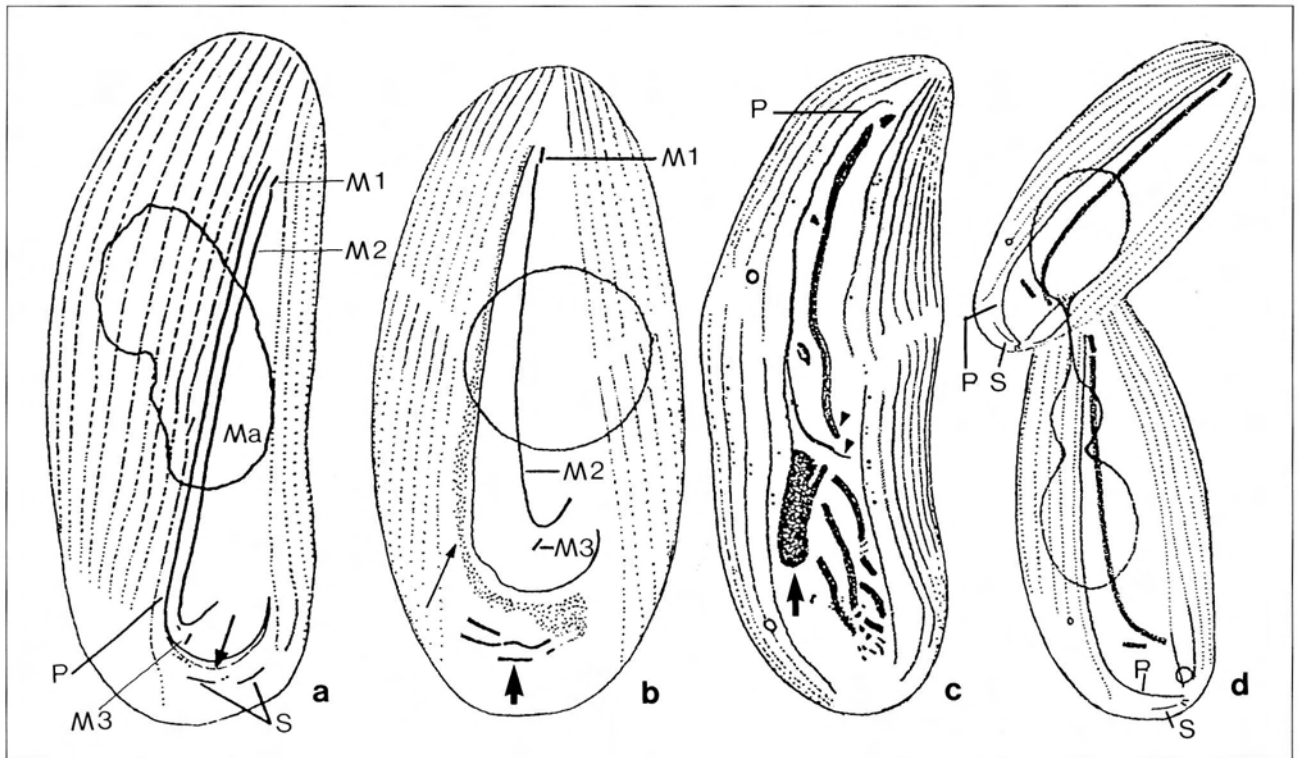
Morphogenetic studies have deeply influenced the classification of cyrtophorids (139–141) and the understanding of ciliate ontogeny in general (Fig. 4 in [24]). Evidence that hypocomids belong to this group, as proposed by Corliss (118) and Deroux

(137), is insufficient, and separation is supported by their homomeric macronucleus (cp. [101, 102, 518]).

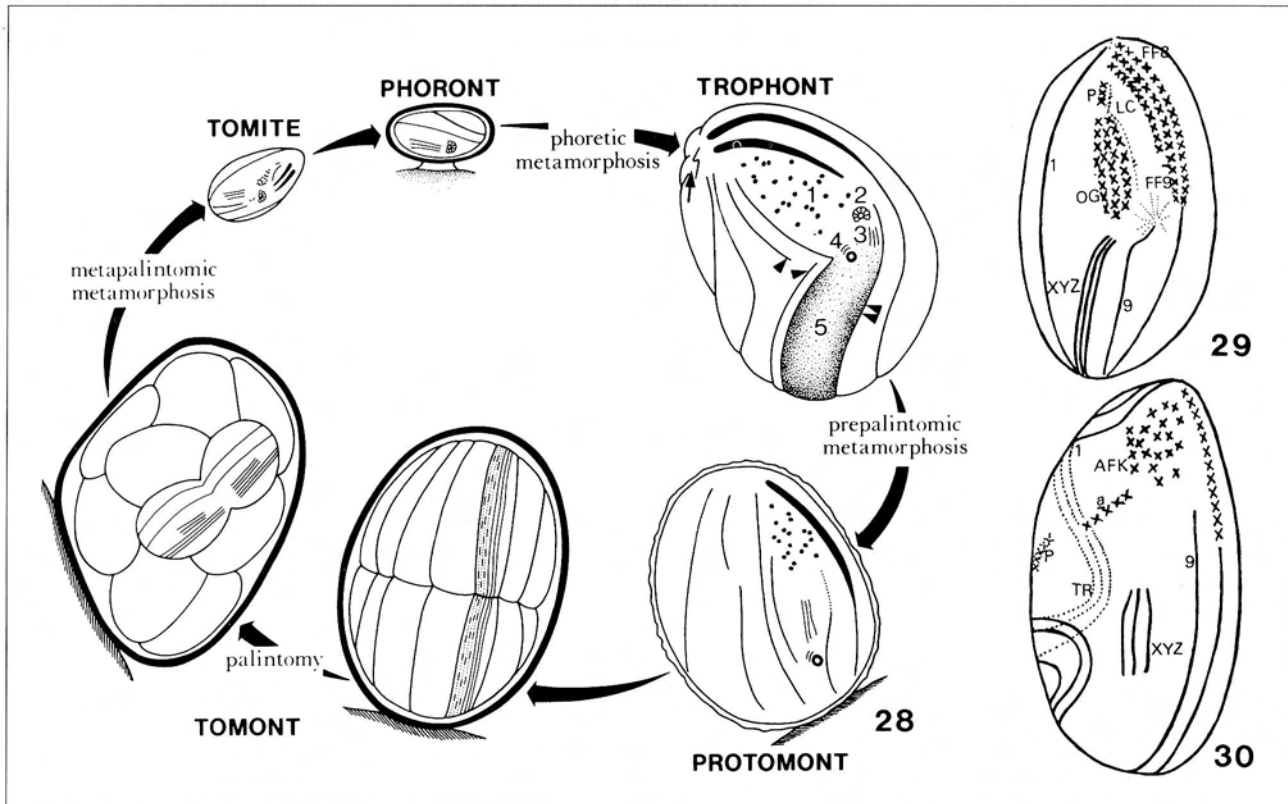
## 7.4.2 Chonotrichs

Few and contradictory data are known from the «collar ciliates», which live on marine and freshwater hosts. Their ciliature is confined to the apical funnel, and it is uncertain whether the chonotrichs have a true oral ciliature or not. It seems to be present in *Chilodochona* (325), but is probably lacking in *Spirochona* (199).

The chonotrichs divide in active condition by forming external or internal buds. Types and variations in swarmer production and life cycle have been comprehensively reviewed by Jankowski (421) and Mohr et al. (551). No stomatogenic mode can be established since, as mentioned above, it is uncertain whether or not an oral infraciliature even



**Fig. 27 a–d:** Scuticobuccokinetal stomatogenesis and oblique transverse fission in the thigmotrich ciliate *Ancistrum mytili* (wet silver nitrate and protargol preparations; from [379]). – **a:** Very early stage showing new basal bodies (arrow) along posterior portion of paroral membrane (P). The scutica (S) is bipartite and the adoral membranelles 1 and 3 (M1, M3) are much smaller than membranelle 2 (M2). – **b:** Early stage showing many disordered basal bodies along the parental paroral membrane (thin arrow) and kinetofragments around the scutica (thick arrow). – **c:** Middle stage. A conspicuous field of basal bodies (arrow), which becomes the opisthe's scutica, and many kinetofragments, which later assemble to the three adoral membranelles, have been produced. The parental oral structures (undulating membranes, membranelle 2) are reorganized (arrowheads). – **d:** Very late stage showing oblique transverse fission. Ma = macronucleus.



**Fig. 28:** Life cycle and palintomic homothetogenic (transverse) fission in the apostome ciliate *Hyalophysa chattoni* (wet silver nitrate and protargol preparations; from [651]). 1 = anterior field of basal bodies, 2 = rosette, 3 = oral kineties x, y, z, 4 = contractile vacuole pore, 5 = metastomial area. Single arrowheads mark «split» ciliary row 2, double arrowhead points to ciliary row number 9, and the arrow marks «split» ciliary row 5.

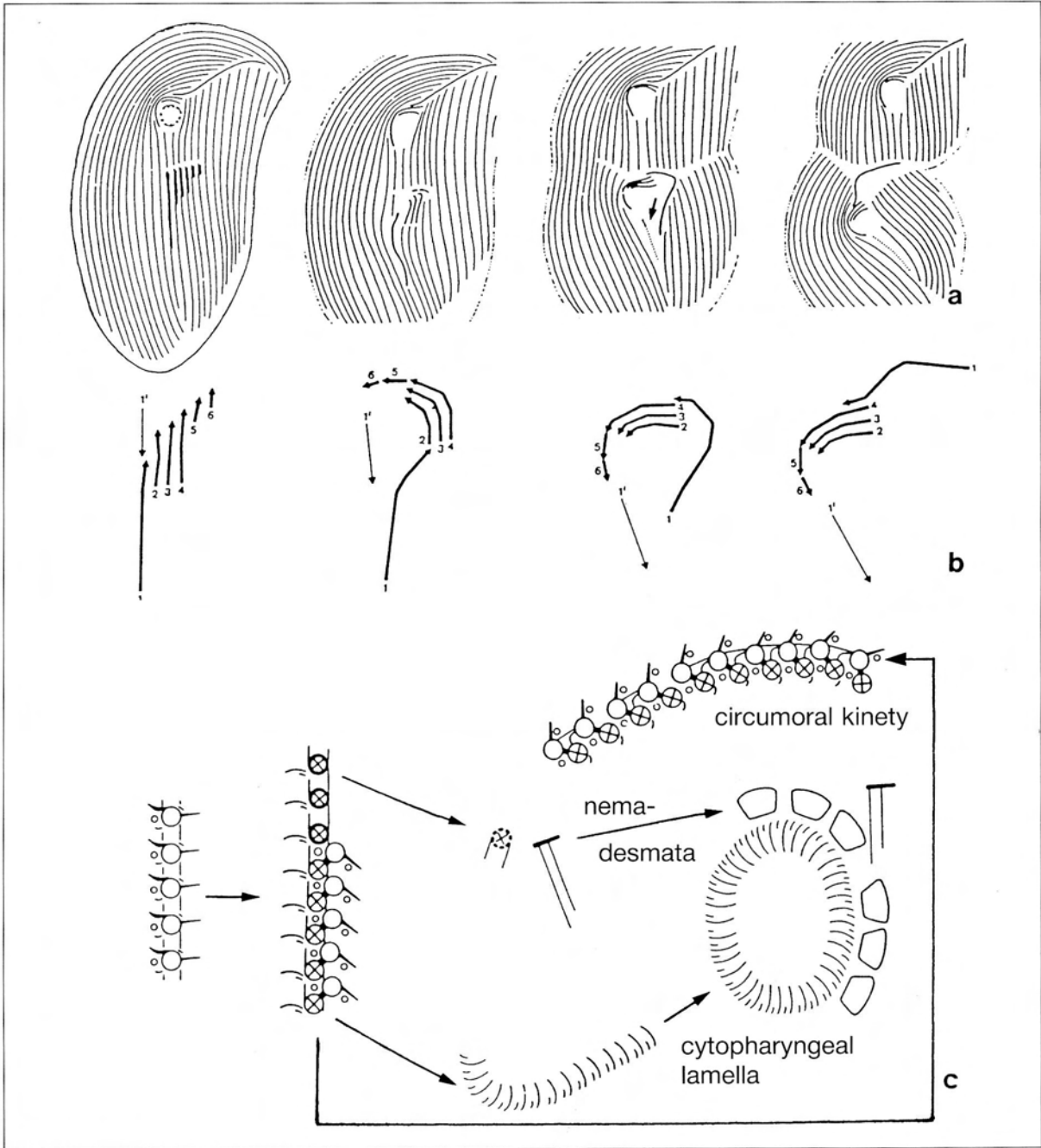
**Figs. 29, 30:** Free-swimming tomite and intermediate stage in the transformation to the macrostome in the apostome ciliate *Hyalophysa chattoni* (protargol impregnation, from [59]). The x's (except for X in xyz) indicate the putative oral ciliature of the microstome and macrostome, respectively. The paroral membrane (P) migrates to the dorsal surface (indicated by dotted x's) following the triple ribbon (TR) formed by ciliary rows 1–3. AFK = anterior field of basal bodies, a = kinety a, FF8, FF9 = falciform fields 8, 9, LC = lateral canal, OG = ogival ciliary field, P = paroral membrane, TR = triple ribbon, XYZ = kineties x, y, z, 1, 9 = ciliary rows 1, 9.

exists. The funnel (somatic) ciliature of the swarmer of *Chilodochona quennerstedti* develops, according to Guilcher (355, 356), by multiplication and elineation of nonciliated cortical basal bodies. Grain and Batisse (325) showed, however, that such nonciliated cortical basal bodies are absent in *Chilodochona quennerstedti* and Guilcher apparently misinterpreted pellicular pores as basal bodies. Thus, an apokinetal origin of the somatic infraciliature is more likely and supported by Matsudo (534), who states that «the kinetosomes appear to develop de novo at the innermost surface of the pouch from concentrations of subpellicular fibrils» in *Lobochona porates*. Unfortunately, these results have been published as an abstract only, like those by Fahrni (198), who definitely states that the two ciliary fields of *Spirochona gemmipara* originate from the parental ciliature. In this species, the mor-

phogenetic area is located in the front of the parental cytostome, which acts as opisthe, the bud as proter; this occurs also in some suctorians (198). Most authors agree that the chonotrichs are closely related to the cyrtophorids s. str. (chlamyodontids and dysterids) and to the suctorians. The heteromeric macronucleus suggests a closer relationship with the cyrtophorids.

### 7.4.3 Suctorians

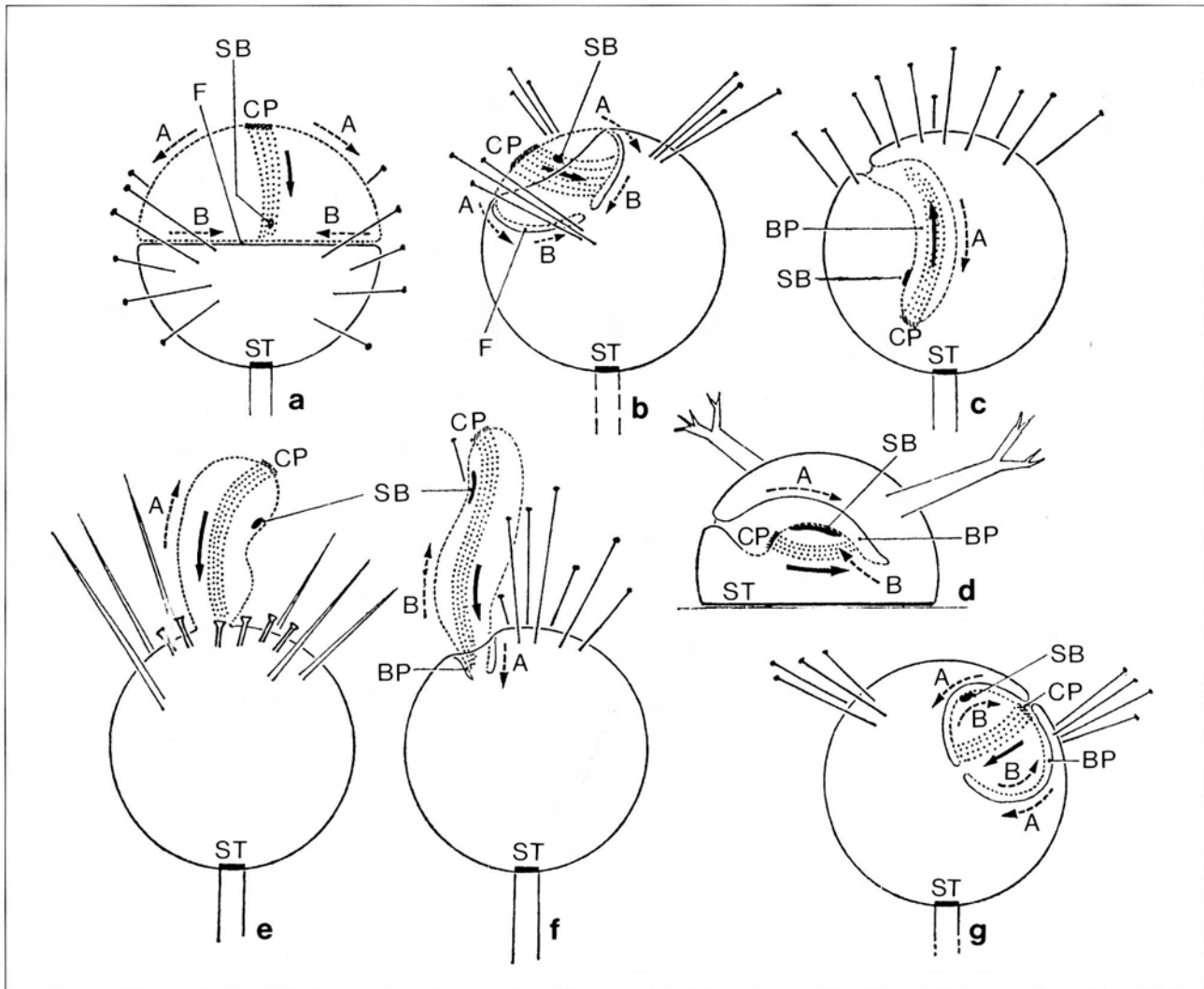
The tentaculate and usually predatory adults are unciliated, but typically they produce one or several ciliated swarmers by exogenous, internal or evaginative budding. The swarmers, after a short swimming existence, lose their cilia and metamorphose into adults. The axes of the adult and the



**Fig. 31 a–c:** Merotelokinetal stomatogenesis and oblique transverse fission in the cyrtophorid ciliate *Trithigmostoma* (from [24]). – **a:** Drawings from silver stained dividing cells. Arrow marks new stomatogenic kinety (cp. Figure b). – **b:** Schematic drawing of the morphogenetic movements of the six stomatogenic kinetofragments. Segment 1' develops anterior to kinetofragment 1, which is the stomatogenic kinety, and becomes the primordium of the opisthe's stomatogenic kinety (cp. Figure a). Note that after completion of the movements the kineties have an inverted polarity. – **c:** The kinetofragments as an anlagen-complex according to transmission electron microscopic investigations. A cross within a circle indicates a nonciliated basal body; the small circles are parasomal sacs. From left to right: Somatic kinety made of monokinetids, transformation into dikinetids, separation of the postciliary microtubules which become the cytopharyngeal lamella, assembly of the anterior basal bodies with their attached subkinetal microtubules to become rods of the cytopharyngeal basket while the remainder of a former kinetofragment becomes part of the circumoral kinety.

swarmer are either the same (homothetogenic; *Podophrya*, *Urnula*) or at right angles (enantiotropic; some *Tokophrya* species); the orientation problem has, however, been studied only in few species, and the axes are difficult to ascertain because the infraciliature of the adult is greatly reduced (477). In a few families (Cyathodiniidae and possibly Encheleymorphidae [15]), the stalkless adult is fleeting, and the enigmatic *Phalacrocleptes verruciformis* lacks a swarmer and basal bodies in all life stages. *Tachyblaston* has two (alternating) generations.

The suctorians divide in active condition, except for *Podophrya grelli*, which produces up to 16 ciliated swarmer in a resting cyst by exogenous (pseudotransverse fission) budding (149). The infraciliature of the swarmer originates from barren «transfer kinetosomes» which are produced during swarmer formation and remain in the adult, typically near the contractile vacuole pore (23, 27, 83, 476). These short, somatic kineties separate from the swarmer infraciliature very early and are often considered to be kinetofragments (118). However, a stomatogenic mode, as used in this review, can-



**Fig. 32 a–g:** Main types of budding in suctorians (from [28]). – **a:** Pseudo-transverse. – **b:** Semi-circumvaginative (a modification of the pseudo-transverse mode where the tomite develops on the tomont). – **c:** Eu-invaginative. – **d:** Infra-circumvaginative. – **e:** Eu-exogenous. – **f:** Semi-invaginative. – **g:** Circumvaginative. Solid arrows indicate direction of kinety growth from the cortical primordium; dashed arrows A and B indicate direction of cortical growth producing the brood pouch and the tomite whose contour is dotted. BP = brood pouch, CP = cortical primordium (usually nonciliated basal bodies near the contractile vacuole pore), F = division furrow, SB = scopuloid of the bud (tomite), ST = scopuloid of the parental organism (tomont).



not be defined, because the suctorians lack a conventional oral apparatus although the tentacles are sometimes considered as a «dispersed» mouth.

Most of our knowledge of suctorian morphogenesis is derived from life and TEM observations. There are only a few silver impregnation studies available. It is reasonable to assume that new and interesting details could be discovered using these methods.

There has been a continuous flow of papers since the fundamental and still indispensable review by Collin (110, 111). Some species were, however, well studied even in the 19th century. The papers by Hertwig (386) on *Ephelota gemmipara* and by Plate (612) on *Dendrocometes paradoxus* have hardly been surpassed by modern workers. In the fifties to seventies, major papers were published by Bardele, Guilcher, Kormos, and Rudzinska. These served as a basis for Batisse's (28) improved classification. During the last 20 years, Curry and Butler (126), Dieckmann (149), Henk and Paulin (385), and Walker and Roberts (791) contributed significantly to our knowledge of the morphogenesis of tentaculate infusorians, which was so unfortunately misinterpreted by the famous Stein (721–723). The formation of the lorica has been studied by Collin (111) and Matthes (538), and the development of the extrusomes (haptocysts) has been investigated by Batisse (26).

Morphogenetic studies contributed significantly to the intragroup classification of the suctorians but did not reveal clear affinities with other ciliates. The fission type and light microscopic and ultrastructural data, however, show convincingly that they form a distinct group within the cyrtophorid ciliates and are possibly most closely related to the chonotrichs (515).

#### 7.4.4 Rhynchodids

The rhynchodids comprise a rather small assemblage of tiny, mouthless ciliates parasitizing freshwater and marine invertebrates. Their ciliature is reduced and thigmotactic. The rhynchodids feed, like the suctorians and some colpodids, by a feeding tube containing toxicysts and microtubular lamellae which have a similar arrangement as those of the nassulid microthoracids (508). The cortical organization indicates a relationship to the cyrtophorids, chonotrichs, and suctorians (631).

The systematic position of these enigmatic ciliates is still controversial, and morphogenetic studies have contributed little in solving the problem. De-

tailed studies are rare, the most important being those by Chatton and Lwoff (102) and Raabe (641). Fission is homothetogenic but, as in cyrtophorids, the axis is slightly oblique; division occurs in active condition either by bipartition (families Hypocomidae, Ancistrocomidae) or by some kind of external budding (family Sphenophryidae). An oral infraciliature is lacking; thus no stomatogenic mode can be established although there are indications that some kind of merotelokinetal stomatogenesis occurs in *Hypocoma*, whose systematic position is, however, uncertain.

#### 7.4.5 Nassulids

The nassulids are free-living, small (microthoracids) to large (nassulids) ciliates united by two derived characters (181, 183): the cortex contains paired alveolocysts, and the cytopharyngeal basket is equipped with special nematodesmal «X-lamellae». The somatic ciliature is holotrichous in synhymenids and nassulids, but strongly reduced in most microthoracids. The subapical oral apparatus consists of a usually conspicuous cytopharyngeal basket («nasse»), an often inconspicuous paroral membrane, and few to many rectangular adoral membranelles, which often form a distinct horizontal ribbon.

Morphogenetic data on nassulids are surprisingly sparse; however, *Furgasonia blochmanni* and *Pseudomicrothorax dubius* have been investigated in great detail and can serve as representative examples (181–184, 597). Unfortunately, ultrastructural and morphogenetic investigations on synhymenids are entirely lacking because *Nassulopsis* is now considered to belong to the nassulids s. str. (710). It is thus questionable whether genera like *Chilodontopsis* and *Zosterodasys* belong to the nassulids.

The nassulids have a homomeric macronucleus and divide in active condition. The available stomatogenic data were critically reviewed by Eisler and Bardele (184). I agree with their interpretation that the paroral membrane is derived from the parental buccal apparatus and that the adoral organelles originate merotelokinetically; stomatogenesis is thus mixokinetal. The parental oral infraciliature is entirely or almost completely reorganized.

The morphogenetic data prove that the nassulids belong to the Cyrtophora but fail to establish a clear sister-group relationship with other ciliates (181); however, most workers would agree that they are rather close to the peniculine hymeno-



stomes. Shi Xinbai (693, 694) even concludes from a comparative study on the morphogenesis of *Paramecium* and *Pseudomicrothorax* that the latter is a true missing link between hymenostomes and gymnostomes.

#### 7.4.6 Prostomatids

This small group of ciliates has long been considered primitive because of its axial symmetry and its simple oral and somatic infraciliature; however, as early as 1968, Puytorac and Savoie (625) suggested that *Prorodon* belongs to the cyrtophorids because it resorbs the parental pharyngeal apparatus during morphogenesis. They also homologized the prorodontid brush kineties with the adoral organelles of the nassulids. Later, Wilbert and Schmall (819) and Foissner (262) suggested that the «dorsal brush» of *Coleps* and related prostomatids is in fact a ventral organelle possibly homologous with the tetrahymenid adoral membranelles. It was only recently that Bardele's group confirmed these vague ideas and presented clear evidence from electron microscopic studies of stomatogenesis in *Coleps* and *Bursellopsis* that the cytostomally directed microtubular ribbons are postciliary microtubules (395, 396, 412). Prostomatids thus have a cyrtos-type basket. The relationship of the prostomatids to other ciliate groups is, however, still unclear (395); very likely they are near the nassulids or oligohymenophoreans. There is a considerable diversity in fission types and division modes as well as in stomatogenesis in taxa currently assigned to the prostomatids (Table 2). This may indicate a high diversity of the group or misclassification of some genera. Typically, stomatogenesis is merotelokinetal (395). *Trimyema compressum* and *Lagynus elegans* have, however, a holotelokinetal stomatogenesis like the haptorids s. str.; they might thus belong to this group. Their brush kineties, however, are very small (as in *Coleps*) and on the oral field, i.e. within the circumoral ciliature. Furthermore, their striated silverline system is very different from the fine-meshed silverline net of the haptorids.

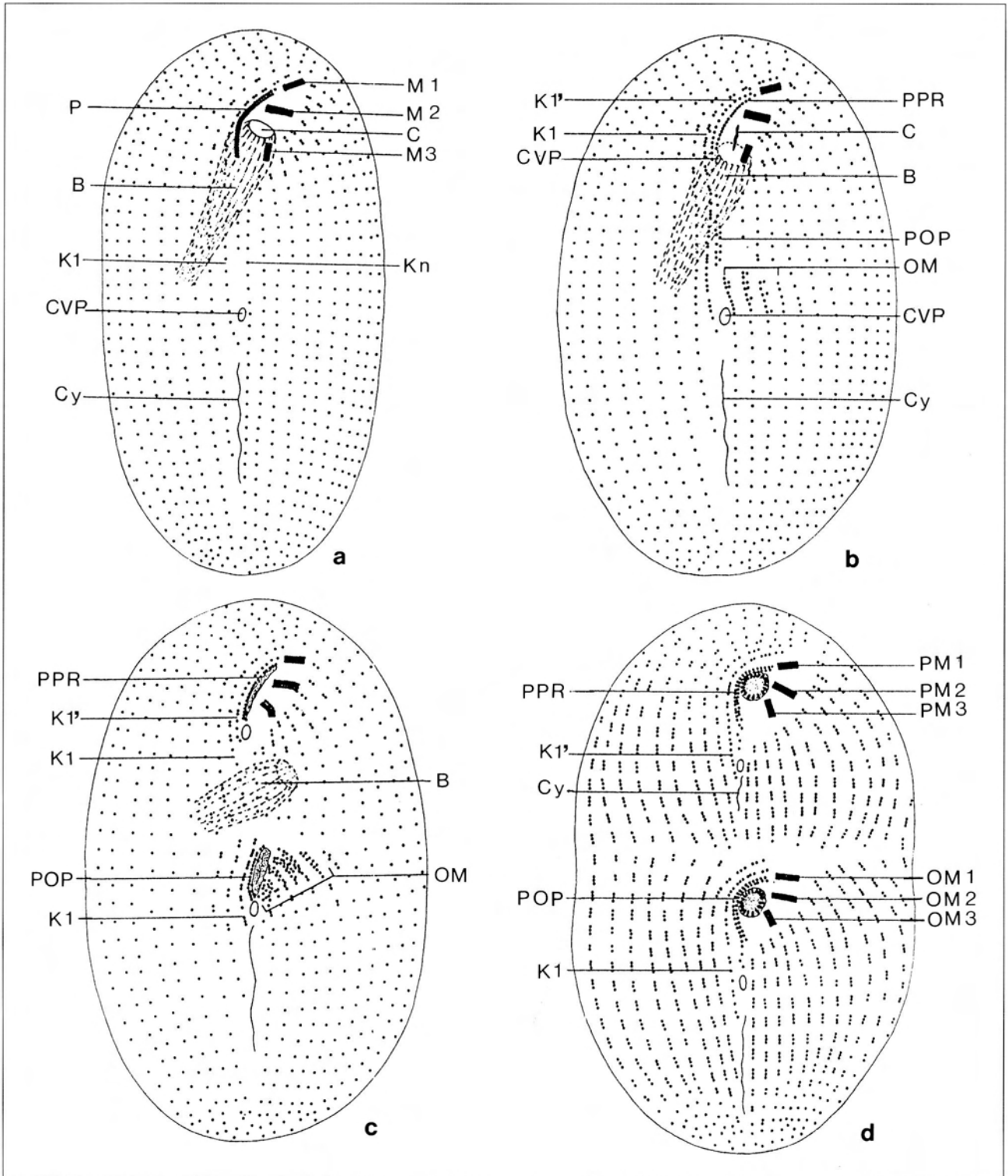
Unfortunately, morphogenetic data on the «true» prostomians, e.g., *Holophrya* and *Metacystis*, are lacking. The available data suggest that the prostomatids consist of two distinct groups (orders?), the Prostomatida (*Metacystis*, *Trimyema*, *Lagynus*) and the Prorodontida (*Prorodon*, *Coleps*, *Urotricha*). *Metacystis* is unusual in having the micronucleus located in the perinuclear space of the macronucleus like several cyrtolophosidid colpodids (847).

#### 7.5 Litostomatea

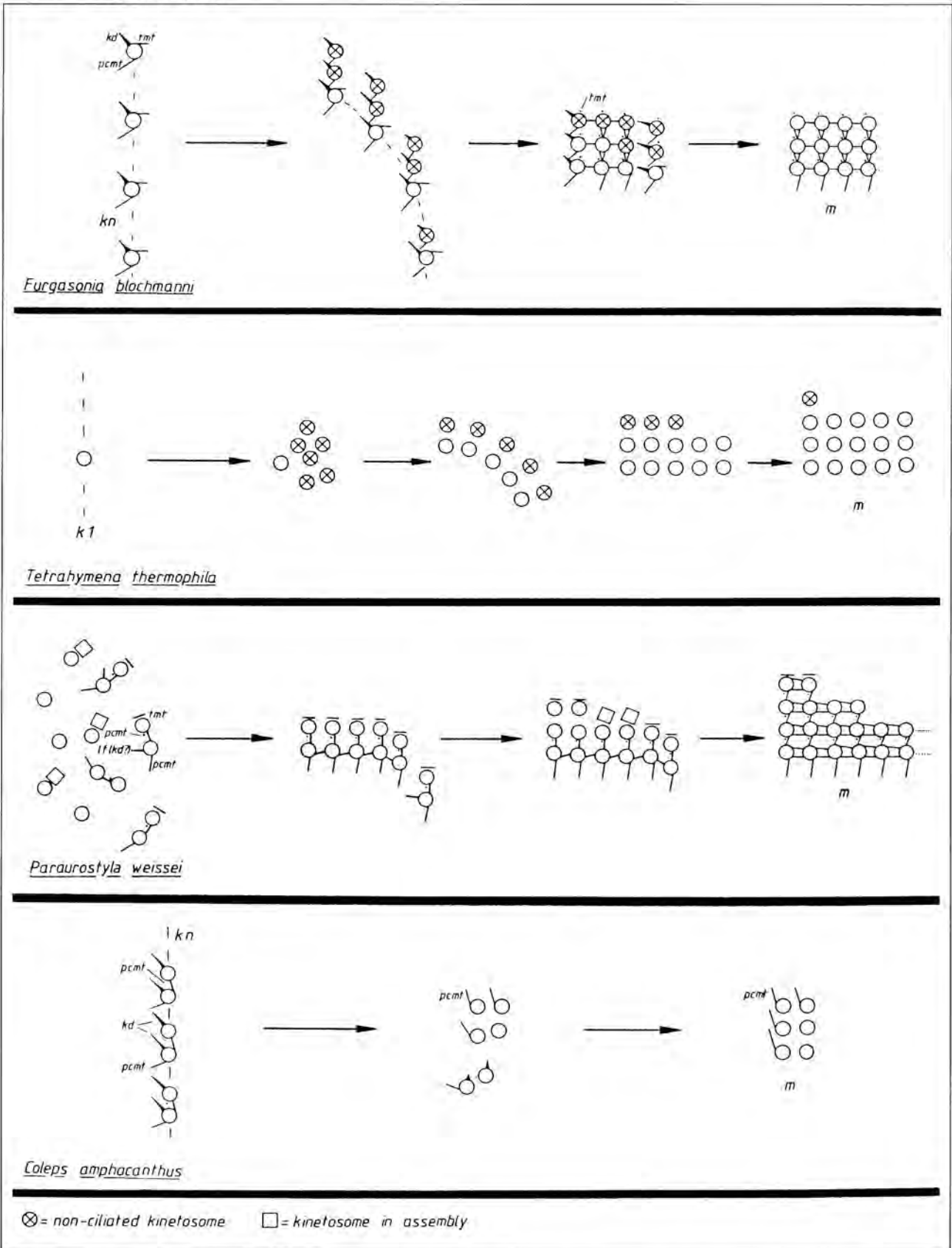
The litostomes are a large and diverse assemblage of free-living and endocommusal or parasitic ciliates which have, in my opinion, two unique apomorphies (derived characters), viz. the rhabdos type oral apparatus and the dorsal brush. This latter organelle is at the anterior end of one or many dorso-lateral somatic kineties and usually composed of paired or heavily staining basal bodies having short, clavate cilia. I suggest that (i) the dorsal brush (270) of the haptorids s. str. (e.g., *Spathidium*), (ii) the kineties extending on the «Konkrementvakuole» (322, 323) of the Buetschliidiidae, Paraisotrichidae, and Blepharocorythidae, (iii) the dextro-oral somatic field (332) of the Balantidiidae, (iv) the kineties in the «crête aborale» (322, 323) of the Isotrichidae, and (v) the paralabial organelle (675) of the entodiniomorphids are homologous structures. The general appearance and the fine structure of these organelles are so similar that there can hardly be any doubt as to their homology.

All litostomes have a homomerous macronucleus and divide in active condition. Stomatogenesis is telokinetal throughout, but at least four subtypes can be distinguished which seem to be of significance at subclass or ordinal level. As far as can be ascertained from the few detailed studies available, the parental oral structures are retained. The telokinetal stomatogenesis unites the litostomates rather firmly; however, it is not a unique character

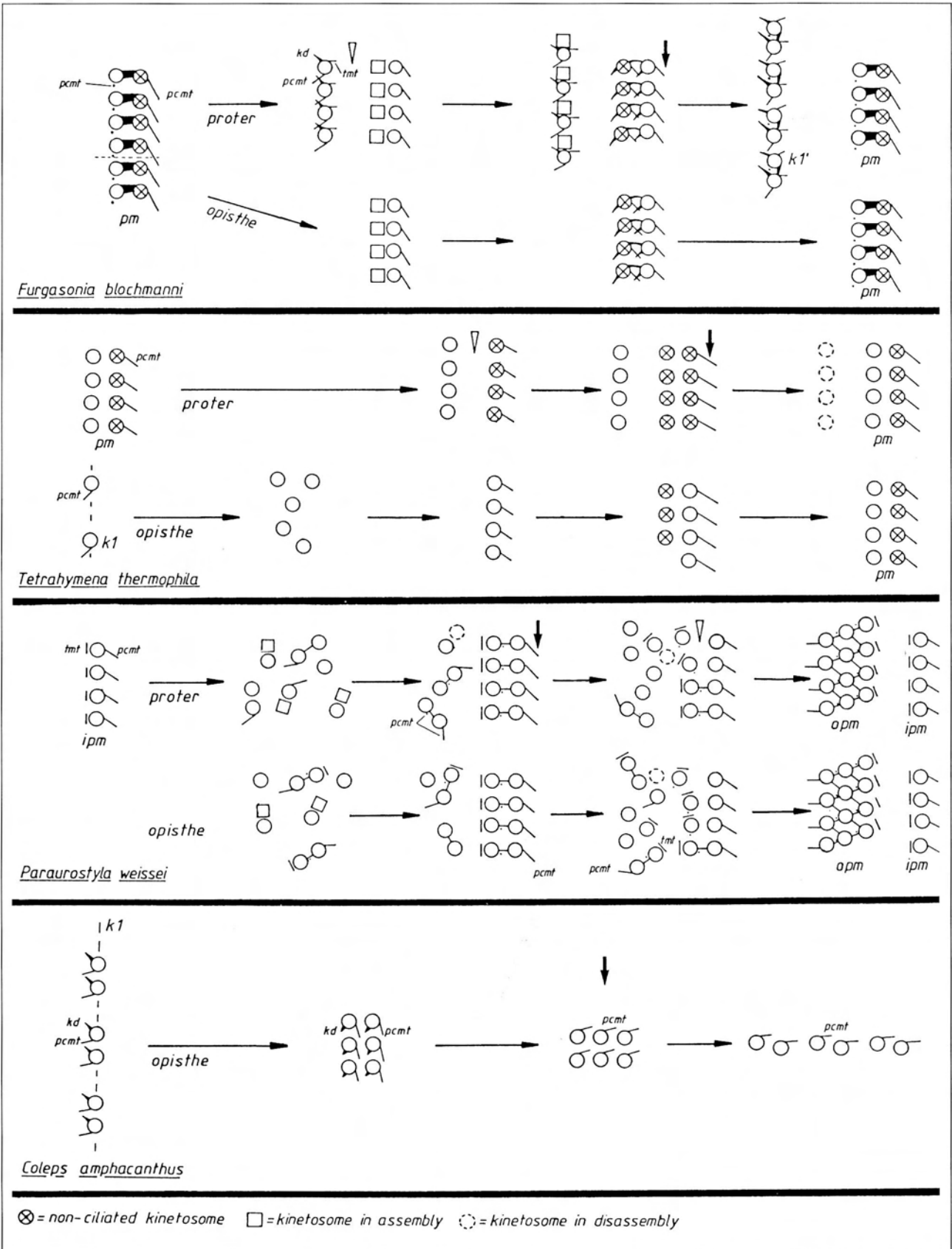
**Fig. 33 a–d:** Mixokinetal stomatogenesis and homothetogenic (transverse) fission in the nassulid ciliate *Furgasonia blochmanni* (wet silver nitrate impregnation; from [184]). – **a:** Interphase specimen. – **b:** Early stage. At the posterior end of the paroral membrane appears the contractile vacuole pore for the proter. The anterior segment of the parental paroral membrane is split longitudinally into the anlage of the paroral membrane of the proter and a new kinety 1'. The posterior segment, representing the anlage of the paroral membrane for the opisthe, is on the way towards the parental pore of the contractile vacuole. At the anterior end of four somatic ciliary rows develop the anlagen (kinetofragments) for the adoral membranelles of the opisthe. – **c:** Middle stage. The parental cytopharyngeal basket becomes resorbed and the opisthe's paroral membrane has reached its final position. The anlagen



for the adoral membranelles of the opisthe have spread over six somatic ciliary rows. In the somatic cortex the proliferation of basal bodies begins on the right side of the opisthe's paroral membrane. — **d:** Late stage. The nematodesmata have separated from the paroral membranes and are now arranged in tube-like structures in the proter as well as in the opisthe. The number of adoral membranelles in the opisthe is reduced to 3 and the proter has developed a new cytophyge. The cleavage furrow becomes apparent and triads of basal bodies are recognizable in most parts of the somatic cortex. B = basket (cyrtos), C = cystostome, Cy = cytophyge, CVP = excretory pore of the contractile vacuole, K1 = ciliary row (kinety) 1, Kn = ciliary row n, M1–M3 = adoral membranelles 1–3, OM = opisthe's adoral membranelles, P = paroral membrane, PM = proter's adoral membranelles, POP = paroral membrane of the opisthe, PPR = paroral membrane of the proter.



**Fig. 34:** Comparison of the development of an adoral membranelle (*m*) during stomatogenesis in *Furgasonia blochmanni*, *Tetrahymena thermophila*, *Paraurostyla weissei*, and *Coleps amphacanthus* according to electron microscopic investigations (from [181]). *k1* = ciliary row 1, *kn* = ciliary row *n*, *kd* = kinetodesmal fiber, *pcmt* = postciliary microtubules, *tmt* = transverse microtubules.



**Fig. 35:** Comparison of the development of the paroral membrane during stomatogenesis in *Furgasonia blochmanni*, *Tetrahymena thermophila*, *Paraurostyla weissei*, and *Coleps amphacanthus* according to electron microscopic investigations (from [181]). The bold vertical arrows point to the developmental stage in which the postciliary microtubules of the paroral membrane are involved in the formation of the cytopharynx. In this stage the paroral membrane is always a «stichodyad». The arrowheads point to the stage where the «stichodyad» of *F. blochmanni*, *T. thermophila*, and *P. weissei* splits longitudinally. k1 = ciliary row 1, k1' = new ciliary row 1, kd = kinetodesmal fiber, ipm = inner paroral membrane, opm = outer paroral membrane, pcmt = postciliary microtubules, pm = paroral membrane, tmt = transverse microtubules.

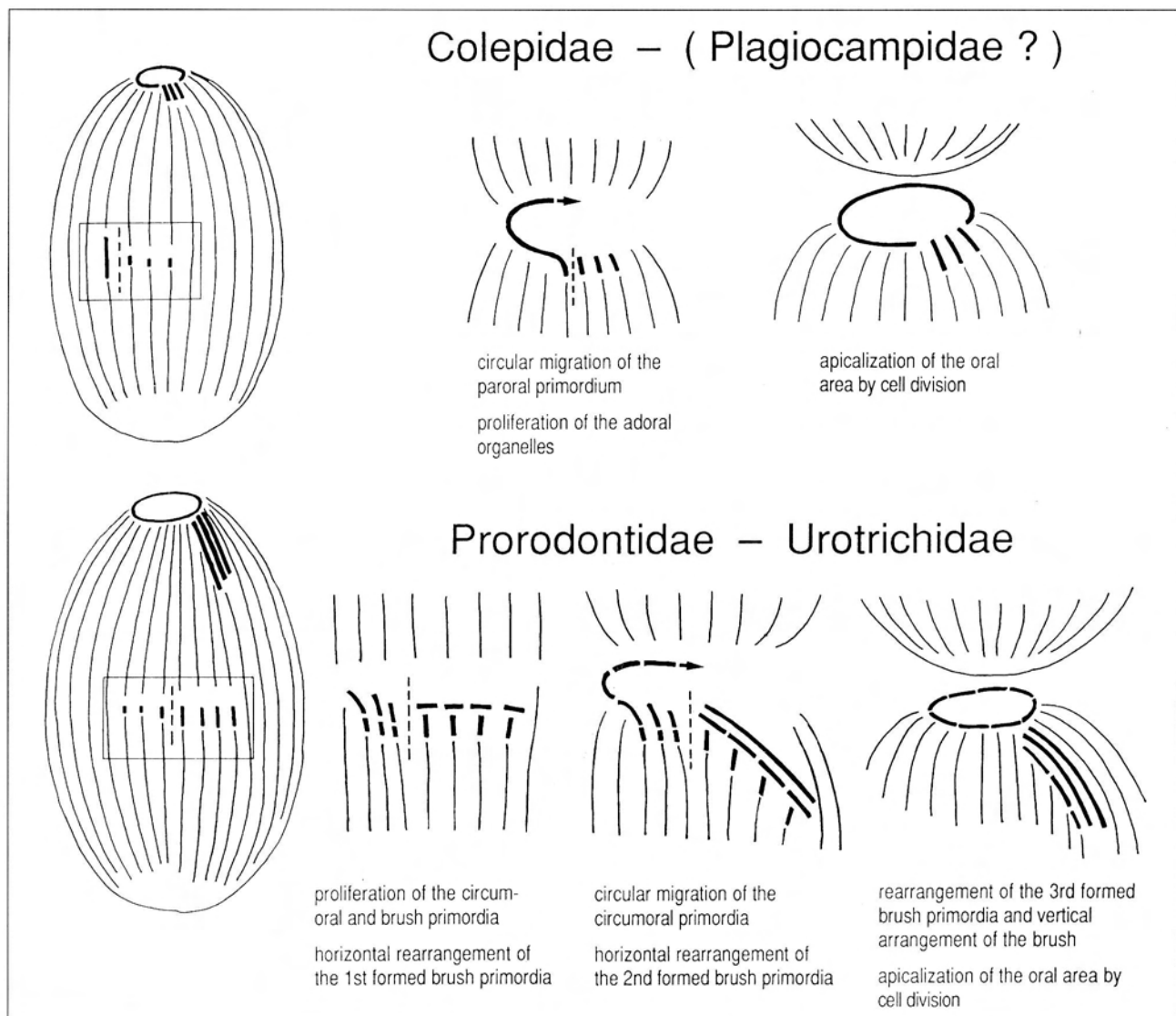
because it occurs also in other, possibly rather distantly related groups, like some heterotrichs and all colpodids.

### 7.5.1 Haptorids and archistomatids

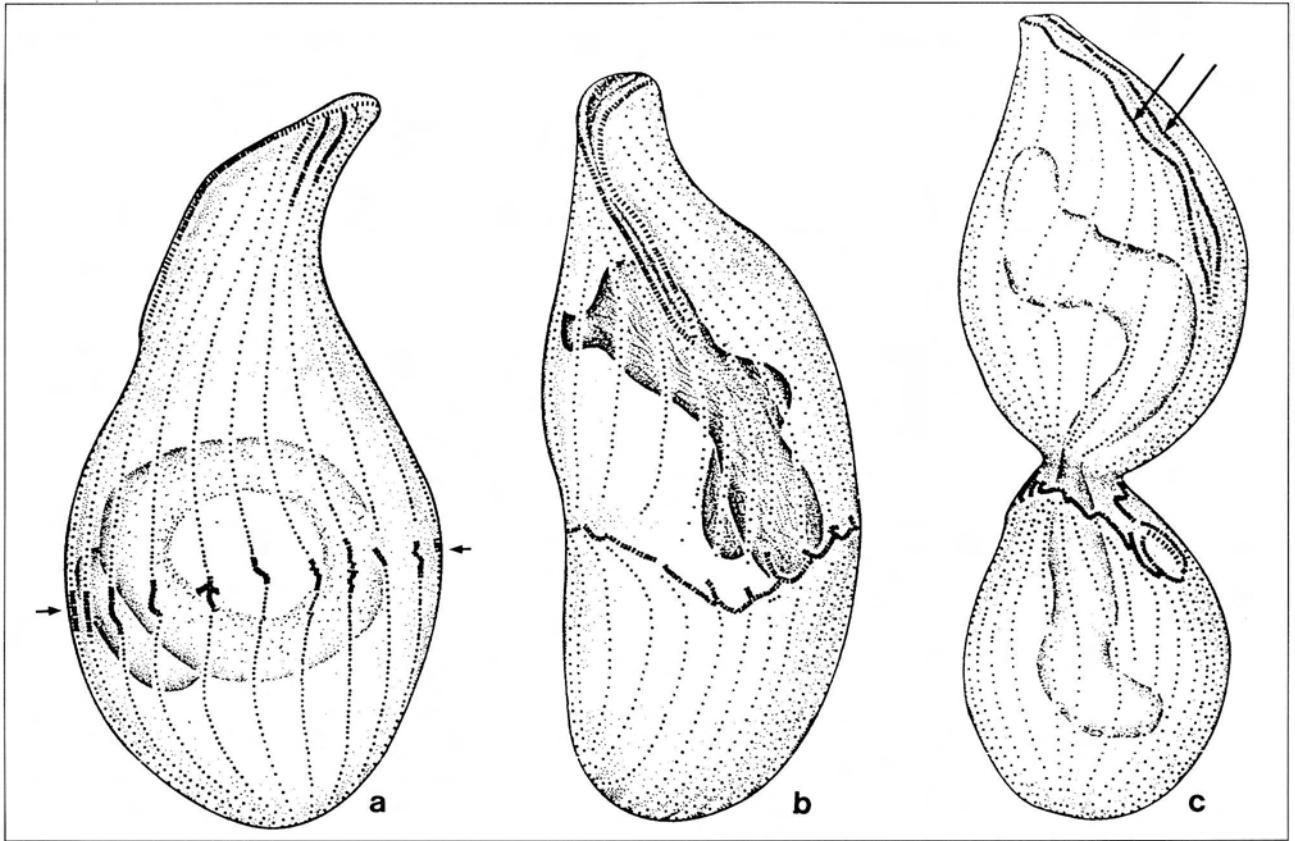
Most members of this group are sac or barrel-shaped with the oral opening at or near the anterior end. Many are rapacious, free-living carnivores; the archistomatids, however, live endocommensally in large mammals. The somatic ciliature is often uniformly holotrichous, except for the dorsal

brush, which is underlain by a unique «Konkrementvakuole» in the archistomatids. The oral infraciliature is usually simple and the oral basket (rhabdos) often made up of oralized somatic kinetids (270). A typical feature is the presence of toxicysts, usually located within the cytostome and used to capture prey; they are absent in the endocommensal species.

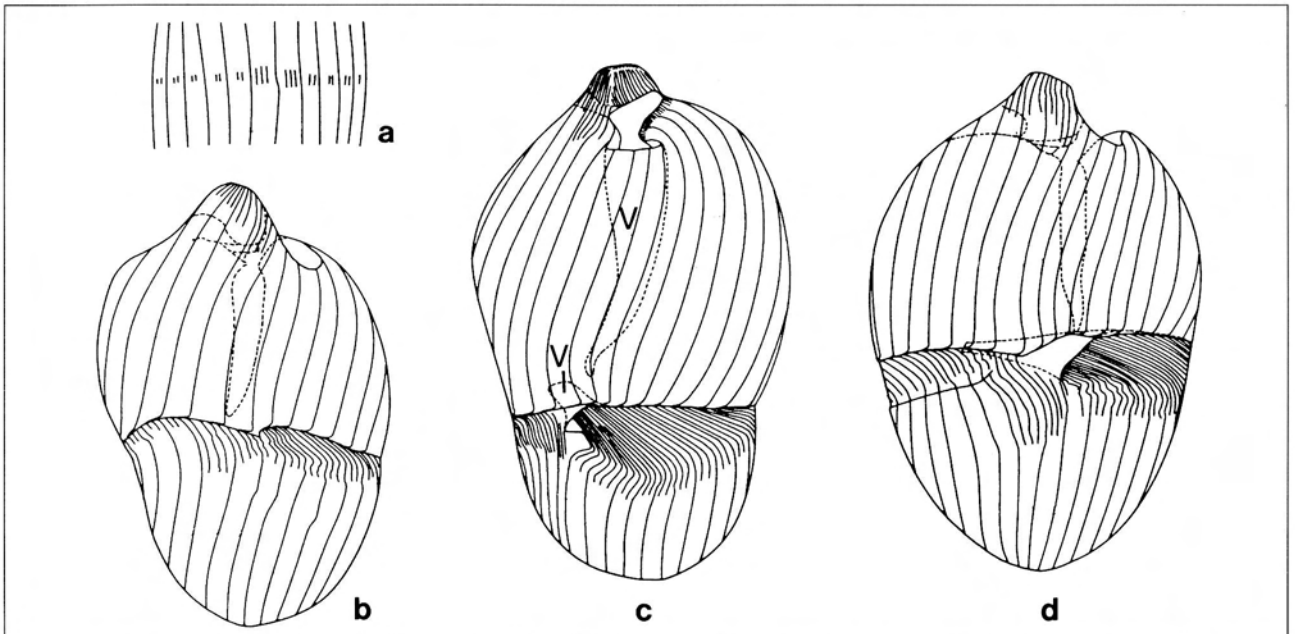
Great changes occurred in the classification of the haptorids during the last few years. Foissner and Foissner (270) revised the entire subclass and added, among others, the Archistomatina (Buetschliidae), and Lipscomb and Riordan (504) added



**Fig. 36:** Schematic illustration of the merotelokinetal stomatogenesis and homothetogenic (transverse) fission in prostomatid ciliates according to silver preparations (from [395]). The stomatogenic area is framed in the leftmost drawings, which show early dividers. The two groups of stomatogenic kineties – a left one forming the adoral («brush») primordia and a right one forming the paroral primordia (circumoral kinety) – are separated by a dashed line. The whole oral ciliature is formed from kinetofragments which are produced at the anterior end of a few ventrolateral ciliary rows.

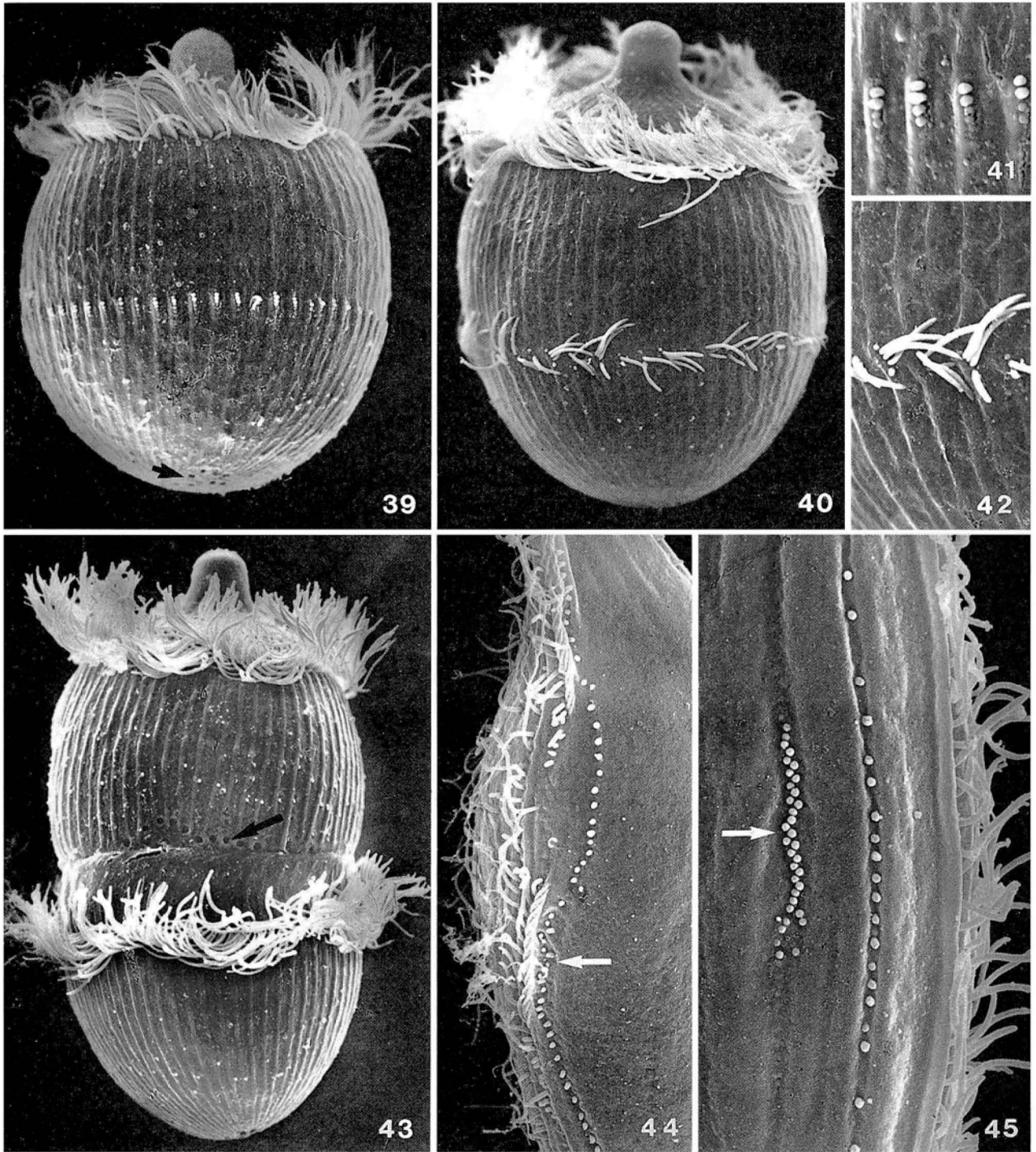


**Fig. 37 a–c:** Holotelokinetal stomatogenesis and homothetogenic (transverse) fission in the haptorid ciliate *Arcuospathidium* (protargol impregnation; from [38]). – **a:** Early stage. Kinetofragments (arrows) consisting of paired basal bodies are produced in all ciliary rows close behind the prospective division furrow. – **b:** Middle stage. The kinetofragments elongate by proliferation of dikinetids and rotate clockwise forming an irregular circumoral kinety. The macronucleus condenses. – **c:** Late stage showing distinct division furrow. The kinetofragments orientate one behind the other along the prospective oral opening. The macronucleus elongates. The parental circumoral kinety is retained (arrows).



**Fig. 38 a–d:** Intertelokinetal stomatogenesis and homothetogenic (transverse) fission in the vestibuliferan ciliate *Paraisotricha* (silver impregnation; from [323]). Kinetofragments are generated within and between the parental somatic ciliary rows. This produces a dense anterior ciliature which is used to cover the deep vestibulum (V).

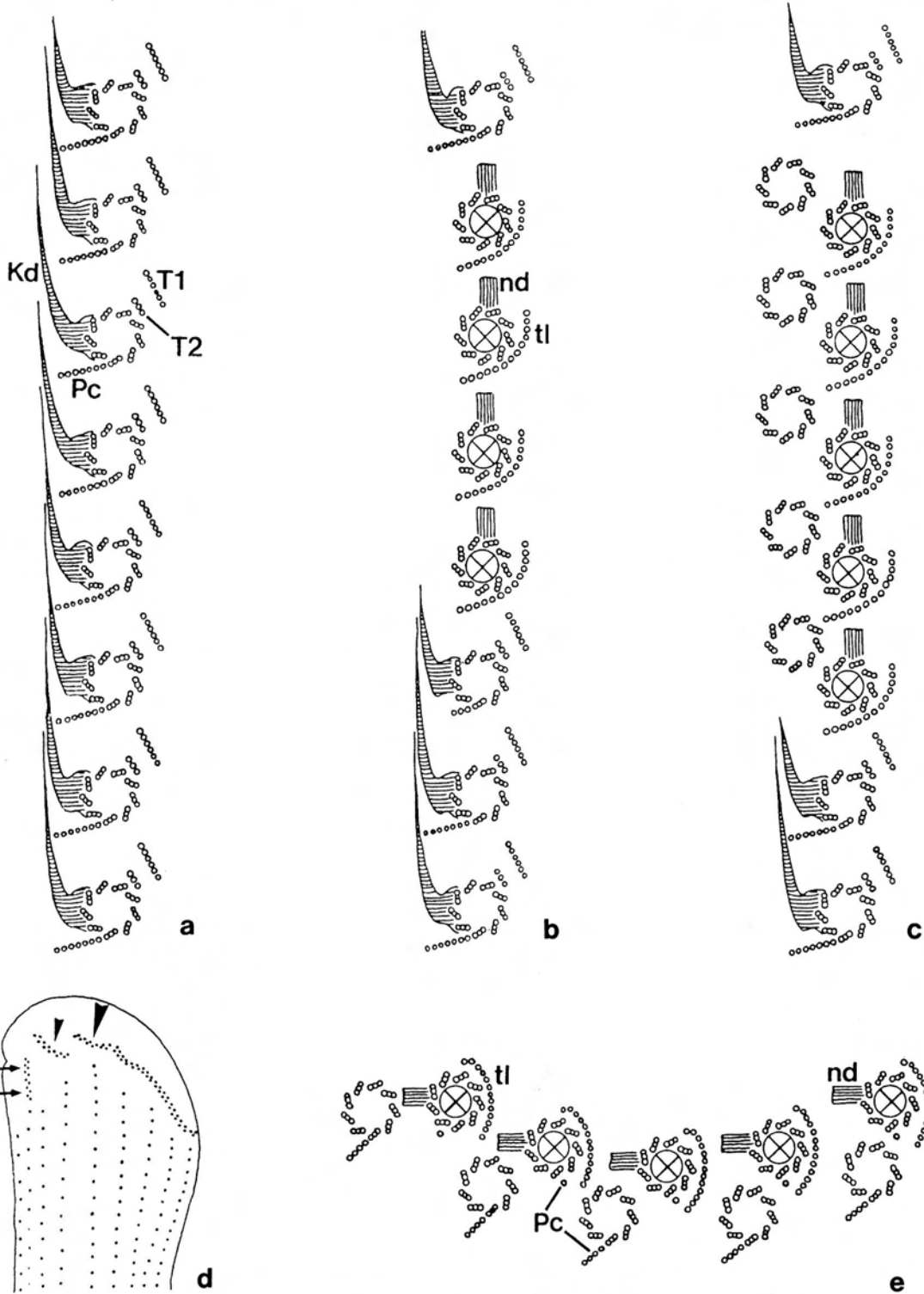




**Figs. 39–43:** SEM-micrographs of the holotelokinetal stomatogenesis and homothetogenic (transverse) fission in the haptorid ciliate *Monodinium* (originals). – **39, 41:** Early stage showing short kinetofragments in all somatic ciliary rows which are nonciliated in this genus except for a dense, subapical ciliary wreath. Arrow marks contractile vacuole pores. – **40, 42:** Middle stage. The kinetofragments elongate and rotate clockwise; cilia grow out. – **43:** Late stage showing distinct division furrow and completed ciliary wreath in the opisthe. New excretory pores (arrow) have been formed at the posterior end of the proter whose ciliary wreath is retained unchanged.

**Figs. 44, 45:** SEM-micrographs of the monotelokinetal stomatogenesis in the pleurostomatid ciliate *Litonotus* (originals). Kinetofragments (arrows) are produced only in the somatic subequatorial portion of the parental perial (Fig. 44) and brush (Fig. 45) kineties.





**Fig. 46 a–e:** Schematic illustration of the development of the circumoral kinety in the hapteroid ciliate *Homalozoon* according to transmission electron microscopic investigations (from [501]). *Homalozoon* has a holotelokinetal stomatogenesis, i.e. all somatic kineties proliferate kinetofragments (cp. Fig. 37, 39–43). A cross within a circle indicates a nonciliated basal body. The first basal body in the row represents the posteriormost basal body of the proter. – **a:** Anterior end of a right lateral somatic ciliary row. – **b:** Early stage. The somatic basal bodies become transformed into oral basal bodies. – **c:** Middle stage. New basal bodies are proliferated adjacent to transformed (formerly somatic) basal bodies. Postciliary microtubules are not depicted because they have not been seen in the anlage but they should hold the same position as in the kinetofragment shown in Fig. 46e. – **d:** Oral kinety anlage (arrows, corresponds to Fig. 46c), migrating kinetofragment (small arrowhead), and integration into a circumoral kinety (large arrowhead; corresponds to Fig. 46e) artificially depicted in a single cell at the same time. – **e:** Kinetofragment as orientated in the interphase circumoral kinety. Both basal bodies of a pair are drawn parallel although they are at angles. Kd = kinetodesmal fiber, nd = nematodesmal microtubules, Pc = postciliary microtubules, tl = transversal lamella, T1, T2 = first and second transverse microtubular ribbon.

the Balantidiidae and Isotrichiidae. The prostomatids, long considered to be closely related to the haptorids, have a cyrtos-type oral basket and are thus now classified as being near the nassulids or oligohymenophorans (395).

Detailed morphogenetic data on haptorids are rather sparse, especially as regards the endocommensal species. A transmission electron microscopic study on the morphogenesis of *Homalozoon* supports the rhabdophora/cyrtophora concept (501, 703). There are also a few transmission electron microscopic studies on excystment and regenerative morphogenesis (460, 461).

Three subtypes of telokinetal stomatogenesis occur in this group. The holotelokinetal mode is found in the free-living haptorids s. str.; the monotelokinetal mode is possibly restricted to the pleurostomatids, and the intertelokinetal mode occurs in the endocommensal Buetschliidiidae.

### 7.5.2 Vestibuliferids

Few taxa remained in this group, because many were transferred to other classes and orders, viz. the Trichospiridae to the hymenostomes, the Trimyemidae to the prostomatids, the Marynidae to the colpodids, and the Blepharocorythidae to the entodiniomorphids. What remained is a rather small assemblage of ciliates having a distinct, ciliated vestibulum, viz. the free-living Plagiopylidae and the endocommensal/parasitic Balantidiidae, Isotrichidae, and Paraisotrichidae.

Stomatogenesis is holotelokinetal in plagiopylids, intertelokinetal in balantidiids and paraisotrichids, and, possibly, merotelokinetal in isotrichids. The intertelokinetal stomatogenesis clearly relates the balantidiids and paraisotrichids to the buetschliidiids, whose oral apparatus, however, lacks a vestibulum and is thus nearer to that of the free-living haptorids (270). The systematic relationship of *Plagiopyla* is still controversial (41, 852).

### 7.5.3 Entodiniomorphids

These bizarre ciliates live in the digestive tract of various ruminants. Their stomatogenesis was considered to be apokinetal for a long time (118, 227, 586). It was only recently that Furness and Butler (293) showed by transmission electron microscopy that it is like the telokinetal process of haptorids. The oral infraciliature develops from a vestigial somatic infraciliature consisting of subcortical barren

basal bodies. A further peculiarity of the entodiniomorphid stomatogenesis is the development of two or more oral primordia, some of which later fuse, in subcortical cavities (pouches) similar to those of some suctorids, oligotrichs, and hypotrichs.

The highly characteristic entodiniomorphid stomatogenic pattern is also found in the Blepharocorythidae, whose buccal infraciliature, however, resembles that known from vestibuliferids (835). Wolska (837) discussed at length a possible homology of the kineties extending on the «Konkrementvakuole» of the buetschliidiids and blepharocorythids; she did not, however, recognize that these organelles are very likely homologous with the paralabial organelle found in entodiniomorphids.

## 7.6 Colpodea

Most colpodids are completely ciliated and have paired cilia or, at least, paired basal bodies (dikinetids). The dikinetids are associated with a highly characteristic fibrillar system, viz. long posterior transverse microtubular ribbons which form a «left kinetodesmal fiber» (LKM-fiber). In contrast, the oral structures show a bewildering diversity, which caused misclassification of many genera. Most genera and species are restricted to terrestrial biotopes, and only very few live in marine environments (266).

All colpodids have a somatic stomatogenesis, i.e. the parental oral structures, which are partially (e.g., *Cyrtolophosis*) or completely (e.g., *Colpoda*, *Bursaria*) reorganized during the division process, are not involved in the formation of mouth structures. «Evolved» bucco- or apokinetal types of stomatogenesis have not yet been reliably documented (see [266] for discussion of the controversial *Woodruffia metabolica*). The new oral ciliary fields originate from kinetofragments by lateral and/or intrafragmental proliferation of basal bodies. The new basal bodies for the somatic kineties of the proter and opisthe originate within the parental ciliary rows. The process starts with a separation of the two basal bodies of a somatic dikinetid and is followed by the appearance of a new basal body in front of the anterior of the two, resulting in typical triads. Shortly afterwards a fourth basal body appears in front of the posterior parental basal body, thus resulting in a quadrupling of basal bodies that later separate to form two dikinetids.

The final positioning of the oral structures and the separation of the daughter cells includes several

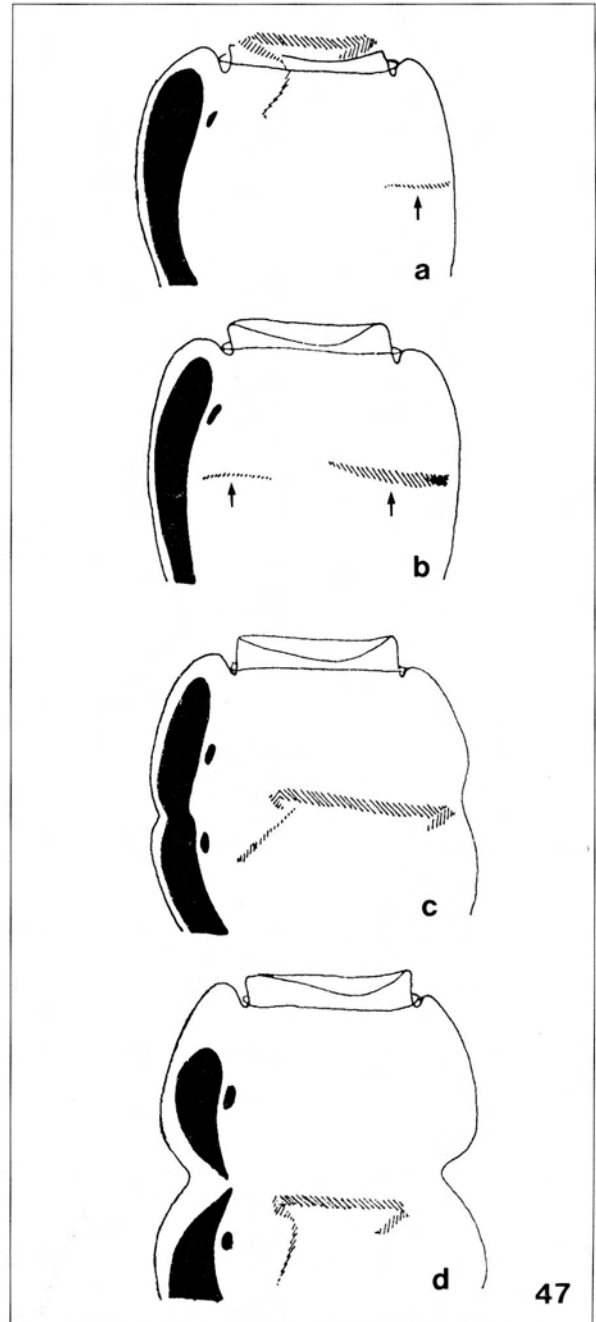
complicated, not yet fully understood rotational movements of the kinetofragments and the daughter cells (266).

The nuclear apparatus divides in the usual way; detailed data are, however, rare. It would be highly interesting to study the division of the cyrtolophosidid macro-micronuclear complex with the electron microscope.

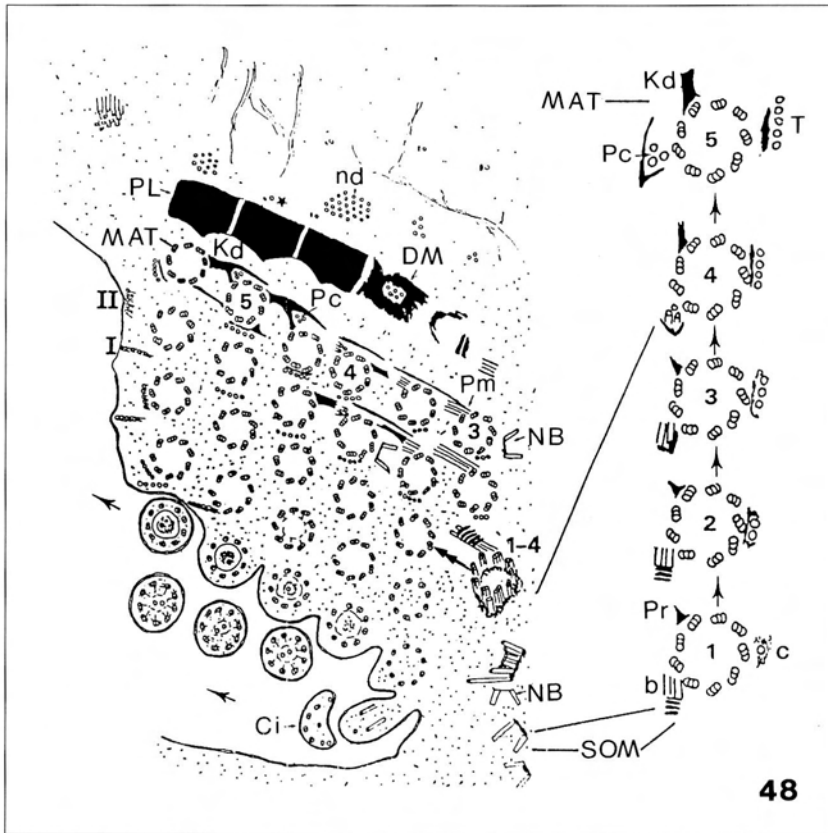
The Colpodida and Grossglockneriida (possibly also the Bryophryida) divide in reproductive cysts and have a merotelokinetal stomatogenesis, i.e. the parental oral structures are resorbed and new ones originate at the anterior ends of some somatic kineties (Figs. 50–52). This greatly resembles the stomatogenesis of prostome and hypostome ciliates, e.g. *Coleps* and *Chilodonella* (24). It is less similar to the holotelokinetal haptorid stomatogenesis in which all somatic kineties proliferate kinetofragments to form the circumoral kinety (38).

All other colpodids (Bursariomorphida, Cyrtolophosidida, Sorogenida, Bryometopida) usually divide in active condition and have some kind of parakinetal stomatogenesis, i.e. the opisthe's oral structures originate as kinetofragments subequatorially within several right lateral somatic kineties (Fig. 49). Foissner (266) named this process «pleurotelokinetal» or, more generally, cyrtolophosidid stomatogenesis.

The morphogenetic data separate two distinct groups of colpodids, but the fibrillar associates of the somatic kinetids are very similar in colpodid and cyrtolophosidid colpodids, indicating either a close relationship or a remarkable convergence. It is not yet possible to reach reliable conclusions from morphogenetic data on the relationships between colpodids and other ciliates although some results suggest affinities with haptorids, nassulids, or hymenostomes (266). During the preparation of this review, I recognized two surprising similarities not yet discussed either by myself (266) or other authors (404). The stomatogenesis of the heterotrich *Nyctotherus* appears similar to that of cyrtolophosidid colpodids, viz. pleurotelokinetal. This could indicate some relationship between cyrtolophosidid colpodids and spirotrichs and strengthens my earlier (266) reservations in assigning bursarid ciliates to the colpodids. The second surprising similarity concerns the right oral ciliary field, which is extremely similar in the Colpodida and some Peniculida (e.g., *Urocentrum*), viz. composed of a doubled-rowed paroral membrane to which an anarchic field of kinetosomes is attached (Fig. 24). This would argue for a relationship between hymenostomes and colpodids (404).

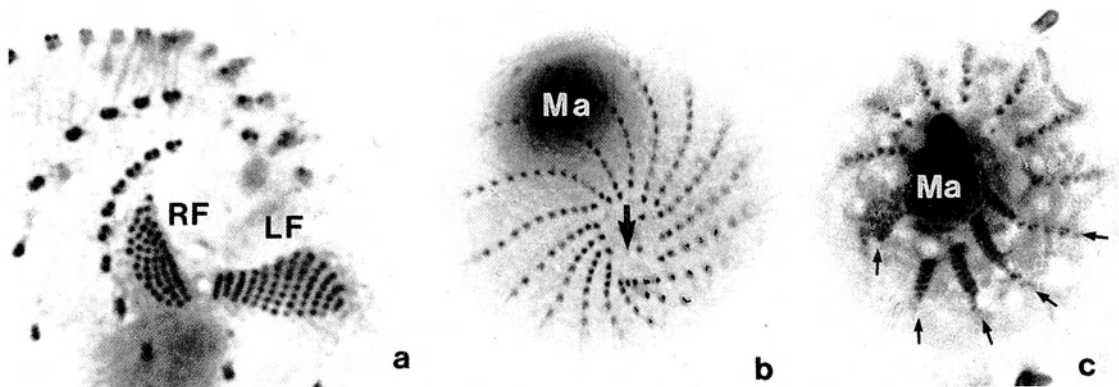


**Fig. 47 a–d:** Cryptotelokinetal stomatogenesis and homothetogenic (transverse) fission in the entodiniomorphid ciliate *Entodinium* (silver carbonate preparations; from [230]). – **a, b:** Two oral primordia (arrows) originate in subcortical pouches from a vestigial somatic ciliature (cp. Fig. 48). – **c, d:** The oral primordia fuse to form a single, long oral polykinetid.

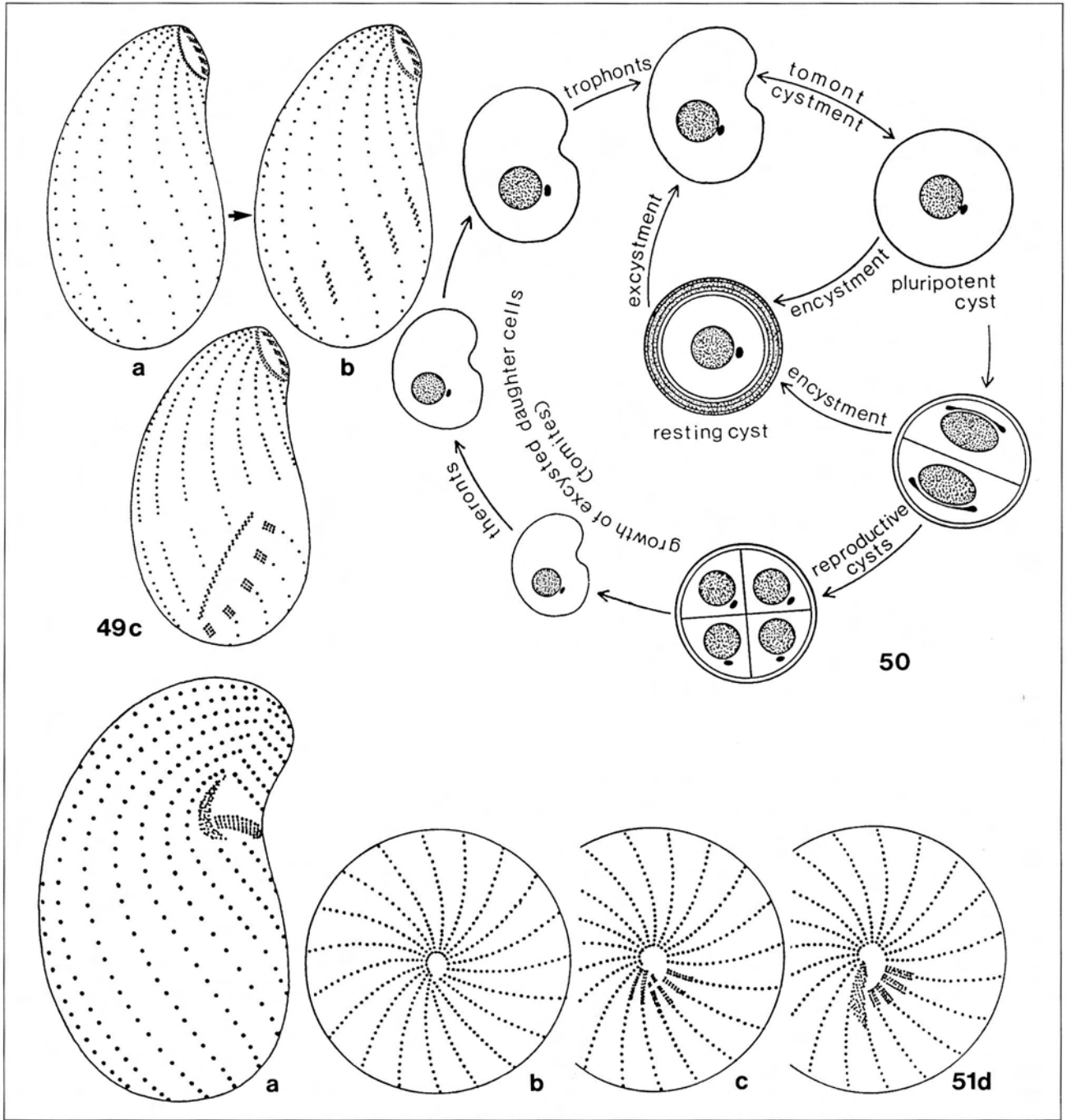


**Fig. 48:** Schematic illustration of kinetid development (stages 1–5) and formation of infraciliature during cryptotelo-kinetal stomatogenesis in the entodiniomorphid ciliate *Eudiplodinium* according to transmission electron microscopic investigations (from [293]). The source of the basal bodies appears to be migration of somatic basal bodies (SOM) and replication among somatic basal bodies and in the new kineties to produce new basal bodies (NB). Stages 1–4 of kinetid development can occur among somatic basal bodies while stages 3–5 most commonly are found in new kineties. To produce mature (MAT) kinetids from somatic ones the basal microtubules (b) become postciliary microtubules (Pc), via intermediate parallel microtubules (Pm). Cortically directed microtubules (c) become transverse microtubules (T). The dense projection (Pr) is located at the connection of the kinetodesmal fiber (Kd).

Dense material (DM) at the base of somatic basal bodies becomes the subkinetosomal plate (PL). Each plate nucleates nematodesmal microtubules (nd) although not all maintain a nematodesmal bundle in the adult (star). Microtubule ribbons type I and II extend from terminal kinetids. Cilium formation (Ci) runs concurrently with kinetid formation. The arrows show direction of maturation of infraciliature, the double headed arrow shows addition of a somatic kinetid to a new kinety.



**Fig. 52 a–c:** Merotelokinetal stomatogenesis in the colpodid ciliate *Colpoda steinii* (silver carbonate impregnation; originals). – **a:** The oral apparatus of the trophic cell has two distinct ciliary fields. – **b:** Tomonts round up, secrete a thin cyst wall, and resorb the oral structures completely. The arrow marks the region where the oral structures have been. – **c:** When division commences, kinetofragments are generated at the anterior end of some somatic ciliary rows (arrows). These fragments proliferate basal bodies laterally, forming the right and left oral ciliary field (Fig. 52a). LF = left oral ciliary field, Ma = macronucleus, RF = right oral ciliary field.



**Fig. 49 a-c:** Schematic illustration of the pleurotelokinetal (cyrtolophosid) stomatogenesis in bursariomorphid, cyrtolophosid, sorogenid, and bryometopid colpodids (silver preparations; from [266]). The oral structures for the opisthe develop from kinetofragments produced within some right lateral parental somatic ciliary rows.

**Fig. 50:** Life cycle of colpodids with reproductive cysts (from [266]).

**Fig. 51 a-d:** Schematic illustration of the merotelokinetal stomatogenesis in colpodid and grossglocknerid colpodids (silver preparations; from [266]). The tomont rounds up (a), forms a thin-walled reproductive cyst, resorbs the oral structures and despiralizes the somatic ciliary rows (b). At the anterior ends of some parental ciliary rows kinetofragments are generated (c, d), which assemble to new oral structures during transverse fission.



**Table 3:** State of characters used in Figure 53.

Apomorph	Plesiomorph
1 stomatogenesis parakinetal	stomatogenesis buccokinetal
2 non-dividing macronucleus	dividing macronucleus
3 fission parallel	fission homothetogenic
4 stomatogenesis epiapokinetal	stomatogenesis parakinetal
5 fibrillar system different	postcilliodesmata
6 stomatogenesis apokinetal	stomatogenesis buccokinetal
7 homomeric macronucleus with reorganization band	homomeric macronucleus without reorganization band
8 cirri	cilia
9 division enantiotropic	division homothetogenic
10 kinetodesmal fiber transient	kinetodesmal fiber permanent
11 somatic infraciliature originates de novo	somatic infraciliature originates intrakinetally
12 stomatogenesis hypoapokinetal	stomatogenesis epiapokinetal
13 somatic monokinetids	somatic dikinetids
14 adoral zone of membranelles partially or completely reduced	adoral zone of membranelles well developed
15 silverline system striated	silverline system narrowly meshed
16 kinetodesmal fibers well developed	kinetodesmal fibers lacking or inconspicuous
17 scutica or stomatogenic kinety	no scutica or stomatogenic kinety
18 stomatogenesis scuticobuccokinetal	stomatogenesis ophryobuccokinetal
19 loss or distinct reduction of somatic infraciliature	with somatic infraciliature
20 with rosette	without rosette
21 stomatogenesis mixokinetal	stomatogenesis ophryobuccokinetal
22 without oral apparatus	with oral apparatus
23 stomatogenesis mixokinetal or telokinetal	stomatogenesis parakinetal, apokinetal or buccokinetal
24 stomatogenesis merotelokinetal or mixokinetal	stomatogenesis pleurotelokinetal, monotelokinetal or cryptotelokinetal
25 cyrtos polymerized («nasse»)	cyrtos indistinct (vice versa in chonotrichs/cyrtophorids)
26 oral apparatus polar	oral apparatus ventral
27 cyrtos not connected with oral kineties in adults	cyrtos connected with oral kineties in adults
28 loss of paroral and adoral ciliary fields	with paroral and adoral ciliary fields
29 cortex with alveolocysts	cortex without alveolocysts

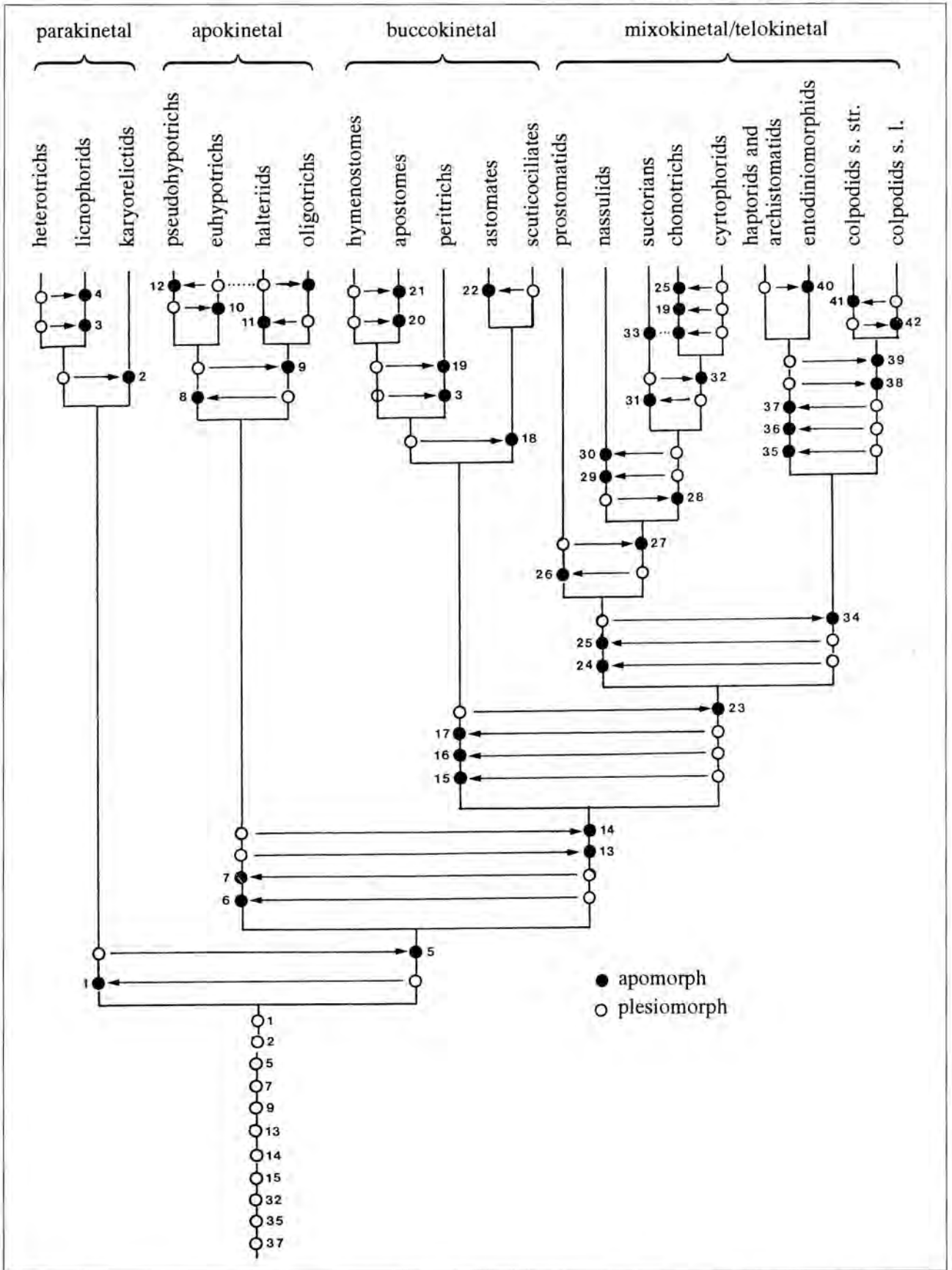
**(Table 3 continued)**

Apomorph	Plesiomorph
30 stomatogenesis mixokinetal	stomatogenesis merotelokinetal
31 with suctorian tentacles	without suctorian tentacles
32 macronucleus heteromeric	macronucleus homomeric
33 budding	normal fission
34 transverse microtubules of somatic kinetids well developed	transverse microtubules of somatic kinetids weakly developed
35 rhabdos type oral apparatus, i.e. transverse microtubules line cytopharynx	cyrtos type oral apparatus, i.e. postciliary microtubules line cytopharynx
36 with dorsal brush	without dorsal brush
37 oral kinetids not organized to distinct fields and indistinctly separate from somatic ciliature	oral ciliature in two distinct fields separate from somatic ciliature
38 with LK <sub>m</sub> fiber	without LK <sub>m</sub> fiber
39 somatic dikinetids	somatic monokinetids
40 stomatogenesis cryptotelokinetal	stomatogenesis different
41 stomatogenesis merotelokinetal	stomatogenesis pleurotelokinetal
42 LK <sub>m</sub> fiber and transverse microtubular ribbon of anterior basal body form V-shaped figure	LK <sub>m</sub> fiber distinctly longer than transverse microtubular ribbon of anterior basal body

## 8 A phylogenetic scenario of ciliates based on ontogenetic data

Many systems of ciliates have been suggested during the past 20 years (e.g., 118, 310, 519, 634, 705, 706). Most were short-lived. The scenario shown in Fig. 53 emphasizes ontogenetic data, but includes also conventional (e.g. macronuclear structure), ultrastructural (cortical fine structure, e.g. [515]) and molecular markers (249, 520, 670). I do not believe that this scheme, which emerged from many trials, is correct in all details, but it at least shows the problems we face if we try to harmonize different data sources. The scheme assumes that the buccokinetal stomatogenic mode is plesiomorph (ancestral). Evidence for this is weak al-





**Fig. 53:** A phylogenetic (cladistic) system of the ciliates mainly based on ontogenetic data. See table 3 for character states. Note that I could not find reliable apomorphies for all taxa included, e.g. for licnophorids and heterotrichs; the lack is not indicated for the sake of clarity.

though the suggestion is supported by a recent hypothesis (182). Furthermore, this assumption produces a rather parsimonious tree, at least with the apomorphies (derived characters) used.

The heterotrichs and karyorelictids cannot be founded as a monophyletic group based on ontogenetic data because those available on the karyorelictids are too scanty and uncertain; however, ultrastructural and molecular characters indicate that they are ancestral and related (249, 310). The heterotrichs, though reduced by the oligotrichs, are very likely still a melting pot, as indicated by their diverse stomatogenic patterns. The typical forms, however, have parakinetal subtypes (PPK, APK, BPK). This suggests that the monoparakinetal and the teloparakinetal subtypes, which occur in many hymenostomes, belong to another main type (buccokinetal?) or evolved convergently. Likewise, parallel fission apparently evolved convergently in licnophorean and peritrich ciliates, possibly due to their sessile mode of life. Whether or not licnophorean stomatogenesis is truly epiapokinetal needs further investigation.

The heterotrich/karyorelictid assemblage is probably the sister group of the hypotrich/oligotrich clade. Most have a distinct adoral zone of membranelles, which was formerly used to unite heterotrichs, hypotrichs, and oligotrichs (118). The hypotrichs and oligotrichs are well-founded as a monophyletic group by the macronuclear reorganization band although a similar structure is found in the orthomere of the heteromeric macronucleus of some cyrtophorids and chonotrichs (645). Furthermore, the hypotrichs and oligotrichs are probably the only ciliates having a true apokinetal stomatogenesis. This is well-founded in oligotrichs, but still uncertain in euhypotrichs. Details of the halteriid/oligotrichid clade are rather clear (324, 610, 851), while those of the euhypotrichs are still bewildering (179, 806, 828).

The Postciliodesmatophorea (at least the heterotrichids) and Spirotrichea both have elaborate oral structures, viz. a distinct zone of adoral membranelles. All other ciliates have few (usually three, e.g., most oligohymenophorans) or none (haptorids). This seems to be a main difference and is thus used for the gross distinction of the six main groups recognized. The Oligohymenophora, which possibly reside at the base of this clade, retained the ancestral buccokinetal stomatogenesis. The scheme suggests that the parakinetal subtypes found, e.g. in tetrahymenids, evolved convergently to those present in heterotrichs or, more likely, are special buccokinetal subtypes. In fact, a scutica-like vestige

occurs during the final stages of stomatogenesis in *Tetrahymena* (345) and the «parakinetal hymenostomes» develop the oral apparatus buccokinetically during physiological reorganization (252, 279). This suggests that the so-called stomatogenic kinty («Richtungsmeridian») of the hymenostomes is a strongly modified scutica or vice versa. Details within the oligohymenophoran clade are not yet clear.

The Cyrtophorea, Litostomatea, and Colpodea have telokinetal or, rarely, mixokinetal (nassulids) stomatogenic subtypes. The pleurotelokinetal mode is probably ancestral because of its similarity with the pleurotelokinetal (?) subtype found in some heterotrichs. The ciliates I unite under the Cyrtophorea have a distinct («polymerized») homonomous cyrtos, a highly characteristic organelle not found in this form in any other ciliate group, and a merotelokinetal or mixokinetal stomatogenesis. Both characters are highly modified in chonotrichs and suctorians. The cyrtophorids and chonotrichids are clearly more closely related to each other than to the suctorians because of their heteromeric macronucleus.

The nematodesmal bundles detach during the late stomatogenic stages in nassulids and cyrtophorids, whereas they remain attached to the paroral dikinetids in prostomatids (181, 184, 402, 403, 412, 625). This appears to be a rather fundamental difference which not only links prostomatids and hymenostomes but can also be used to distinguish two main evolutionary lines within the Cyrtophorea.

The litostomes were included by Gerassimova and Seravin (310) in the Postciliodesmatophorea. This seems correct because they possess, like heterotrichs and karyorelictids, strongly developed postciliary microtubule ribbons, which, however, do not overlap as in heterotrichs, but form a monolayer between the ciliary rows. More recently, Gerassimova (309) united the Archistomatina and Isotrichina into a new taxon, Archiciliatida, which are considered to contain the «most primitive ciliates». Furthermore, this author suggested that the ciliates are most closely related to the Chloromonadina. Both proposals are not supported by recent molecular data (249). A convincing apomorphy between litostomes and colpodeids is still lacking (266); however, both are sharply defined, the colpodeids by the LKM-fiber, and the litostomes by the dorsal brush and the rhabdos type oral apparatus. The merotelokinetal stomatogenesis in the colpodeids s. str. is probably related to their reproduction in cysts and very likely evolved convergently in

the cyrtophorids. See (266, 270, 504) for details and problems within the litostome and colpodid clade.

Three major conclusions are suggested by the scheme discussed: (i) A subphyletic division of the Ciliophora based on a cyrtos or rhabdos type of oral apparatus, as proposed by Small (703), is not supported. Rather, the rhabdos is an apomorphy of a single group, the Litostomatea. The same applies to the cortical fibrillar systems, i.e. the Postciliodesmatophora and Kinetodesmatophora suggested by Gerassimova and Seravin (310). (ii) Some stomatogenic modes evolved either convergently or are only superficially similar, viz. at light microscopic level. (iii) The «eociliate» possibly possessed the following character constellation: a dividing, homomerous macronucleus without a reorganization band; a cyrtos – type oral apparatus composed of a well developed adoral zone of membranelles and a paroral membrane; somatic dikinetids with postciliodesmata; a narrow-meshed silverline system; homothetogenic fission, and buccokinetal stomatogenesis. Fleury et al. (249) suggest that the «eociliate» also possessed a distinct epiplasm. If so, then it has been lost or considerably reduced in those groups which they consider to be most ancestral, i.e. the heterotrichs and karyorelictids. This could serve as a further apomorphy separating the karyorelictid/heterotrich clade from the other clades.

type, division mode, stomatogenic mode (to subtype level), degree of dedifferentiation in the parental oral apparatus during stomatogenesis of the opisthe, macronucleus type, and references. This compilation demonstrates the inadequacy of much of the available data in terms of modern requirements. There is thus an urgent need for refined studies, especially in metopid, odontostomatid, and licnophorid heterotrichs, all karyorelictids, chonotrichs, and rhynchodids, and most thigmotrichs, apostomes, and prostomatids. Hennig's cladistic method was applied to the ontogenetic data and several light microscopic and ultrastructural features as well as molecular markers. Although it was not possible to determine all character states (plesiomorphies, apomorphies) unequivocally and to harmonize all data, the cladogram suggests main pathways in ciliate evolution and three major conclusions: (i) A subphyletic division of the Ciliophora based on a cyrtos or rhabdos type of oral apparatus is not supported; (ii) Some stomatogenic modes evolved either convergently or are only superficially similar, viz. by light microscopy; (iii) The «eociliate» possibly possessed the following character constellation: a dividing, homomerous macronucleus without a reorganization band; a cyrtos-type oral apparatus with a well developed adoral zone of membranelles and a paroral membrane; somatic dikinetids with postciliodesmata; a narrow-meshed silverline system; homothetogenic fission, and buccokinetal stomatogenesis.

## 9 Summary and conclusions

The phenomenology of ontogenesis in ciliated protozoa is reviewed, with emphasis on stomatogenic data published between 1870 and 1993. Three basic types of fission (homothetogenic, enantiotropic, parallel), two basic modes of division (active, cystic), and five main modes of stomatogenesis (apokinetal, parakinetal, buccokinetal, telokinetal, mixokinetal) are distinguished. Within the main stomatogenic patterns several subtypes occur, some of which are, however, possibly not homologous, i.e. they evolved convergently in different ciliate groups. The stomatogenic patterns were extracted from a re-examination of published data on 600 ciliate species. These are listed in Table 2 together with the following details: quality of data, fission

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- With few exceptions, titles of journals are given in accordance with the abbreviations found in the 4th edition of the «World List of Scientific Periodicals», published by Butterworths, London, in 1963–1965. Also practically without exception, all works cited here have been examined first-hand in order that dates, titles, names of journals or books, and complete pagination could be given with accuracy. Chinese references were often difficult to locate because the first and second names were mixed and/or incorrectly abbreviated in the secondary literature. Thus, I neither abbreviated them nor changed the sequence of the names, i.e. they are given as written on the title page of the paper.
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