

Cladistic Relationships and Generic Characterization of Oxytrichid Hypotrichs (Protozoa, Ciliophora)

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Summary: The relationships of 13 common oxytrichid genera were analysed using cladistic methods (HENNIG, PAUP). Twenty-three characters in four groups were selected, viz. the morphology of the oral apparatus (three characters), infraciliature of ventral and dorsal side (ten characters), cortical features (two characters), and ontogenetic particulars (eight characters). All characters and character states are described and discussed using published and original data. Half of the characters originated independently in several genera at least twice, making it very difficult to follow oxytrichid evolution. The autapomorphies of the family Oxytrichidae are 18 characteristically arranged fronto-ventral-transverse cirri and the fragmentation of at least one dorsal kinety. The cladograms show two major branches, termed subfamily Oxytrichinae JAN-KOWSKI and subfamily Stylonychinae n. subfam. The Oxytrichinae have a unique synapomorphy, viz. the participation of cirrus V/3 in primordia formation. This subfamily contains the genera *Cyrtohymena*, *Gonostomum*, *Notohymena*, *Onychodromopsis*, *Oxytricha*, *Tachysoma*, *Urosoma*, *Urosomoida* and, very likely, *Australocirrus*, *Parurosoma* and *Pseudostrombidium*. The Stylonychinae have three synapomorphies, viz. the rigid body, an oral apparatus of more than 40% of body length, and the lack of cortical granules. This subfamily comprises *Coniculostomum*, *Histiculus*, *Steinia*, *Sterkiella*, *Stylonychia* and, very likely, *Parastylonychia* and *Pleurotricha*. The family Oxytrichidae, its subfamilies, and the genera included are characterized and keyed. An unambiguous terminology is established for oxytrichid hypotrichs, and synonymy and nomenclature of genera are discussed.

Key Words: *Histiculus histrio*; Key to genera; Morphogenesis; Oxytrichidae; Oxytrichinae; Phylogeny; Stylonychinae.

Introduction

Oxytrichid ciliates are very common in freshwater and soil. Thus, several species were already described by the pioneers of protozoology (MÜLLER 1786; EHRENBERG 1838; STEIN 1859) and placed in the genera *Oxytricha*, *Stylonychia*, and *Pleurotricha*. Later, DIESING (1866), STERKI (1878), KENT (1880–1882), KOWALEWSKIEGO (1882), and STOKES (1887) established further oxytrichid genera, viz. *Steinia*, *Histrio*, *Opisthotricha*, *Urosoma* and *Tachysoma*, using details of the oral apparatus or the length of the dorsal cilia and caudal cirri as main diagnostics. KAHL (1932) recognized all genera, but lowered most of them to subgeneric rank. Forty years later, BOR-

ROR (1972) synonymized *Steinia*, *Urosoma* and *Opisthotricha* with *Oxytricha*, considering the differences in the oral apparatus and the length of the caudal cirri as insufficient for a generic or subgeneric distinction. However, this simplification was only partially accepted by other specialists, who re-established *Steinia* and *Urosoma* because of autapomorphies in the shape of the undulating membranes and, respectively, the arrangement of some cirri in the frontal area (GROLIÉRE 1975; FOISSNER 1982, 1983a; VOSS & FOISSNER 1995).

Since then many detailed studies on the morphology and morphogenesis of oxytrichids were performed and

several new genera were established, viz. *Australocirrus*, *Cyrtohymena*, *Notohymena*, and *Sterkiella* (FOISSNER & ADAM 1983a, b; FOISSNER 1984, 1987a, b, 1988, 1989, 1995; HEMBERGER 1985; BERGER et al. 1985; WIRNSBERGER et al. 1985a, 1986; WILBERT 1986; BERGER & FOISSNER 1987, 1988a, 1989a; GANNER et al. 1987; BLATTERER & FOISSNER 1988, 1990; SONG & WILBERT 1989; KAMRA & SAPRA 1990; SONG 1990; FOISSNER et al. 1991; VOSS 1991a, b; AUGUSTIN & FOISSNER 1992; KAMRA et al. 1994; VOSS & FOISSNER 1995). Simultaneously, some oxytrichids became an extensively used model for experimental and biochemical research (e.g. SCHLEGEL & STEINBRÜCK 1986; RICCI et al. 1991; SCHLEGEL et al. 1991; BAROIN-TOURANCHEAU et al. 1992; MITCHAM et al. 1994). The most detailed molecular biological studies were performed on *Oxytricha nova* (KLOBUTCHER et al. 1981), a nomen nudum species, that is a taxon not existing according to the International Code of Zoological Nomenclature (ICZN 1985). More than 50 papers have been published on *O. nova*, but nobody knows its identity, i.e. whether it is a new or a known species.

Certainly, not only molecular and cell biologists have problems in assigning oxytrichid hypotrichs to a certain genus but also morphologists (HEMBERGER 1982; WIRNSBERGER et al. 1986). This is due not only to insufficient data but also to the lack of a comprehensive evaluation and clear presentation of the data accumulated. The history of *Histriculus muscorum* can serve as a representative example of the problems tantalizing oxytrichid students. *Histriculus* (originally described as *Histrio* [STERKI 1878], but replaced by CORLISS [1960] because of homonymy) was established to separate *Stylonychia histrio* MÜLLER, 1773 from other *Stylonychia* species (EHRENBERG 1838), because the marginal cirral rows are posteriorly confluent and caudal cirri are lacking. However, later KAHL (1932) and BORROR (1972) added species with inconspicuous caudal cirri, obviously assuming that STEIN (1859) and STERKI (1878) overlooked them. Morphogenetic studies proved that such species indeed have inconspicuous caudal cirri, especially *Histriculus muscorum*, one of the most widespread oxytrichids (FOISSNER 1982; BERGER et al. 1985). It was thus a great surprise for us to find a species exactly matching the original diagnosis of STERKI (1878), demanding that species assigned to *Histriculus* by KAHL (1932) and BORROR (1972) be referred to a new genus, *Sterkiella* (FOISSNER et al. 1991). Thus, a single species has accumulated three generic combinations over time: *Oxytricha (Histrio) muscorum* (KAHL 1932), *Histriculus muscorum* (CORLISS 1960; BORROR 1972), *Sterkiella histriomuscorum* (FOISSNER et al. 1991). In the latter binomen, the species name has changed too, because KAHL (1932) named three other species *Oxytricha muscorum*,

namely *O. (Opisthotricha) muscorum*, *O. (Steinia) muscorum*, and *O. (Stylonychia) muscorum*. All these are primary homonyms, because a subgeneric name does not affect homonymy (Article 57d of ICZN 1985). Thus, three species had to be renamed, among them also *Histriculus muscorum*, now called *Sterkiella histriomuscorum* (FOISSNER et al. 1991).

In the present paper we characterize all sufficiently investigated oxytrichid genera and analyse the cladistic relationships among the common ones, a difficult task addressed by few morphologists (WIRNSBERGER et al. 1986; KAMRA et al. 1994; VOSS & FOISSNER 1995) and molecular biologists (e.g. SCHLEGEL et al. 1991; BAROIN-TOURANCHEAU et al. 1992). However, the time is ripe for such a comprehensive evaluation of data because detailed morphological and morphogenetical investigations have become available from almost all type species, i.e. from the authoritative measure of the supraspecific taxa. Finally, we have tried to establish an unambiguous terminology for oxytrichid hypotrichs.

Many classifications of hypotrichs, including oxytrichids, were suggested in the last decades (e.g. BORROR 1972; CORLISS 1979; JANKOWSKI 1979; SMALL & LYNN 1985; TUFFRAU 1987). With few exceptions (BORROR 1972; WIRNSBERGER et al. 1985a) they were established without detailed discussion of the characters used.

Without doubt, the classification of the oxytrichids is in a chaotic and provisional state. Many of the characters used for genus and species distinction appear, at first glance, inconspicuous and difficult to rate. Thus, they must be described and discussed in great detail, which is why the present paper became rather lengthy. On the other hand, molecular biological evidence (SCHLEGEL & STEINBRÜCK 1986; SCHLEGEL et al. 1991) indicates that oxytrichids are even more diverse than morphologists presently assume. We hope that our approach will be helpful to both classical morphologists and modern molecular biologists.

Materials and Methods

Most of the material presented in this paper is based on previous investigations by our group. We thus refer to these publications as concerns the origin of the material and detailed descriptions of the methods used (FOISSNER 1982, 1989; BERGER et al. 1985; BERGER & FOISSNER 1987, 1988a; BLATTERER & FOISSNER 1988; FOISSNER et al. 1991; VOSS & FOISSNER 1995). Briefly, all species were investigated alive and after protargol impregnation (FOISSNER 1991). Most of the scanning electron micrographs are shown for the first time and were obtained by the method described in FOISSNER (1991). Line drawings were made with a camera lucida.

The data of *Histriculus histrio* are from a population found in August 1986 in the periphyton of a small lake (Teu-

felsee) near Berlin (Germany). A culture was set up in a petri dish with table water (Volvic, France) and some crushed wheat grains to support growth of bacteria and small ciliates which served as food organisms.

Terminology is explained in detail in the results section. Cladistic analysis was carried out both traditionally, i.e. by HENNIG's (1966) method (construction of the cladogram by head and hand) and with the computer program PAUP. The traditional method has been described in detail by AX (1984, 1995), HENNIG (1966, 1982), and SUDHAUS & REHFELD (1992). In contrast to computer analysis, HENNIG's method requires that the plesiomorphic and apomorphic state of a character is defined before the analysis is performed (MEIER 1992). To distinguish plesiomorphies from apomorphies out-group (e.g. holostichids) and in-group comparison was used (AX 1984). Computer analysis was conducted with the PAUP program (SWOFFORD 1991) using the successive weighting procedure and holostichids as outgroup. With both methods, only apomorphies are used for reconstructing phylogeny. For further details see LIPSCOMB (1992).

Results and Discussion

Genera concerned

For the present purposes we define as Oxytrichidae (= oxytrichids) hypotrichs usually having 18 fronto-ventral-transverse (FVT) cirri clustered to six distinct groups and at least one fragmented dorsal kinety. The FVT cirri originate from six longitudinal primordia (anlagen, generally numbered I–VI) segregating 1, 3, 3, 3, 4, and 4 cirri, respectively. Six or fewer parental FVT cirri participate in primordia formation. Usually, dorsal kinety 3 fragments, producing kinety 4 (Figs. 1, 26, 38, 44). This complex morphostatic and morphogenetic pattern has been described for at least eighteen distinct groups (genera) and shows such a high stability that it can be used to characterize the family. However, only those genera are considered in the cladistic analysis for which detailed morphogenetic data, especially on the type species, are available, viz. *Coniculostomum*, *Cyrtohymena*, *Gonostomum*, *Histriculus*, *Notohymena*, *Onychodromopsis*, *Oxytricha*, *Steinia*, *Sterkiella*, *Stylonychia*, *Tachysoma*, *Urosoma*, *Urosomoida*. Consequently, *Australocirrus*, *Parastylonychia*, *Parurosoma*, *Pleurotricha*, and *Pseudostrombidium* are excluded from the cladistic analysis. For completeness, however, they are characterized and included in the key.

One of the genera mentioned, *Histriculus*, has been reinvestigated (Figs. 29–37). Briefly, this genus has confluent marginal rows and lacks caudal cirri, characters exactly matching the original description (Fig. 29). The lack of caudal cirri is confirmed by the morphogenesis of the dorsal infraciliature (Figs. 35–37). The origin of the FVT cirri highly resembles oxytrichids with a

rigid cortex, i.e. the postoral ventral cirrus V/3 is not involved in primordia formation (Fig. 33).

Genera not considered

The following genera, although classified by some authors (BORROR 1979; CORLISS 1979; FOISSNER 1982, 1984, 1987b; WIRNSBERGER et al. 1986; FOISSNER et al. 1987; BERGER & FOISSNER 1988b, 1989a; SZABÓ & WILBERT 1995) as Oxytrichidae and/or Oxytrichidae sensu lato, were not considered in our analysis because they lack the typical 18 FVT cirral pattern: *Ancystropodium* (CORLISS 1979), *Engelmanniella* (FOISSNER 1982), *Gastrostyla* (WIRNSBERGER et al. 1986), *Hemisincirra* (FOISSNER 1982, 1984), *Lamtostyla* (BERGER & FOISSNER 1988b), *Laurentiella* (SZABÓ & WILBERT 1995), *Onychodromus* (FOISSNER et al. 1987; SZABÓ & WILBERT 1995), *Paraurostyla* (BORROR 1979; WIRNSBERGER et al. 1986), *Pattersoniella* (FOISSNER 1987b), *Terricirra* (BERGER & FOISSNER 1989a), *Territricha* (BERGER & FOISSNER 1988b).

Ancystropodium is a monotypic, very poorly known genus, having a ventral infraciliature obviously rather similar to that of *Gastrostyla* (FAURÉ-FREMIET 1909). Detailed redescription necessary.

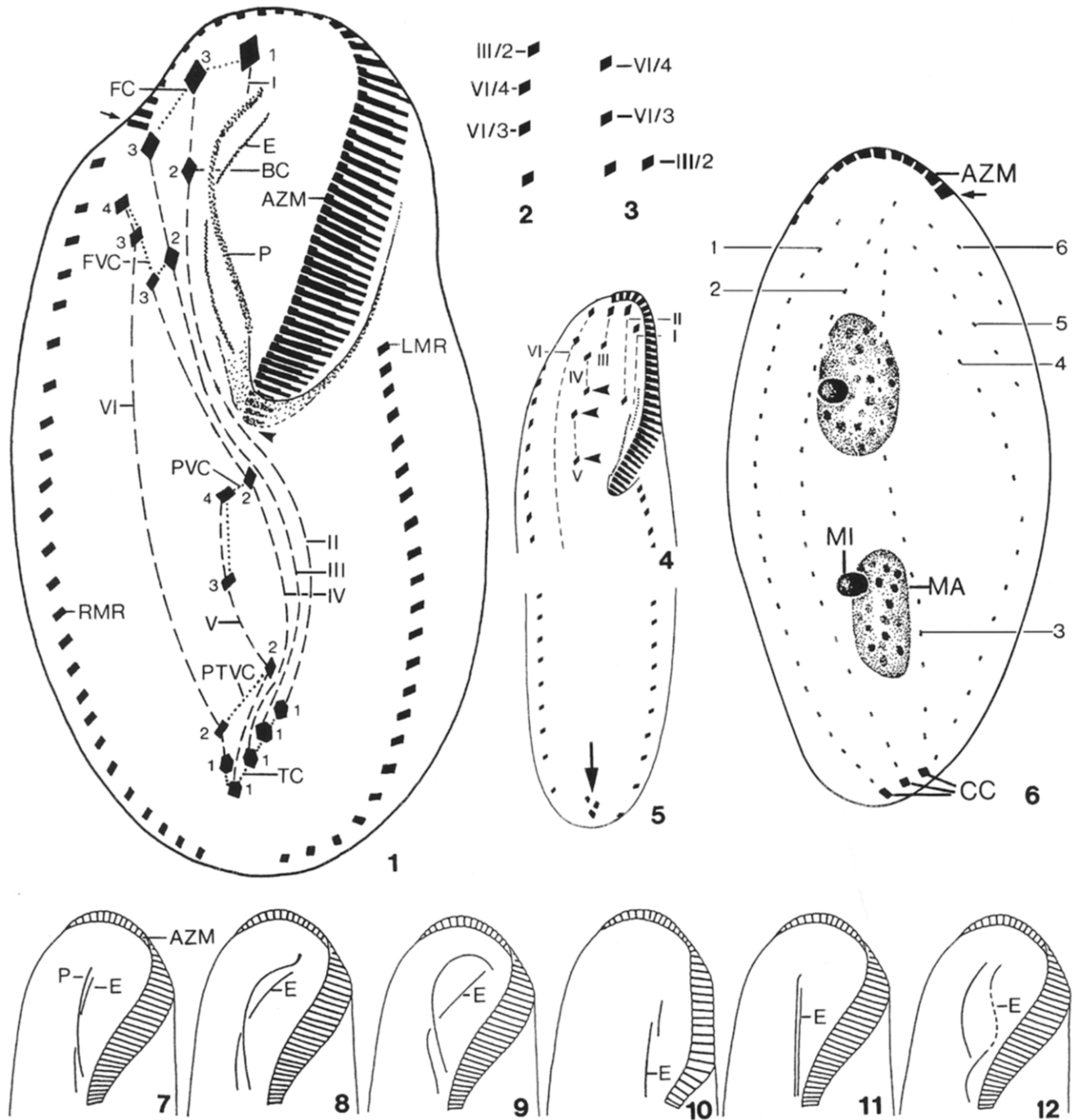
Engelmanniella was only provisionally assigned to the Oxytrichidae (FOISSNER 1982). Later, morphogenetic data revealed that it is very likely a kahliellid (WIRNSBERGER-AESCHT & FOISSNER 1989; EIGNER 1995).

Gastrostyla has distinctly more than 18 FVT cirri (FOISSNER 1982), which form a more or less continuous frontoventral row, suggesting a close relationship with the amphisiellids (WICKLOW 1982; EIGNER & FOISSNER 1994). However, the amphisiellids lack fragmentation of dorsal kineties, which is common in *Gastrostyla*. In fact, the dorsal morphogenesis of *Gastrostyla* proceeds as in *Oxytricha* (WALKER & GRIM 1973).

Hemisincirra comprises several, usually very slender soil inhabiting species which have, however, not a very uniform infraciliature (FOISSNER 1982, 1984; HEMBERGER 1985). Some of them (e.g., *H. polynucleata*) have the frontoventral cirri very similar arranged as *Urosoma* (see below). Detailed morphogenetic and molecular biological data are needed to ascertain the phylogenetic relationships of this genus.

Lamtostyla was originally classified in the Holostichidae (BUTKAMP 1977a), and later transferred to the Cladotrichidae (SMALL & LYNN 1985), however, without detailed explanation. Others (BERGER & FOISSNER 1987, 1988b) proposed a classification in the Oxytrichidae because of morphogenetic similarities. Recently, PETZ & FOISSNER (1996) provided convincing morphogenetic evidences that *Lamtostyla* belongs to the amphisiellids.

Laurentiella, *Onychodromus*, and *Pattersoniella* are usually classified as oxytrichids sensu lato (MARTIN et



Figs. 1–12. Schematic illustrations of the oxytrichid infraciliature and some characters and character states used in the cladistic analysis. **1.** Ventral infraciliature of *Sterkiella cavicola* showing position, designation, and numbering of cirri. Arrow marks distal, arrowhead proximal end of adoral zone of membranelles. Cirri originating from the same primordium are connected by broken lines. Cirral groups, e.g. frontal cirri are connected by dots. Modified from BERGER & FOISSNER (1987). **2, 3.** Character 6, arrangement of frontoventral cirri in *Urosoma* and in some species (e.g. *Stylonychia*) with rigid body. Note the different arrangement of cirrus III/2. **4.** Character 7, apomorphic position of postoral ventral cirri (arrowheads) in *Gonostomum*. From BERGER & FOISSNER (1988a). **5.** Characters 8 and 9, reduced number of pretransverse ventral and transverse cirri (arrow) in *Urosomoida agiliformis*. From FOISSNER (1982). **6.** Dorsal infraciliature of *Sterkiella histriomuscorum*. From BERGER et al. (1985). Arrow marks distal end of adoral zone of membranelles. **7–12.** Characters 1 and 3, shape of adoral zone of membranelles and arrangement of paroral and endoral. From FOISSNER et al. (1991). For details, see text and Figs. 13–25. **7.** *Oxytricha* pattern. **8.** *Notohymena* pattern. **9.** *Cyrtohymena* pattern. **10.** *Gonostomum* pattern. **11.** *Stylonychia* pattern. **12.** *Steinia* pattern. AZM = adoral zone of membranelles, BC = buccal cirrus, CC = caudal cirri,

al. 1983; FOISSNER 1987b; FOISSNER et al. 1987), i.e. as sister group of the 18 FVT cirri oxytrichids. However, the comparison of small subunit ribosomal RNA sequences places *Onychodromus quadricornutus* very close to *Stylonychia* (SCHLEGEL et al. 1991). The three genera mentioned have some conspicuous characters in common, viz. a rigid body, a very large oral apparatus, lack of cortical granules, and a complicated dorsal ciliary pattern (multiple fragmentation and/or retention of parental dorsal kineties). The first three features match the autapomorphies of the *Stylonychia* branch exactly (Fig. 49a, b), strongly supporting the classification inferred from the RNA sequences (SCHLEGEL et al. 1991). Possibly, these genera evolved from a *Australocirrus octonucleatus*- and/or *Coniclostomum*-like hypotrich, both also having a complex dorsal ciliature, by secondary polymerization of the anlagen (*Pattersoniella*) and/or secondary polymerization of cirri within the anlagen (*Onychodromus*, *Laurentiella*), as proposed by SCHLEGEL et al. (1991).

Paraurostyla was originally classified in the Urostylidae (BORROR 1972), and later transferred to the oxytrichids because of similarities in ventral morphogenesis with the 18 FVT cirri oxytrichids (BORROR 1979). Furthermore, dorsal morphogenesis proceeds as in *Oxytricha* (WIRNSBERGER et al. 1985b). However, it is difficult to ascertain whether *Paraurostyla* branches off from the base of the cladogram, as suggested by the high (ancestral?) number of cirri or if it is a member of the Oxytrichinae (see below) with a secondarily increased number of fronto-ventral-transverse cirri.

Terricirra includes three soil inhabiting species with green to blue-green cortical granules, spindle-shaped food vacuoles, short undulating membranes forming an acute angle, and one short frontoventral row (BERGER & FOISSNER 1989a). The ventral infraciliature is highly reminiscent of that of *Lamtostyla* (see above), which is now classified in the family Amphisiellidae (PETZ & FOISSNER 1996). Morphogenetic data are needed to clarify the systematic position of *Terricirra*.

Territricha, a monotypic genus, was originally placed in the Urostylidae. It has some sort of midventral rows but a typical oxytrichid cirral pattern in the frontal area (BERGER & FOISSNER 1988b). Thus, a position between urostylids and oxytrichids was proposed. However, the fragmentation in dorsal kinety 3 suggests that *Territricha* branches off from the oxytrichids.

Characters, character states, parallelisms and terminology

The generic characterizations and the cladistic analysis are based on four groups of characters: the morphology of the oral apparatus (characters 1–3), the infraciliature of the ventral and dorsal side (characters 4–13), cortical features (e.g. flexibility of body; characters 14, 15), and on the morphogenesis of the ventral and dorsal infraciliature (characters 16–23). The characters and character states used are summarized in Table 1, and their distribution in the taxa is given in Table 2. To preserve terminological consistency, we use terms as defined by previous authors (WALLENGREN 1900; KAHL 1932; BORROR 1972; CORLISS 1979). However, some minor changes and emendations are necessary and will be introduced in the appropriate sections.

The basic morphology of the oxytrichid cell is explained in Figs. 1, 6. Briefly, the ventral side bears the oral apparatus, usually 18 FVT cirri arranged in six groups, and two (rarely more) rows of marginal cirri. The adoral zone of membranelles extends near the left body margin from the anterior end to about mid-body; right of the zone are two undulating membranes bordering a more or less wide and deep buccal cavity. The dorsal side bears 3–6, rarely more, longitudinal kineties usually having short (about 3 µm) cilia (bristles) and three caudal cirri attached to kineties 1, 2, 4. The majority of oxytrichids have two macronuclear nodules and two micronuclei; a few have four or even eight nodules. The contractile vacuole is in or near mid-body, close to the left margin. Some species form giants (e.g. ROSATI et al. 1988) and most, probably all, are omnivorous and at least the larger species even predatory.

Character 1: Shape of the adoral zone of membranelles (Figs. 1, 4, 7, 10, 13, 16, 20, 22). The adoral zone is formed like a question mark in most oxytrichids, as in the majority of hypotrichs, indicating that this configuration is plesiomorphic (Figs. 1, 13, 20). Only in *Urosoma* and *Gonostomum* is the middle portion straight and extends along the left margin of the cell, causing the proximal part of the zone to become abruptly bent towards the centre of the body (Figs. 4, 10, 16, 22). Obviously, this is a rare and thus derived configuration.

Character 2: Relative length of the adoral zone of membranelles. The ratio of the length of the adoral zone to the length of the cell is possibly of cladistic significance in oxytrichid hypotrichs. It is less than 40% (usually 25–35%)

E = endoral, FC = frontal cirri, FVC = frontoventral cirri, LMR = left row of marginal cirri, MA = macronuclear nodule, MI = micronucleus, P = paroral, PTVC = pretransverse ventral cirri, PVC = postoral ventral cirri, RMR = right row of marginal cirri, TC = transverse cirri, I–VI = primordia (anlagen) I–VI, 1–4 and 1–6 = numbering of cirri within a primordium and numbering of dorsal kineties, respectively. Dorsal rows 5 and 6 are termed dorsomarginal kineties.

Table 1. Characters, character states, and coding used for the construction of the cladograms shown in Figs. 49a, b. Character state matrix see Table 2. Definition of plesiomorphic and apomorphic states refer only to the traditionally constructed cladogram (Fig. 49a).

No.	Character	Character states	
		Plesiomorphic	Apomorphic
1	Shape of adoral zone of membranelles	formed like a question mark (coded 0)	<i>Gonostomum</i> pattern (coded 1)
2	Relative length of adoral zone of membranelles	≤40%, usually 25–35%, of body length (coded 0)	≥40%, usually 45–50%, of body length (coded 1)
3	Arrangement of paroral and endoral	<i>Oxytricha</i> pattern (coded 0)	<i>Gonostomum</i> pattern (coded 1) <i>Notohymena</i> pattern (coded 2) <i>Cyrtohymena</i> pattern (coded 3) <i>Stylonychia</i> pattern (coded 4) <i>Steinia</i> pattern (coded 5)
4	Frontal cirri ^a		
5	Buccal cirrus ^a		
6	Arrangement of frontoventral cirri	V-shaped (coded 0)	longitudinal (coded 1)
7	Position of postoral ventral cirri	underneath adoral zone (coded 0)	right of adoral zone (coded 1)
8	Number of pretransverse ventral cirri	2 (coded 0)	1 (coded 1)
9	Number of transverse cirri	usually 5, rarely 4 (coded 0)	less than 4 (coded 1)
10	Number of marginal rows	2 (coded 0)	more than 2 (coded 1)
11	Distance between posterior ends of marginal rows	present (coded 0)	absent (coded 1)
12	Number of dorsal kineties	5 or 6 (coded 0)	4 (coded 1) 3 (coded 2) >6 (coded 3)
13	Caudal cirri	present (coded 0)	absent (coded 1)
14	Body	flexible (coded 0)	rigid (coded 1)
15	Cortical granules	present (coded 0)	absent (coded 1)
16	Primary primordia	absent (coded 0)	present (coded 1)
17	Origin of proter's primordia V and VI	from frontoventral cirrus IV/3 (coded 0)	de novo (coded 1) primordium V from cirrus V/4 and primordium VI from cirrus V/3 (coded 2) from cirrus V/4 (coded 3)
18	Origin of opisthe's primordia V and VI	from postoral ventral cirri V/3 and/or V/4 (coded 0)	de novo (coded 1)
19	Postoral ventral cirrus V/3	not involved in primordia formation (coded 0)	involved in primordia formation (coded 1)
20	Origin of opisthe's primordium IV	cirrus IV/2 (coded 0)	cirrus V/4 (coded 1)
21	Origin of proter's primordium II	cirrus II/2 (coded 0)	oral primordium (coded 1)
22	Origin of right marginal row(s)	new formation of 1 row, no parental marginal cirri retained (coded 0)	new formation of 2 or more rows, no parental marginal cirri retained (coded 1) new formation of 1 row, parental marginal cirri retained (coded 2)
23	Morphogenesis of dorsal kineties	<i>Oxytricha</i> pattern (coded 0)	<i>Urosomoida</i> pattern (coded 1) <i>Gonostomum</i> pattern (coded 2) <i>Tachysoma</i> pattern (coded 3) <i>Coniculostomum</i> pattern (coded 4)

^a Not used in cladistic analysis.

Table 2. Distribution of characters in the 18 cirri oxytrichids. Coding see Table 1. – = not used; ? = not-applicable.

<i>Coniculostomum</i>	014-	-00001	0301103001	124
<i>Cyrtohymena</i>	003-	-00000	0000001010	000
<i>Gonostomum</i>	111-	-01010	020001??1?	002
<i>Histiculus</i>	010-	-00000	101110?00?	000
<i>Notohymena</i>	002-	-00000	0000001010	000
<i>Onychodromopsis</i>	000-	-00001	0000002010	010
<i>Oxytricha</i>	000-	-00000	0000002010	000
<i>Steinia</i>	015-	-00000	0001103000	000
<i>Sterkiella</i>	010-	-00000	000110?100	000
<i>Stylonychia mytilus</i>	014-	-00000	0001103001	100
<i>Stylonychia vorax</i>	014-	-00000	0001100000	000
<i>Tachysoma</i>	000-	-00000	001001??1?	003
<i>Urosoma</i>	101-	-10000	010001??1?	001
<i>Urosomoida</i>	000-	-00110	0100001010	001
holostichids	000-	-?0000	0??000??0?	002

in genera with a flexible body and in most other hypotrichs (except euplotids), indicating that such values represent the ancestral state. Exceptions are rare, e.g. *Cyrtohymena quadrinucleata* (FOISSNER 1984) and *Gonostomum* spp., whose adoral zone is 40–50% of body length, as in all genera with a rigid body.

A correlation between the relative length of the zone and the mode of nutrition is neither known nor apparent. However, such a correlation possibly exists with the absolute size of the buccal cavity; usually, species with a small cavity (e.g. *Oxytricha setigera*, *Tachysoma pellationum*) feed on bacteria and small protists, while those with a large buccal cavity are rapacious carnivores (e.g. *Sterkiella cavicola*, *Cyrtohymena* spp.).

Character 3: Paroral, endoral, and buccal cavity (Figs. 1, 7–25). The terms paroral and endoral membrane were introduced by STERKI (1878). However, he used the first one to describe the rightmost cilia of the hypotrich adoral membranelles, which often beat independently of the remaining part of the membranelles. But for some decades the term paroral membrane has been rather uniformly used in a wide variety of ciliates for the right portion of the oral ciliature (EISLER 1992). We follow LYNN (1988) in that we use paroral and endoral as nouns. Synonyms of the hypotrich paroral are undulating membrane (used e.g. in KAHL 1932; BORROR 1972; FOISSNER et al. 1991), paroral formation 2 (FERNANDEZ-LEBORANS 1985), external paroral kinety (FERNANDEZ-LEBORANS 1985), and outer preoral membranelle (JERKA-DZIADOSZ 1981). Synonyms of the endoral are paroral formation 1 (FERNANDEZ-LEBORANS 1985), internal paroral kinety (FERNANDEZ-LEBORANS 1985), and inner preoral kinety (JERKA-DZIADOSZ 1981).

The shape of the paroral and endoral and their arrangement are very important for distinguishing oxytrichid genera (FOISSNER 1989). In general, the paroral extends at the outer margin of the buccal cavity, i.e. on the cell surface, while the endoral is on the bottom and right border of the cavity. This means, the membranes extend at clearly different lev-

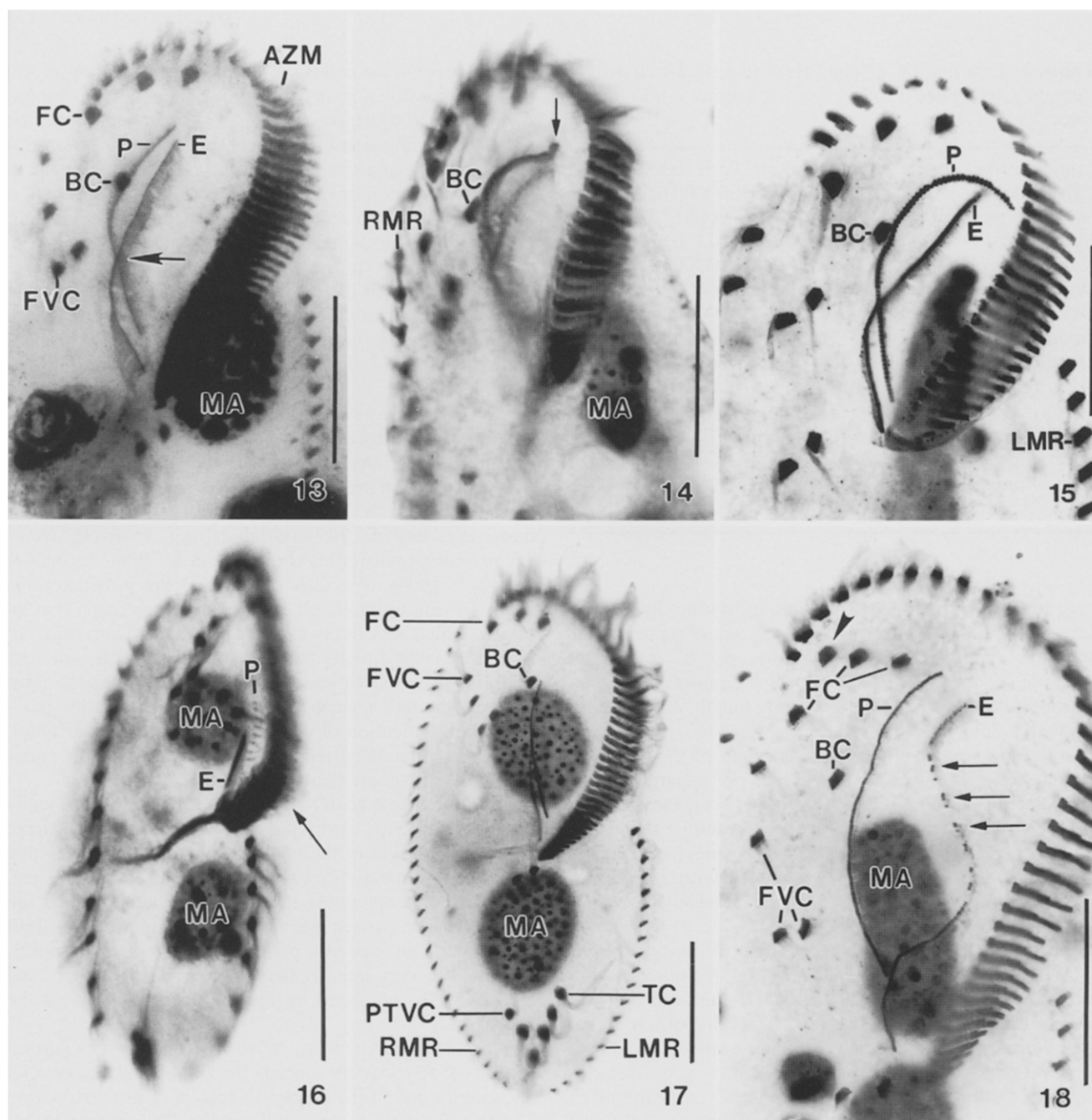
els. However, if the cell is viewed from ventral, they appear to lie side by side (e.g. in *Stylonychia*, Figs. 11, 17) or intersect (e.g. in *Oxytricha*, Figs. 7, 13), depending on their shape and arrangement. The buccal cavity is also rather different in shape and size and is described by the terms flat or deep and wide or narrow. Flat means that the buccal field is only slightly hollowed, whereas a deep cavity extends almost to the dorsal surface, making the buccal field conspicuously bright. In a wide buccal cavity the paroral, i.e. the right margin of the cavity, is in the midline of the cell, whereas in a narrow buccal cavity the paroral is displaced to the left, that is very close to the adoral zone. The six known patterns of character 3 are described in the following paragraphs.

Oxytricha pattern (Figs. 1, 7, 13, 19, 20): The paroral and endoral are slightly curved and optically intersect at about the middle. The buccal cavity is usually rather flat and narrow. This pattern prevails and occurs in *Oxytricha*, *Tachysoma*, *Urosomoida*, *Sterkiella*, and *Histiculus*, but also in many taxa outside the oxytrichids, e.g. *Urostyla*, *Holosticha*, and amphisiellids (FOISSNER et al. 1991; EIGNER & FOISSNER 1994). We thus consider it the plesiomorphic state. In our opinion, all other patterns, except that of *Steinia* which very likely evolved from the *Stylonychia* pattern, originated directly from the *Oxytricha* state, but very likely at different times and comparatively late, as indicated by the rather great homogeneity of the family, making the classification of oxytrichid hypotrichs so difficult. The assumption of a direct evolution provides a more parsimonious cladogram than a series of transformations. As concerns the time scale, HAECKEL's ontogenetic principle can be applied. All oxytrichids and related hypotrichs have an identical origin of the undulating membranes, viz. they are formed in parallel rows right of the primordium. Then, when the oral apparatus invaginates in late dividers, an *Oxytricha*-like pattern becomes recognizable for a short time. The genus-specific patterns described below, originate only in very late dividers and early postdividers and are obviously produced by the particular shaping of the buccal cortex.

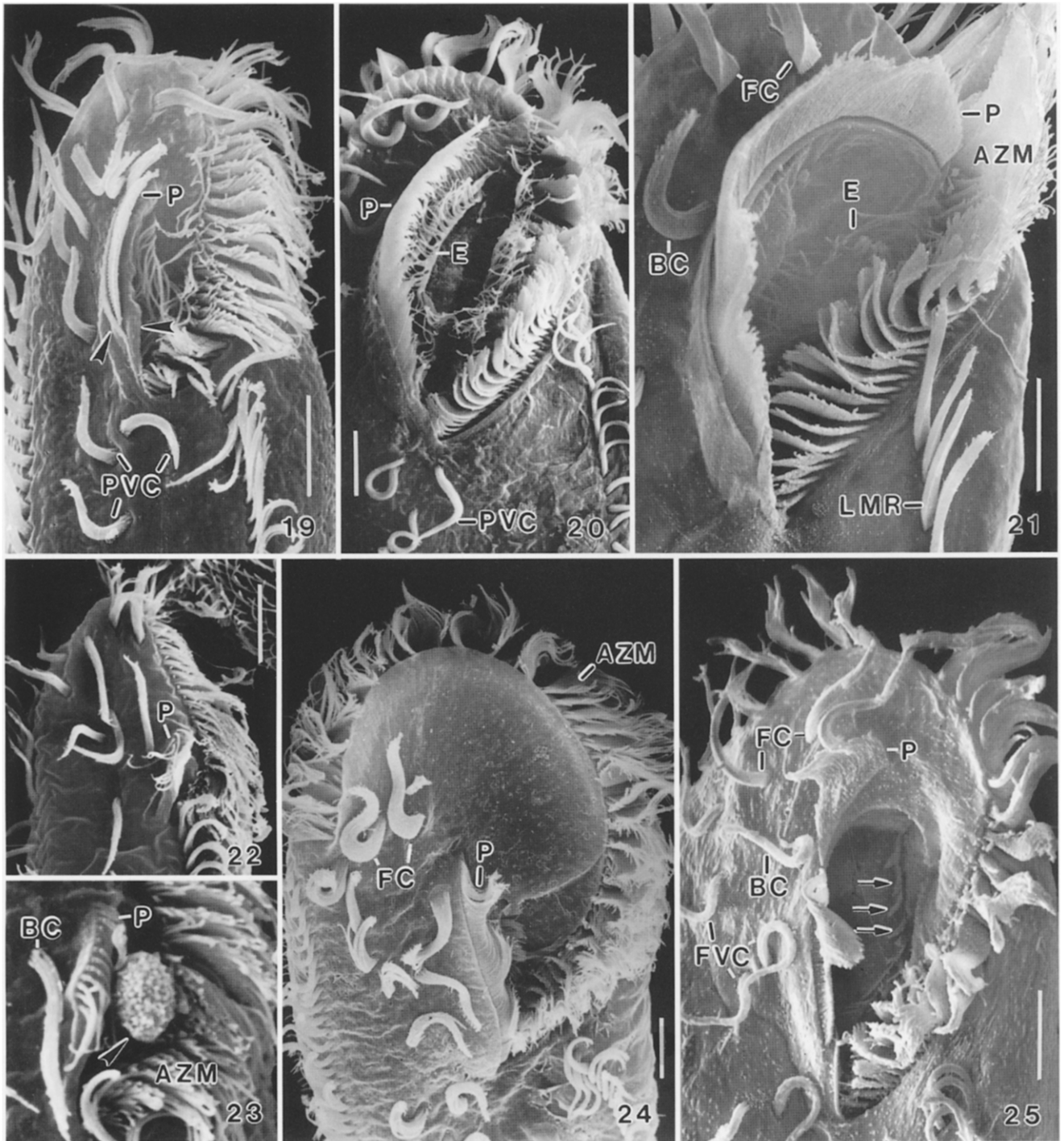
Gonostomum pattern (Figs. 4, 10, 16, 22, 23): The paroral consists of few, widely spaced cilia and extends far beyond the anterior end of the endoral, which is of usual structure. The buccal cavity is very small and flat. This pattern occurs in *Gonostomum* and *Urosoma* and very likely evolved concomitantly with the peculiar shape of their adoral zone (character 1).

Notohymena pattern (Figs. 8, 14): The *Notohymena* pattern differs from the *Oxytricha* state in that the paroral, which is often more distinctly curved, has a hooked distal end bent anteriorly and ventrally. The buccal cavity is moderately wide and rather deep. This pattern occurs only in *Notohymena*.

Cyrtohymena pattern (Figs. 9, 15, 21): This pattern is very prominent, but has often been confused, e.g. by KAHL (1932), with the *Steinia* pattern, because both genera have a very deep and wide buccal cavity. The cavity is bordered by a long paroral whose distal portion is semicircularly curved. The straight anterior part of the endoral extends diagonally on the bottom of the buccal cavity, while its pos-



Figs. 13–18. Characters 1 and 3, shape of adoral zone of membranelles and arrangement of paroral and endoral in oxytrichids after protargol impregnation. Bars = 20 μ m. **13.** Plesiomorphic *Oxytricha* pattern in *Sterkiella histriomuscorum*. The paroral and endoral are slightly curved and intersect optically (arrow). The adoral zone is formed like a question mark as in all derived states, except for the *Gonostomum* pattern (Fig. 16). **14–18.** Derived states. **14.** *Notohymena* pattern in *Notohymena rubescens*. Arrow marks hooked distal end of paroral. From BLATTERER & FOISSNER (1988). **15.** *Cyrtohymena* pattern in *Cyrtohymena quadrinucleata*. The distal portion of the paroral is semicircularly curved and the straight anterior half of the endoral extends diagonally on the bottom of the buccal cavity, while its posterior half is curved and at the right buccal wall and thus intersects optically with the posterior half of the paroral. **16.** *Gonostomum* pattern in *Gonostomum affine*. The proximal part of the adoral zone is abruptly bent towards the body centre (arrow). The paroral consists of few, widely spaced cilia and extends beyond the anterior end of the endoral. **17.** *Stylonychia* pattern in *Stylonychia pustulata*. The paroral and endoral are straight or slightly curved and arranged side by side. From FOISSNER et al. (1991). **18.** *Steinia* pattern in *Steinia sphagnicola*. The sinusoidal endoral is fragmented (arrows) and does not intersect with the curved paroral. The specimen shown has a surplus frontal cirrus (arrowhead). From VOSS & FOISSNER (1995). AZM = adoral zone of membranelles, BC = buccal cirrus, E = endoral, FC = frontal cirri, FVC = frontoventral cirri, LMR = left row of marginal cirri, MA = macronuclear nodule, P = paroral, PTV = pretransverse ventral cirri, RMR = right row of marginal cirri, TC = transverse cirri.



Figs. 19–25. Characters 1 and 3, oral apparatus of oxytrichids in the scanning electron microscope. Bars = 10 μm. **19, 20.** Plesiomorphic *Oxytricha* pattern in *Oxytricha granulifera* and *Sterkiella cavicola*. The slightly curved paroral, which borders the rather flat and narrow buccal cavity, inserts in a narrow furrow of the buccal lip (arrowheads). **21.** *Cyrtohymena* pattern in *Cyrtohymena quadrinucleata*. Note semicircularly curved distal portion of paroral and straight anterior part of endoral extending diagonally on the deep and wide buccal cavity. **22, 23.** *Gonostomum* pattern in *Gonostomum affine*. The paroral consists of few, widely spaced cilia. The endoral, which lies in the very small buccal cavity, is not recognizable. Note the peculiar shape of the adoral zone. Arrowhead marks a food particle. **24.** *Stylonychia* pattern in *Stylonychia mytilus*. The undulating membranes are straight and arranged in parallel. The buccal cavity is flat and wide. **25.** *Steinia* pattern in *Steinia sphagnicola*. The paroral is slightly curved, the endoral is fragmented (arrows) and extends on the bottom of the deep and moderately wide buccal cavity. AZM = adoral zone of membranelles, BC = buccal cirrus, E = endoral, FC = frontal cirri, FVC = frontoventral cirri, LMR = left row of marginal cirri, P = paroral, PVC = postoral ventral cirri.

terior half is curved and at the right buccal wall and thus optically intersects with the posterior portion of the paroral. Consequently, the anterior parts of the membranes form a figure like an archer's bow. This configuration is restricted to *Cyrtohymena*.

Stylonychia pattern (Figs. 11, 17, 24): The paroral and the endoral are straight or very slightly curved and arranged almost in parallel. The buccal cavity is wide and flat. This pattern also occurs in *Coniculostomum*. A very similar configuration is described for the type species of *Onychodromopsis* (PETZ & FOISSNER 1996; Fig. 54). This must be explained as parallelism, because many other significant characters assign this genus as a sistergroup of *Oxytricha* (Figs. 49a, b). However, other *Onychodromopsis* species have the plesiomorphic *Oxytricha*-pattern indicating that this parallelism evolved within *Onychodromopsis*.

Steinia pattern (Figs. 12, 18, 25): *Steinia* has the most complex pattern, not only in oxytrichids but also as compared with the hypotrichs in general. The sinusoidal endoral is fragmented in the middle part and does not intersect with the curved paroral. At the anterior end of the buccal cavity close to the left anterior margin of the endoral there is a unique cavity of unknown function extending to the dorsal surface (Fig. 27). In life, the *Steinia* pattern resembles the *Cyrtohymena* configuration because of the large and bright anteriorly semicircularly excavated buccal field.

There is some evidence that further patterns exist, especially within the genus *Oxytricha*, which is very likely paralog polyphyletic (e.g., *O. siseris* in FOISSNER 1982). Furthermore, the differences mentioned above probably concern not only the shape of the membranes but also their fine structure (FERNANDEZ-LEBORANS 1985; FOISSNER 1995).

Character 4: Frontal cirri (Figs. 1, 13, 25). This group, named anterior frontal cirri by some authors (e.g. FOISSNER & ADAM 1983b), invariably consists of three cirri in the 18 FVT cirri oxytrichids, viz. I/1, II/3, and III/3. Thus, it cannot be used as phylogenetic marker. Usually, the frontal cirri are slightly to distinctly enlarged as compared with the frontoventral cirri (character 6).

BORROR (1972) designated the leftmost frontal cirrus (cirrus I/1) as buccal and later (BORROR 1979; BORROR & WICKLOW 1983) as paroral cirrus because it originates from the same anlage as the undulating membranes (Figs. 1, 26, 33; see character 5 for further details on this confusing terminology). However, a special name for this cirrus seems superfluous, because there are also several other cirri, especially in the opisthe, which originate from the oral primordium (Figs. 38–43).

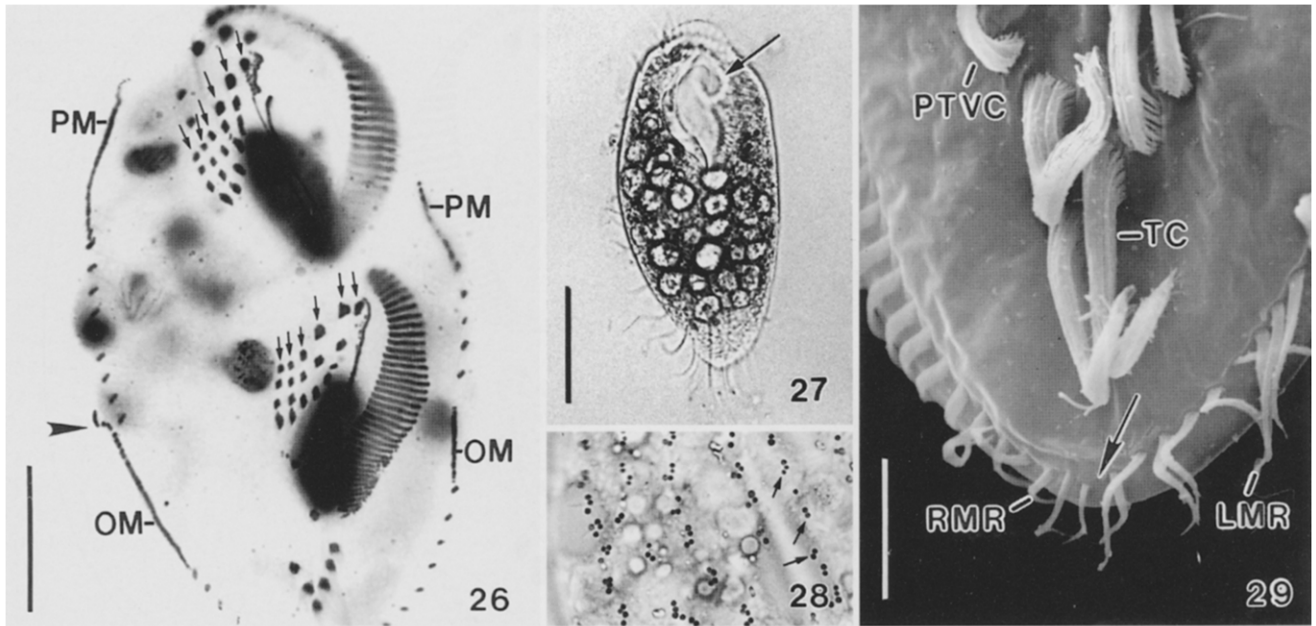
Character 5: Buccal cirrus (Figs. 1, 13, 25). This term is used for cirrus II/2, invariably close to the right and often near the anterior end of the paroral. While its position along the paroral has no cladistic significance, its morphogenetic activity is a valuable apomorphy for some genera (see character 21).

There is great confusion about the terminology of cirrus II/2. BORROR (1972) introduced the term buccal cirrus for cirrus I/1, that is the leftmost frontal cirrus in our terminology (Fig. 1). According to him, the "buccal cirrus" (cirrus I/1) may occur to the immediate right of the paroral, or be located elsewhere near the anterior end of the ventral sur-

face. This is obviously incorrect, because cirrus I/1 is invariably located in front of the undulating membranes and never right of the paroral. Very likely BORROR (1972) confused cirri I/1 and II/2. Furthermore, he erroneously labelled cirrus II/2 as buccal cirrus, and not cirrus I/1, as intended, in his schematic Fig. 1. Presumably, this misleading labelling caused some taxonomists (BUTKAMP 1977a, b; FOISSNER 1982) to use the term buccal cirrus for cirrus II/2, which was not specifically named by either BORROR (1972, 1979) or previous authors. Subsequently, the name buccal cirrus was used in the latter sense by many taxonomists (e.g. FOISSNER 1983a, 1984, 1987b, 1988; FOISSNER & ADAM 1983a, b; BERGER et al. 1985; HEMBERGER 1985; WIRNSBERGER et al. 1985a, b, 1986; GANNER et al. 1987; BERGER & FOISSNER 1988a, b, 1989a; BLATTERER & FOISSNER 1988, 1990; SONG & WILBERT 1989; FOISSNER et al. 1991; VOSS 1991a, b; AUGUSTIN & FOISSNER 1992; VOSS & FOISSNER 1995). The confusion was further increased by BORROR (1979) in that he introduced the term paroral cirrus, a replacement name for "buccal cirrus" (cirrus I/1) sensu BORROR (1972). Finally, BORROR & WICKLOW (1983) introduced the term malar cirrus for cirrus II/2. Thus, malar cirrus is a synonym of our preferred term buccal cirrus. In conclusion, we strongly recommend using descriptive terms concomitantly with the well-established and simple numbering system introduced by WALLENGREN (1900).

Character 6: Frontoventral cirri (Figs. 1, 13, 25). This group comprises four cirri (III/2, IV/3, VI/3, VI/4) between the anterior portion of the right marginal row and the paroral. The V-shaped arrangement shown in Fig. 1 is widespread and thus possibly the plesiomorphic state, as also suggested by the computer generated tree. In *Urosoma* cirrus III/2 is in front of the other three cirri, which thus form a longitudinal row (Fig. 2). No other genus-specific patterns have been distinguished. However, cirrus III/2 shows a tendency to be placed more posteriorly in species having a rigid body, e.g. in *Stylonychia mytilus*, *Steinia* spp., and *Histriculus histrio* (Figs. 3, 18, 31, 62). Furthermore, the frontoventral cirri are displaced posteriorly in *Oxytricha setigera* and related species (FOISSNER 1982; SONG & WILBERT 1989). The frontoventral cirri VI/3 and VI/4, which never form primordia during morphogenesis, are homologous to the migratory cirri (BORROR & WICKLOW 1983; = frontoterminal cirri of HEMBERGER 1985) of the urostylids (WIRNSBERGER et al. 1985a).

Character 7: Postoral ventral cirri (Figs. 1, 4, 19, 20). This term is commonly used for the cirri IV/2, V/3, and V/4, which are underneath the proximal end of the adoral zone. These three cirri form a narrow group close to the buccal vertex in *Oxytricha*, *Onychodromopsis*, *Urosomoida*, *Urosoma*, *Cyrtohymena*, *Notohymena*, and *Tachysoma* (Figs. 51, 53–56, 58–60). By contrast, cirrus V/3 (posterior postoral ventral cirrus) is distinctly separated from the other two cirri in some genera with a rigid body, e.g. *Sterkiella* and *Steinia* (Figs. 1, 65). However, transitions exist and thus this character is of cladistic significance only in *Gonostomum*, where morphogenetic studies (HEMBERGER 1982; SONG 1990) revealed that the postoral ventral cirri are displaced right of the proximal portion of the adoral zone of membranelles (Fig. 4).



Figs. 26–29. Important cladistic characters in oxytrichids. **26.** Ventral ciliature in a late divider of *Stylonychia pustulata* after protargol impregnation. The FVT cirri of oxytrichids originate from six longitudinal anlagen (arrows) segregating 1, 3, 3, 3, 4 and 4 cirri. A dorsomarginal kinety (arrowhead) originates near the anterior end of the opisthe's right marginal row primordium. Bar = 20 μ m. **27.** *Steinia sphagnicola* in vivo showing the extraordinary pit (arrow) in the anterior region of the buccal cavity (character state 3–5). Bar = 50 μ m. **28.** Character 15, cortical granules (arrows). The example shows *Notohymena rubescens* whose granules are about 1 μ m across, spherical and reddish. From BLATTERER & FOISSNER (1988). Most types of cortical granules can be seen in live specimens only. Thus, in vivo observation is indispensable for identification and classification of oxytrichids because cortical granules occur only in the subfamily Oxytrichinae. **29.** Character 11, confluent marginal rows (arrow) in *Histriculus histrio*. Bar = 10 μ m. LMR = left row of marginal cirri, OM = opisthe's primordia of marginal rows, PM = prother's primordia of marginal rows, PTVC = pretransverse ventral cirrus, RMR = right row of marginal cirri, TC = transverse cirri.

Character 8: Pretransverse ventral cirri (Figs. 1, 29). This new term is introduced for ventral cirri V/2 and VI/2, which are in front of the transverse cirri. This state (two cirri), which occurs also in holostichids (FOISSNER 1982, 1984), is very likely plesiomorphic. The loss of one of these cirri, e.g. in *Urosomoida*, is considered an autapomorphy (Fig. 5).

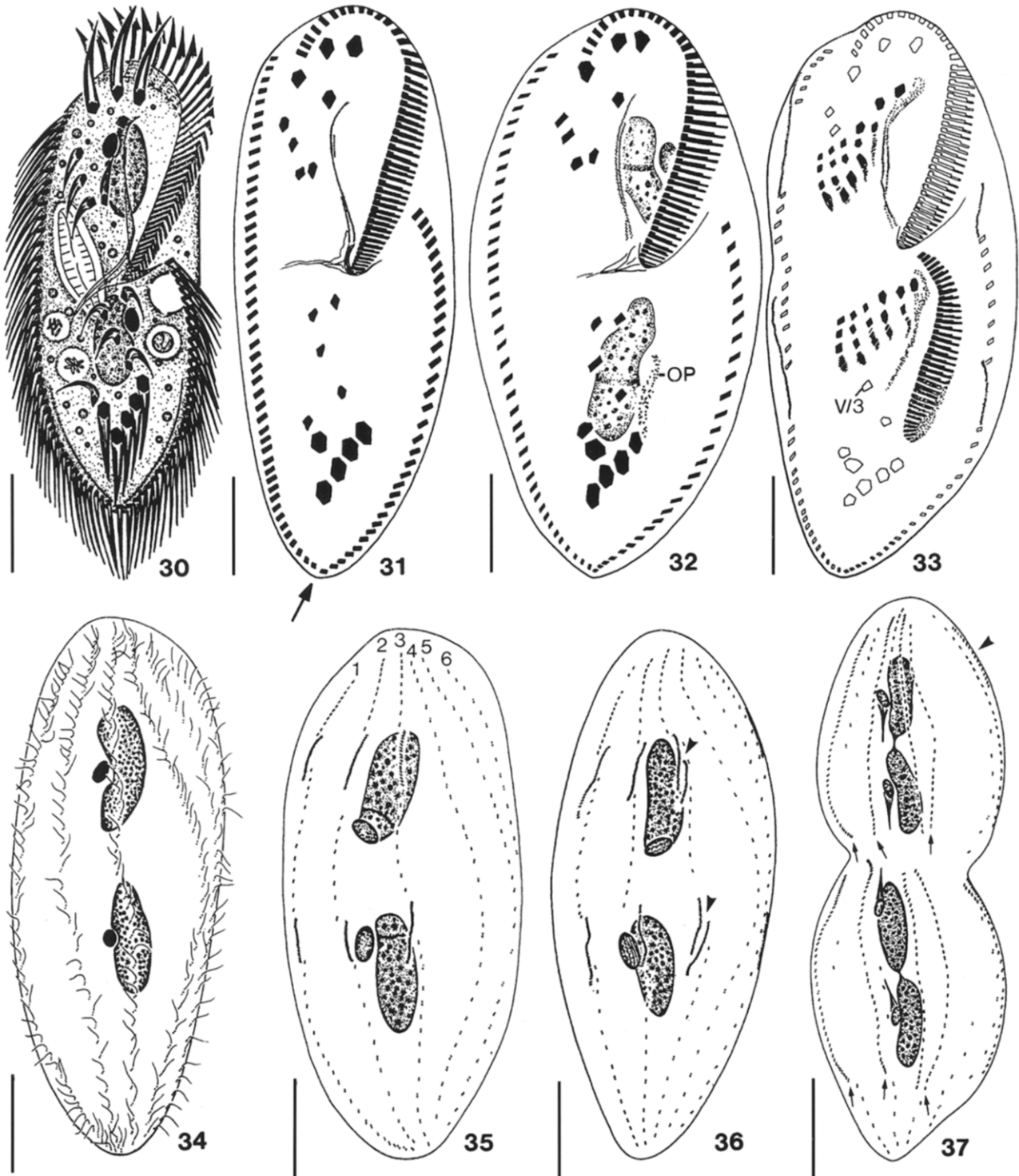
Character 9: Transverse cirri (Figs. 1, 17, 29). This group is in the posterior quarter of the cell. The basic pattern comprises five cirri, namely II/1, III/1, IV/1, V/1, and VI/1. The loss of cirrus II/1 undoubtedly occurred independently in different genera because species with four or five transverse cirri are found even in the same genus, e.g. in *Cyrtohymena*. Thus, only a reduction of the number to ≤ 3 is used as generic autapomorphy. The transverse cirri are often distinctly enlarged as compared with the pretransverse ventral cirri, e.g. in *Histriculus histrio* (Fig. 31) and/or separated into two distinct groups, e.g. in *Stylonychia mytilus*, *Coniculostomum* spp., and *Steinia sphagnicola* (Figs. 61, 62, 64, 65).

Characters 10, 11: Number and arrangement of marginal cirral rows (Figs. 1, 17). Most oxytrichids have one left and one right row of marginal cirri, suggesting this to be the plesiomorphic state. Consequently, an increased number is the

apomorphic configuration which very likely evolved, however, at least twice independently, viz. in genera with a flexible (*Onychodromopsis*, *Parurosoma*; Figs. 54, 56) and a rigid body (*Coniculostomum*, *Pleurotricha*; Figs. 61, 64). Usually, the marginal rows are more or less distinctly separated posteriorly, i.e. not confluent; the gap is often difficult to recognize because it is seemingly occupied by the caudal cirri which, however, insert on the dorsal surface (Fig. 6). Only in *Histriculus* are the marginal rows in fact confluent, suggesting this as derived condition (Figs. 29, 31).

Character 12: Number of dorsal kineties (Fig. 6). Most oxytrichids have five or six dorsal kineties (WIRNSBERGER et al. 1986). Lower or higher numbers are considered to be derived states.

Dorsal kineties consist of basal body pairs. The anterior basal body bears a 2–15 μ m (usually 3–6 μ m) long, stiff cilium, frequently named bristle (GRIMES & ADLER 1976). GÖRTZ (1982) found that the mature dorsal dikinetid of *Stylonychia mytilus* differs from that of *S. pustulata* and *Oxytricha* sp. (GRIMES & ADLER 1976) in that the posterior basal body is reduced to a fibrous structure after cell division. Possibly, this is an autapomorphy of species of the *S. mytilus*-complex; however, data on closely related taxa,



Figs. 30–37. Morphology and morphogenesis of *Histriculus histrio*. Bars = 20 μm. (Fig. 30, from life; 31–37, protargol impregnation). **30, 31, 34.** Ventral and dorsal views of morphostatic specimens. Arrow marks confluent marginal rows (character 11). **32.** Morphogenesis commences with the formation of an oral primordium close to the left transverse cirrus. **33.** Ventral side of a middle divider showing that the posterior postoral ventral cirrus V/3 is not involved in primordia formation. This is the plesiomorphic state of character 19 and thus assigns *Histriculus* unambiguously to the subfamily Stylylonychinae. Parental cirri are depicted by contour, new cirri are shaded black. **35–37.** Morphogenesis of the dorsal ciliature. Arrowheads in Fig. 36 mark fragmenting dorsal kinety 3, arrowhead in Fig. 37 marks proter's dorsomarginal kineties (dorsal kineties 5 and 6). Note that no caudal cirri are formed at the posterior end of the dorsal kineties (arrows), which is the apomorphic condition of character 13. OP = oral primordium, V/3 = posterior postoral ventral cirrus, 1–6 = dorsal kineties.

like *Coniculostomum* and *Steinia*, are needed to evaluate this feature reliably.

Character 13: Caudal cirri (Fig. 6). These are at the posterior margin of the dorsal surface and originate from the end of dorsal kineties 1, 2, and 3 or 4 (see character 23). Since they are widespread in oxytrichids, their presence is considered as plesiomorphy (WIRNSBERGER et al. 1986). Consequently, the absence of caudal cirri in e.g. *Tachysoma* and *Histiculus* is an apomorphy which was, however, obtained independently as suggested by the cladogram (Figs. 49a, b). The relative length of the caudal cirri was used by KAHL (1932) as character for the genera *Opisthotricha* and *Stylonychia*. However, at the present stage of knowledge, the length is of significance for species distinction only.

Character 14: Flexibility of body and body shape. A difference in the flexibility of hypotrichs was already mentioned by STEIN (1859) and later used by KENT (1880–1882), KAHL (1932), BORROR (1972), and SMALL & LYNN (1985) to distinguish several oxytrichids. Suppleness is typical for about half of the oxytrichid genera (e.g. *Oxytricha*, *Tachysoma*, *Notohymena*, *Urosoma*) and also for many (all? except for euplotids and the curious *Psilotricha*; see KAHL 1932 and FOISSNER 1983b) other hypotrichs, indicating that this is the ancestral state. The difference in body flexibility is correlated with ultrastructural specializations, although evidence is still scanty. Oxytrichids with a rigid body have several, in *Stylonychia* arranged crosswise, layers of subpellicular microtubules (PUYTORAC et al. 1976; CALVO et al. 1986), while hypotrichs with a flexible body have only a single sheet of parallel, polar microtubules (GRIMES 1972; WIRNSBERGER-AESCHT & FOISSNER 1989).

The flexibility of the body is of central importance in our cladogram, because it provides rather parsimonious and reasonable trees uniting taxa with considerable morphogenetic similarities, which are, however, plesiomorphic. Admittedly, the flexibility is a difficult character to judge because it is a relative measure often needing the comparison with the extremes on the scale. Flexible hypotrichs bend laterally while moving unhampered on the substratum, when swimming they are often curved and when touching an obstacle their anterior half contracts slightly. Rigid hypotrichs never bend in any direction while creeping and look like a rotating board when swimming.

Most flexible oxytrichids have a slender body, i.e. the ratio of body width to length is <40%, usually about 30%, while it is ≥40% in oxytrichids with a rigid body. Furthermore, tailed species occur only in flexible oxytrichids, especially in *Urosoma*, *Urosomoida*, and *Parurosoma* (Figs. 56, 59).

Character 15: Cortical granules (Fig. 28). These structures, often some sort of extrusome, are of great value for species identification (FOISSNER 1982; BORROR & WICKLOW 1983). They are widespread in hypotrichs and at least one species with cortical granules is known in all flexible oxytrichid genera, suggesting that cortical granules are plesiomorphic. Surprisingly, cortical granules are entirely lacking in rigid oxytrichids. Thus, we consider this character as a useful phylogenetic marker very likely correlated in some way with the cortical fine structure. Obviously, the

granules were lost in the last common ancestor of the rigid oxytrichids.

Character 16: Primary primordia (Fig. 39). *Urosoma* and *Gonostomum* develop long cirral streaks during early morphogenesis (FOISSNER 1983a; SONG 1990). Later, these so-called primary primordia divide transversely to form secondary primordia, i.e. the usual oxytrichid cirral anlagen in proter and opisthe. This type of primordia formation has also been described for *Tachysoma pellationellum*, but not for *T. terricola* (HEMBERGER 1982), suggesting either poly- or paraphyly of *Tachysoma*, or independent evolution of primary primordia in the *Gonostomum-Urosoma* group and *Tachysoma*, respectively. All other oxytrichids develop at least some cirral streaks independently in proter and opisthe. Thus, separated cirral primordia are considered to be the plesiomorphic character state (Fig. 38).

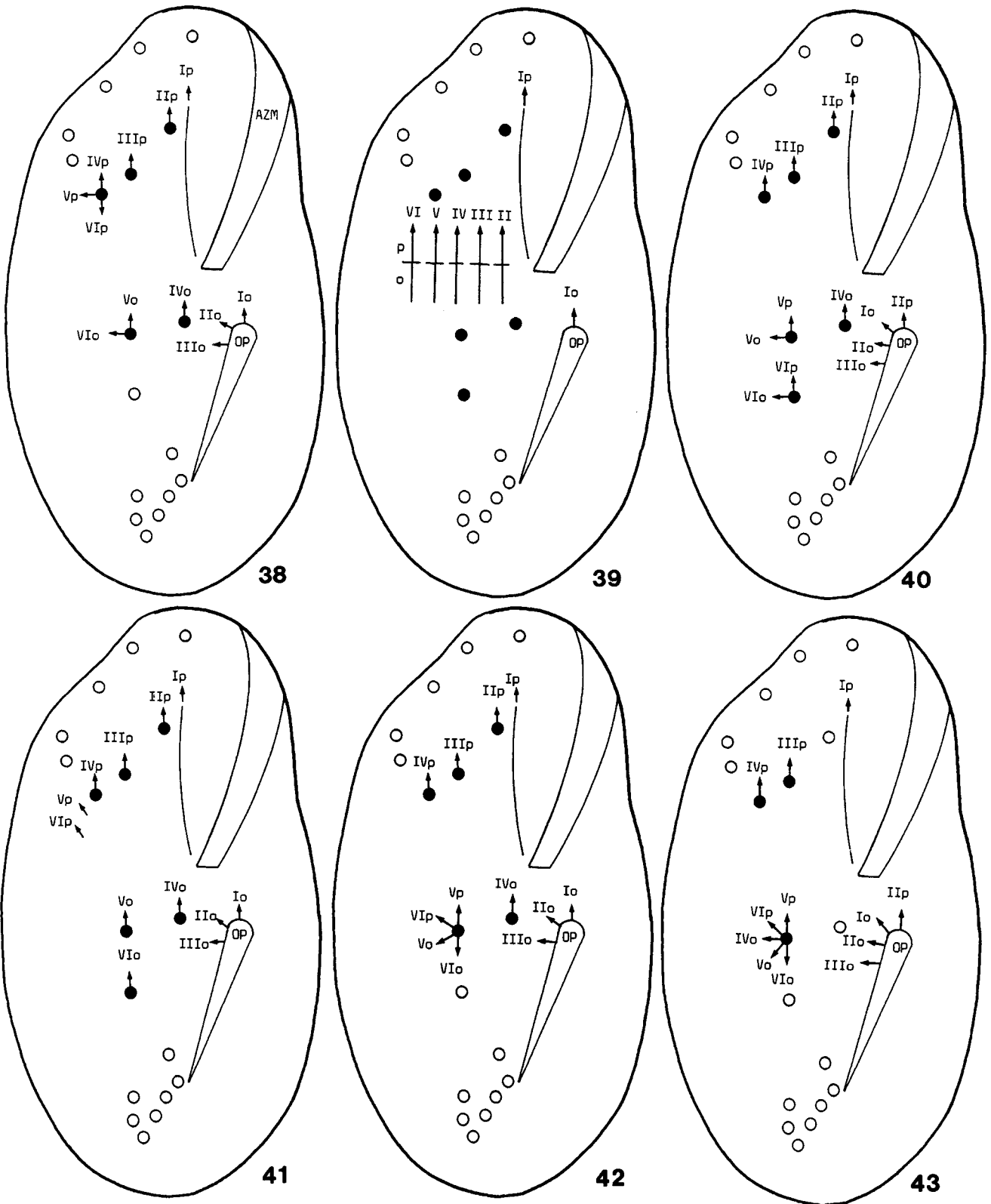
Character 17: Origin of primordia V and VI of the proter. The origin of these anlagen is very likely of great cladistic significance. Four states are recognizable (Table 1).

First state (Table 3 and Fig. 38): Primordia V and VI originate from cirri located in the anterior half of the cell, i.e. from the parental frontoventral cirri III/2 and/or IV/3. This configuration occurs in *Stylonychia pustulata* and *S. vorax*, where both anlagen originate from the parental frontoventral cirrus IV/3. Second state (Table 3 and Fig. 41): In *Urosomoida*, *Notohymena*, and *Cyrtohymena* both primordia are formed de novo. Third state (Table 3 and Fig. 40): In *Oxytricha granulifera*, *O. longa*, and in *Onychodromopsis flexilis* primordium V of the proter originates from the postoral ventral cirrus V/4 and primordium VI from the posterior postoral ventral cirrus V/3. The data on *O. longa* are from the populations 3 and 4 of *Urosomoida agilisformis* sensu GANNER et al. (1987). These populations also have a significantly higher number of pretransverse ventral and transverse cirri than the type populations of *U. agilisformis* (see Table I in GANNER et al. 1987), suggesting that they are not conspecific. Fourth state (Table 3 and Figs. 42, 43): In *Steinia*, *Coniculostomum*, and in species of the *Stylonychia mytilus*-complex, both primordia originate from the postoral ventral cirrus V/4.

It is difficult to ascertain the ancestral and the derived states. We assume that the first state is the plesiomorphic condition, because all primordia of the proter derive from cirri located in the oral half of the cell, i.e. all primordia originate independently in the proter and the opisthe (Fig. 38). This mode is also found in *Paraurostyla* (JERKA-DZIASZ & FRANKEL 1969; WIRNSBERGER et al. 1985b) and *Gastrostyla* (HEMBERGER 1982), members of assemblages branching possibly at the base of the oxytrichids (WIRNSBERGER et al. 1985b, 1986).

Character 18: Origin of primordia V and VI of the opisthe. These primordia usually originate from the postoral ventral cirri. Thus, de novo formation in *Sterkiella cavicola* (F. W., unpubl. data) and, possibly, also in *S. histriomuscorum* (Table 2) have to be considered as a derived condition.

Character 19: Participation of cirrus V/3 in anlagen formation (Table 3 and Figs. 33, 38–43). The cladistic significance of this cirrus was first recognized by WIRNSBERGER et al. (1986). It may or may not be involved in primordia formation. WIRNSBERGER et al. (1986) considered its inactivity



Figs. 38–43. Schematic illustration of characters 16–21, ontogenesis of primordia I–VI. For designation of FVT cirri see Fig. 1. Cirri involved in primordia formation are symbolized by black dots. The direction of the arrows has no meaning. Marginal rows omitted. For details, i.e. definition of states see characters 16–21 and Table 1. **38.** *Stylonychia pustulata* and *S. vorax*. **39.** Primary primordia. This apomorphic type of anlagen formation occurs in *Gonostomum*, *Urosoma*, and

as apomorphy and thus obtained *Stylonychia* and *Sterkiella* as a sister-group. We assume the very opposite using the hypothesis by WIRNSBERGER (1987) that anlagen V and VI of the oxytrichids are homologous to the two posteriormost (rightmost) and morphogenetically inactive anlagen in holostichids. Using holostichids as outgroup, the inactivity of cirrus V/3 is a plesiomorphy, whereas its participation is an autapomorphy, uniting all genera with a flexible cortex. Usually, in these genera cirrus V/3 is arranged very close to the remaining postoral ventral cirri (e.g., Figs. 51, 55).

Character 20: Origin of primordium IV of the opisthe (Table 3 and Figs. 38, 43). This primordium usually originates from postoral ventral cirrus IV/2, indicating that this is the ancestral condition. In *Coniculostomum* and species of the *Stylonychia mytilus*-complex cirrus IV/2 is not involved in primordia formation, and anlage IV of the opisthe originates from the postoral ventral cirrus V/4. Thus, the ontogenetic inactivity of cirrus IV/2 is considered as apomorphy.

Character 21: Origin of primordium II of the proter (Table 3 and Figs. 38, 43). This primordium usually originates from the parental buccal cirrus, suggesting that this mode is plesiomorphic. Only in species of the *Stylonychia mytilus*-complex and in *Coniculostomum* is it generated solely by the oral primordium. However, some participation of the oral primordium in formation of anlage II has been described in *Oxytricha granulifera* and *Sterkiella histriomuscorum* (Table 3).

Character 22: Origin of right marginal cirral rows (Figs. 26, 33). Most oxytrichids have one left and one right marginal row, originating by simple within row formation. Two or more right marginal rows are obtained by two different strategies, viz. by new formation of all marginal rows, e.g. in *Onychodromopsis* (PETZ & FOISSNER 1996), or, as in *Coniculostomum* (KAMRA & SAPRA 1990), by retention of parental marginal rows (Fig. 61).

Character 23: Morphogenesis of the dorsal ciliature (Figs. 44–48). The value of the dorsal morphogenetic patterns for

Table 3. Origin of the FVT primordia in several oxytrichids.

Species (Reference)	Primordium ^a											
	Ip	IIp	IIIp	IVp	Vp	VIp	Io	IIo	IIIo	IVo	Vo	VIo
<i>Urosomoida agilisformis</i> (1)	um	II/2	III/2	IV/3	de novo	de novo	OP	OP	OP	IV/2	V/4	V/3
<i>Urosomoida agilis</i> ^b (2)	um	II/2	III/2	IV/3	de novo	de novo	?	?	?	?	?	?
<i>Cyrtohymena muscorum</i> (3)	um	II/2	III/2	IV/3	de novo	de novo	OP	OP	OP+	OP+	V/3	V/3
									IV/2?	V/4?		
<i>Notohymena rubescens</i> (4)	um	II/2	III/2	IV/3	de novo	de novo	OP	OP	OP	IV/2	V/4	V/3
<i>Oxytricha granulifera</i> (5)	um	II/2 + part of IIo	III/2	IV/3	V/4	V/3	OP	OP	OP	IV/2	V/4	V/3
<i>Oxytricha longa</i> ^c (6)	um	II/2	III/2	IV/3	V/4	V/3	OP	OP	OP	IV/2	V/4	V/3
<i>Onychodromopsis flexilis</i> (7)	um	II/2	III/3	IV/3	V/4	V/3	OP	OP	OP	IV/2	V/4	V/3
<i>Sterkiella histriomuscorum</i> (8)	um	II/2 + part of IIo	III/2	IV/3	IV/3	de novo or part of Vo or VIo ^c	OP	OP	OP	IV/2	V/4 ^d	V/4 ^d
<i>Stylonychia pustulata</i> (9)	um	II/2	III/2	IV/3	IV/3	IV/3	OP	OP	OP	IV/2	V/4	V/4
<i>Stylonychia vorax</i> (9)	um	II/2	III/2	IV/3	IV/3	IV/3	OP	OP	OP	IV/2	V/4	V/4
<i>Steinia sphagnicola</i> (10)	um	II/2	III/2	IV/3	V/4	V/4	OP	OP	OP	IV/2	V/4	V/4
<i>Stylonychia mytilus</i> (11)	um	OP of o	III/2	IV/3	V/4	V/4	OP	OP	OP	V/4	V/4	V/4
<i>Coniculostomum monilata</i> (12)	um	OP of o	III/2	IV/3	V/4 or de novo?	V/4	OP	OP	OP	V/4	V/4 or de novo?	V/4

References: 1 = FOISSNER & ADAM 1983a; 2 = BUITKAMP 1975; 3 = VOSS 1991a; 4 = VOSS 1991b; 5 = FOISSNER & ADAM 1983b; 6 = GANNER et al. 1987; 7 = PETZ & FOISSNER 1996; 8 = BERGER et al. 1985; 9 = WIRNSBERGER et al. 1985a; 10 = VOSS & FOISSNER 1995; 11 = WIRNSBERGER et al. 1986; 12 = KAMRA & SAPRA 1990.

^a Abbreviations: o, opisthe; OP, oral primordium; um, undulating membranes; Io–VIo, primordia I–VI of opisthe; Ip–VIp, primordia I–VI of proter.

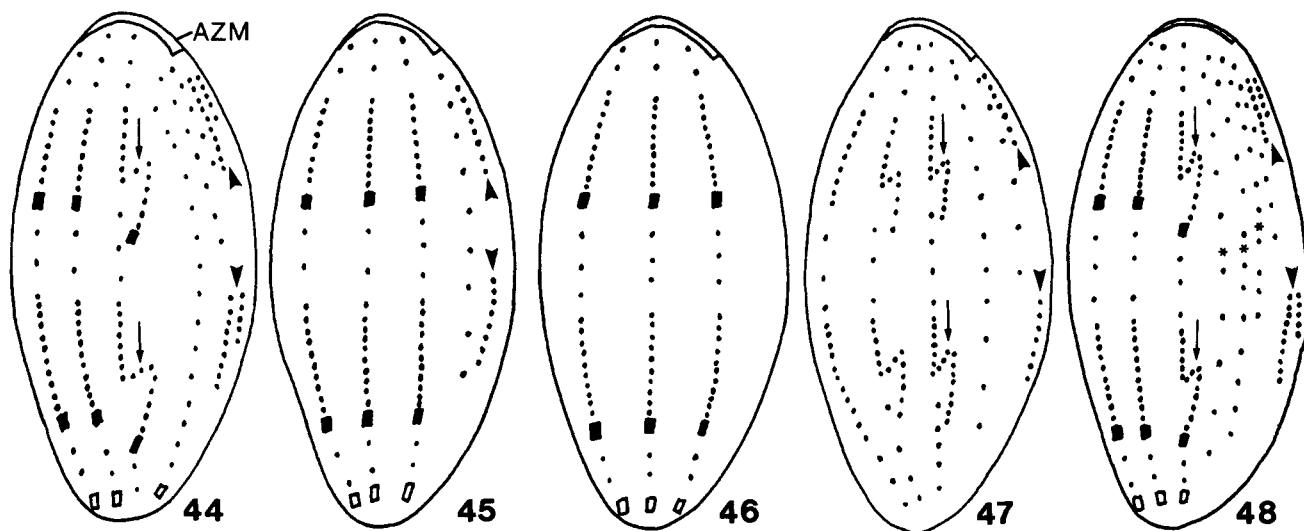
^b The origin was ascertained by BERGER et al. (1985) from Figs. 3 and 4 in BUITKAMP (1975).

^c Possibly originates from cirrus IV/3.

^d In the type species, *Sterkiella cavicola*, primordia Vo and VIo originate de novo (W. F., unpubl. data).

^e Populations 3 and 4 in GANNER et al. (1987).

Tachysoma pellionellum. **40.** *Oxytricha* and *Onychodromopsis*. **41.** *Urosomoida*, *Notohymena*, and *Cyrtohymena*. In *Cyrtohymena* primordium V of the opisthe originates from cirrus V/3 (see Table 3). **42.** *Steinia*. **43.** *Stylonychia mytilus* and *Coniculostomum*. AZM = adoral zone of membranelles, OP = oral primordium, Io–VIo = primordia I–VI of opisthe, Ip–VIp = primordia I–VI of proter.



Figs. 44–48. Schematic illustration of character 23, ontogenesis of the dorsal ciliature in oxytrichids. Arrows mark fragmentation of dorsal kineties, arrowheads denote dorsomarginal kineties. New dorsal kineties narrowly, old (parental) ones widely spaced. Black squares are new caudal cirri, white squares are old ones. **44.** The plesiomorphic *Oxytricha* pattern is characterized by fragmentation of dorsal kinety 3 and formation of one or two dorsomarginal kineties. No parental ciliature is retained after division. **45.** The *Urosomoida* pattern evolved from the *Oxytricha* pattern by the loss of fragmentation in kinety 3 and one of the two dorsomarginal kineties. **46.** The *Gonostomum* pattern evolved from the *Urosomoida* pattern by the loss of the dorsomarginal kinety. **47.** The *Tachysoma pellionellum* pattern evolved from the *Oxytricha* pattern by additional fragmentation of dorsal kinety 2. **48.** The *Coniculostomum* pattern evolved from the *Oxytricha* pattern by retention of some parental kineties (asterisks). AZM = adoral zone of membranelles.

sorting hypotrichs and evaluating their phylogenetic relationships was recognized only recently (MARTIN 1982; FOISSNER & ADAM 1983b; MARTIN et al. 1983). All oxytrichids have at least three dorsal kineties which form an anlage each in the proter and the opisthe by intrakinetal proliferation of basal bodies (Fig. 35). Furthermore, dorsomarginal kineties (MARTIN 1982) originate from or very close to the primordium of the right marginal row (Fig. 26). However, specializations occur and thus five patterns of dorsal ciliature formation can be distinguished in the oxytrichids cladistically analyzed.

Oxytricha pattern (type 4 in FOISSNER & ADAM 1983b; Fig. 44). Kinety 3 fragmentates into two unequal pieces, the posterior one becoming kinety 4, and one or two dorsomarginal kineties are formed. This is the most common and thus very likely plesiomorphic state. It is found in many *Oxytricha* species and in all *Onychodromopsis*, *Notohymentha*, *Cyrtohymentha*, *Sterkiella*, *Histiculus*, *Stylonychia*, and *Steinia* species investigated so far. This type occurs in no other group of hypotrichs, except for *Gastrostyla* and *Paraurostyla* genera usually considered to be closely related to the Oxytrichidae (HEMBERGER 1982; WIRNSBERGER et al. 1985b, 1986; FLEURY et al. 1992).

Urosomoida pattern (type 2 in FOISSNER & ADAM 1983b; Fig. 45). Fragmentation of kinety 3 is lost and only one dorsomarginal kinety is formed. This pattern occurs in the genera *Urosomoida* and *Urosoma* and in some species of the genus *Oxytricha* (e.g., *O. lanceolata*; BERGER & FOISSNER 1989a). These genera are in different clades, indicating that

the loss of the fragmentation was independently achieved three times.

Gonostomum pattern (type 1 in FOISSNER & ADAM 1983b; Fig. 46). New kineties are formed only by intrakinetal proliferation of basal bodies. This strategy is confined to *Gonostomum*, and we assume that it evolved from the *Urosomoida* pattern by the loss of the dorsomarginal kineties.

Tachysoma pattern (Fig. 47). This configuration is unique to *Tachysoma pellionellum*, type of the genus. It differs from the ancestral state in that not only dorsal kinety 3 but also kinety 2 fragmentates. One dorsomarginal kinety is formed, so that altogether six dorsal kineties are obtained as in the ancestral state (HEMBERGER 1982). Unfortunately, this pattern does not match that described for *T. terricola* (HEMBERGER 1982, 1985), which shows the *Oxytricha* pattern, suggesting that *Tachysoma* is not monophyletic.

Coniculostomum pattern (Fig. 48). This pattern is identical to the plesiomorphic state, except that some parental dorsomarginal kineties are retained after division. The retention of a parental dorsal kinety in *Parakahliella*, which very likely belongs to the Kahliellidae (BERGER et al. 1985; BERGER & FOISSNER 1989b; EIGNER 1995), is rather likely a kind of parallelism.

Generally, two trends in dorsal ciliature formation can be observed within the Oxytrichidae. On the one hand a tendency to simplification (loss of fragmentation of dorsal kinety 3 and/or loss of dorsomarginal kineties) in the soft-bodied genera and on the other hand a tendency to complication (multiple fragmentation, retention of parental kine-

ties) in the genera with a rigid body. Very likely, each of the derived states evolved independently from the plesiomorphic *Oxytricha* state – except for the *Gonostomum* pattern which is obviously a transformation of the *Urosomoida* pattern – because no parsimonious tree was obtained if, for instance, the simple *Gonostomum* pattern was used at the base of the cladogram. In this case it has to be assumed that dorsomarginal kineties and fragmentation of dorsal kinety 3 evolved independently at least twice, which is unlikely.

Cladistic analysis

WIRNSBERGER et al. (1986) used HENNIG's cladistic method (HENNIG 1982; AX 1984) to search for the branching sequences of seven common oxytrichid genera (their "oxytrichids s. str."). Since then the number of genera has increased significantly and more data on morphology and morphogenesis became available (BERGER & FOISSNER 1987, 1989a; GANNER et al. 1987; BLATTERER & FOISSNER 1988; FOISSNER 1989; KAMRA & SAPRA 1990; FOISSNER et al. 1991; VOSS 1991a, b; KAMRA et al. 1994; VOSS & FOISSNER 1995). Thus, a new attempt to elucidate the phylogenetic relationships within this family seemed appropriate. We used both the traditional method (Fig. 49a) and a computer program (Fig. 49b). As expected, the results (cladograms) were very similar. Thus, first the hand-generated tree is discussed followed by a discussion of the differences with the computer generated tree.

The autapomorphies of the Oxytrichidae are 18 characteristically arranged and evolving FVT cirri and fragmenting dorsal kineties, as outlined by WIRNSBERGER et al. (1986). Both characters are slightly modified in *Urosomoida*, *Urosoma*, and *Gonostomum*. Some other genera, e.g. *Paraurostyla*, *Gastrostyla*, *Laurentiella*, and *Territricha* have a rather deviating cirral pattern, but fragmentation of dorsal kinety 3 occurs too, strongly suggesting a close relationship with the 18 FVT cirri oxytrichids. Very likely, molecular biological data are needed for a better classification of these genera.

The cladogram based on 21 characters divides the oxytrichids into two major branches, termed *Oxytricha* branch or subfamily Oxytrichinae and *Stylonychia* branch or subfamily Stylonychinae, respectively (Fig. 49a). The other clades are not named because, as is widely known, preliminary cladistic results suffer from the same instability as phenetic or intuitively derived classifications.

The *Oxytricha* branch: This clade is defined by a distinct ontogenetic autapomorphy, the participation of cirrus V/3 in primordia formation (character 19). The *Gonostomum-Urosoma-Tachysoma* lineage has primary primordia (character 16) as the sole synapomorphy.

However, in *Tachysoma* primary primordia occur only in *T. pellionellum*, the type of the genus, and not in *T. terricola*, the second species so far morphogenetically characterized (HEMBERGER 1982). Different strategies not only in the ventral but also in the dorsal morphogenesis suggest that *Tachysoma* is an artificial assemblage unified by the loss of caudal cirri, a character which very likely evolved independently in several oxytrichids, viz. *Tachysoma*, *Histiculus*, *Pleurotricha*, and *Parastylonychia*.

Gonostomum differs the most from the other oxytrichids treated in our paper. It has a peculiar oral apparatus (characters 1, 3) and an unusual position of the postoral ventral cirri right of the adoral zone of membranelles (Figs. 4, 52). Furthermore, the decreased number of transverse cirri and the simplification of dorsal ciliature formation (character state 23-2) are valuable autapomorphies. However, *Gonostomum* has synapomorphies (characters 1, 3, 12, 23) with *Urosoma*, supporting the sister group relationship proposed by FOISSNER (1983a). WIRNSBERGER et al. (1986) ignored the primary primordia (character 16) and the distinctive oral apparatus (characters 1, 3), but used the decreased number of pretransverse ventral and transverse cirri as autapomorphies. Thus, they arrived at *Gonostomum* and *Urosomoida* as sister groups. *Kahliella* (BERGER & FOISSNER 1987) and *Wallackia* (BERGER & FOISSNER 1989a) have a similar oral apparatus as *Gonostomum* and *Urosoma* indicating parallelism or a close relationship of oxytrichids and kahliellids, as recently proposed by EIGNER (1995).

The *Oxytricha-Onychodromopsis-Urosomoida-Notohymena-Cyrtohymena* lineage lacks an autapomorphy, i.e. its monophyly is questionable (Fig. 49a). However, two strong (ontogenetic) apomorphies occur in the following dichotomy, viz. special types of primordia formation (character states 17-1, 17-3), confirmed in seven species including the types. Unfortunately no autapomorphy could be found for *Oxytricha*, indicating an almost unchanged survival of the stem species and/or misidentified states of some characters. The important cladistic characters of *Urosomoida* are the loss of some pretransverse ventral and transverse cirri (characters 8, 9) and the loss of the fragmentation of dorsal kinety 3 (character state 23-1). These reductions also occur in the *Urosoma-Gonostomum* group and must thus be explained in Fig. 49a as parallelisms. We did not find a synapomorphy for the genera *Notohymena* and *Cyrtohymena*. However, both have a valuable autapomorphy, namely a distinctive pattern of the undulating membranes (character 3). Possibly, *Cyrtohymena* differs from *Notohymena* and *Urosomoida* in the origin of the anlagen II–V of the opisthe (Table 3). However, data on other *Cyrtohymena* species are needed to evaluate the significance of this difference.

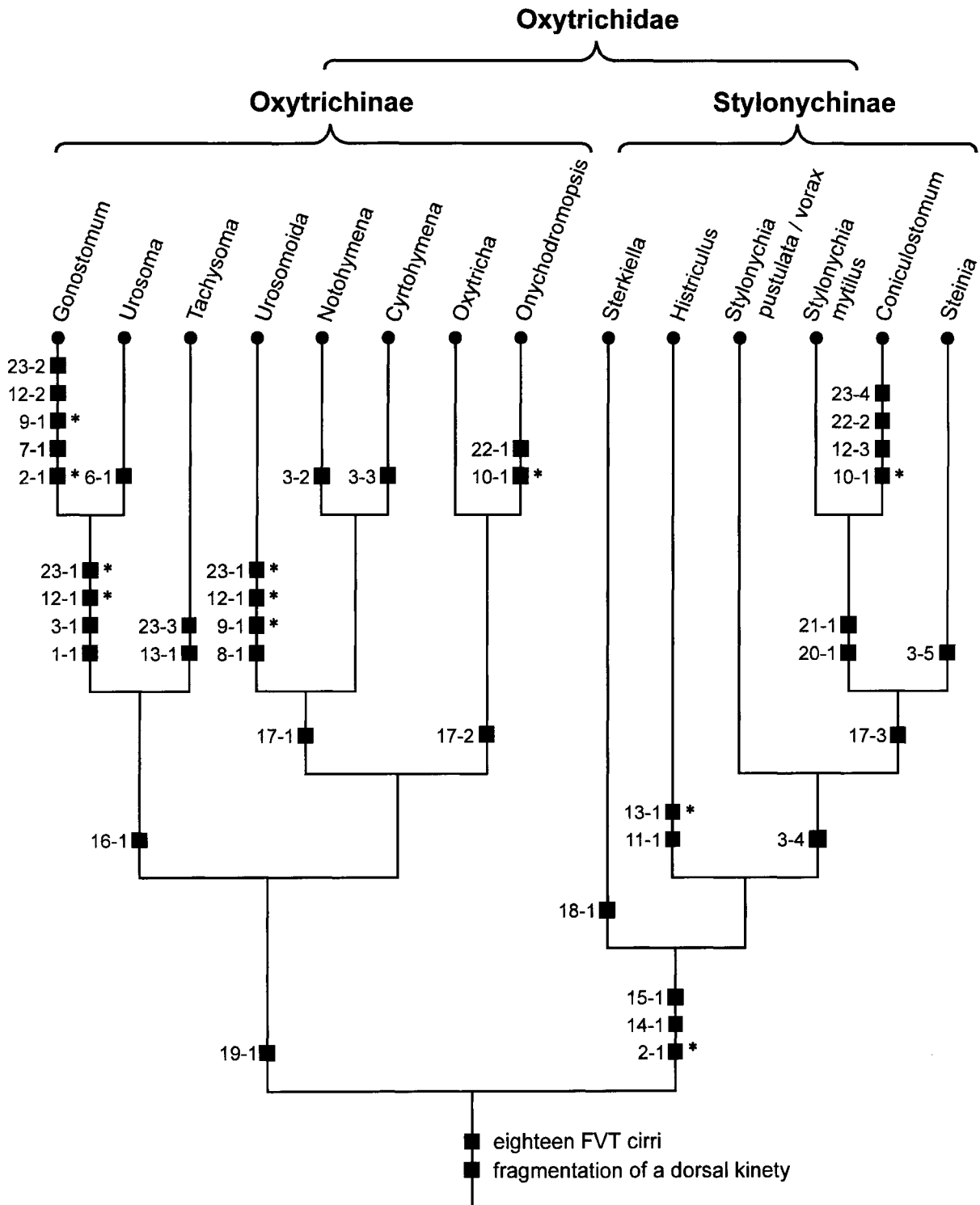


Fig. 49a. Cladogram of common oxytrichid genera generated by the traditional method. Character states see Table 1 and section on characters and character states. Only autapomorphies (black squares) are shown. Parallelisms are starred.

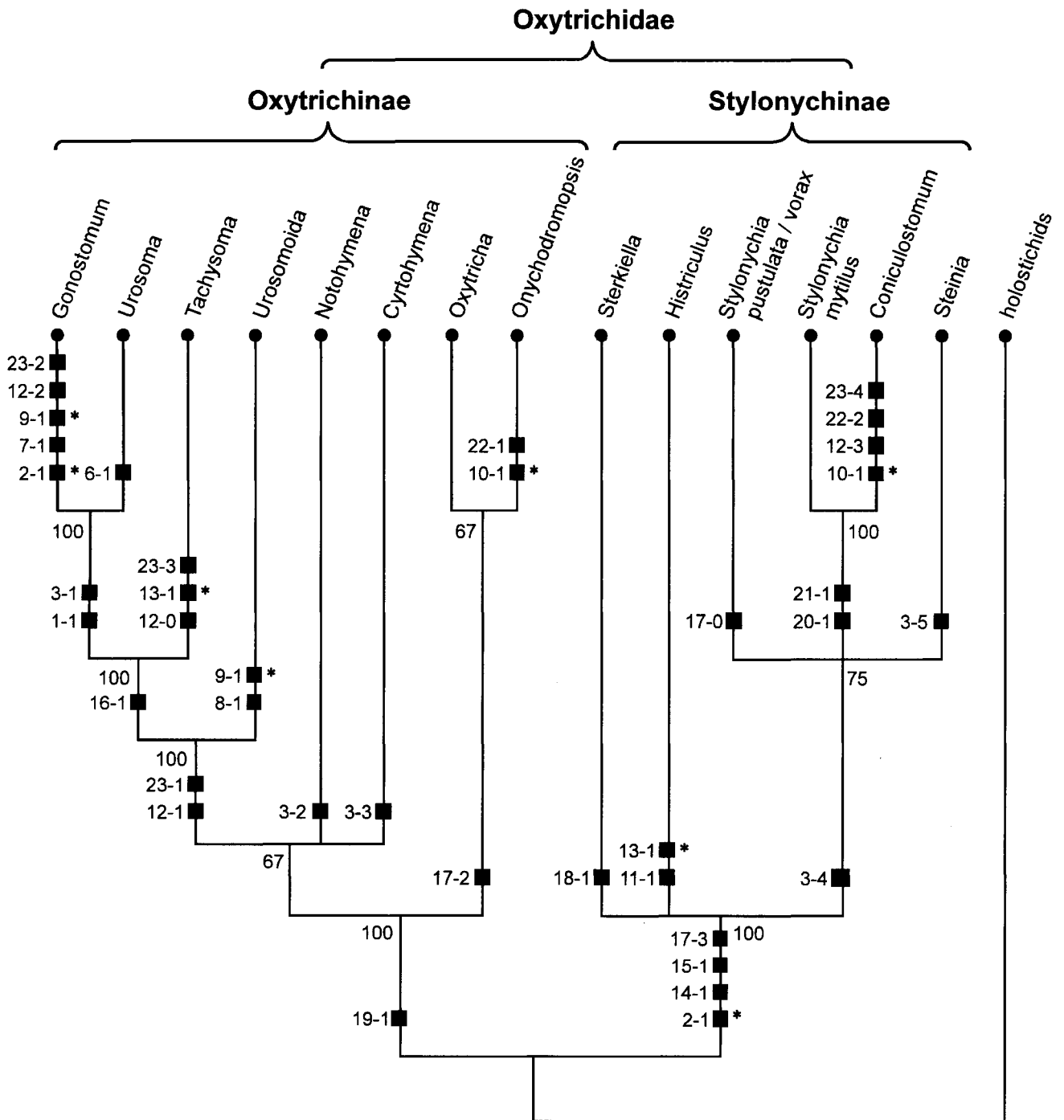


Fig. 49b. Cladogram of common oxytrichid genera generated by computer analysis. The tree is the 50% majority-rule consensus of 72 trees. Length = 39 steps, RC = 0.94, RI = 97. Only autapomorphies are shown. Parallelisms are starred.

The *Stylonychia* branch: This clade (subfamily) is characterized by three autapomorphies, viz. the long oral apparatus (character 2), the rigid body (character 14), and the lack of cortical granules (character 15). Admittedly, these are not very strong characters, but we were unable to find better ones. However, the distinction is strongly supported by molecular biological data which show that *Oxytricha granulifera* (our *Oxytricha* branch) is distinctly separated from *Stylonychia pustulata*, *Onychodromus quadricornutus*, and "*Oxytricha nova*" (which is in fact a *Sterkiella*; PRESCOTT, D. M. & FOISSNER, W., unpubl data), taxa having a rigid cortex and thus belonging to our *Stylonychia* branch.

Sterkiella is well defined by a unique, but sophisticated combination of morphological characters (body rigid or only slightly flexible, undulating membranes bent and intersecting, marginal rows separated posteriorly, caudal cirri present). However, the only autapomorphy we could find is the de novo formation of primordia V and VI of the opisthe (character 18).

Character 11, confluent marginal rows (Fig. 29), is a valuable autapomorphy of *Histriculus*. It is the last genus within the *Stylonychia* branch with the plesiomorphic *Oxytricha* pattern of undulating membranes. However, *Pleurotricha* (excluded from the cladogram because of insufficient morphogenetic data) shows the same membrane pattern (Fig. 64) and also lacks caudal cirri (character 13), indicating a sister group relationship between *Histriculus* and *Pleurotricha*.

The *Stylonychia-Coniculostomum-Steinia* group is characterized by parallel undulating membranes (character state 3–4). The cladogram reveals some peculiarities within this group: 1) *Stylonychia pustulata* and *S. vorax* are distinctly separate from the type species, *S. mytilus*, suggesting that *Stylonychia* is diphyletic. This is supported by molecular biological data (SCHLEGEL & STEINBRÜCK 1986); 2) *Steinia* is very likely the sister group of *S. mytilus* and *Coniculostomum*, because they share a peculiar morphogenetic feature, viz. primordia V and VI of the proter originate from cirrus V/4 (character 17-3). This is why we assume that the *Steinia* pattern of the undulating membranes (character state 3-5) is a transformation of the *Stylonychia* pattern (see character discussion). The peculiar fragmentation of the endoral in *Steinia* is one of the most impressive autapomorphies within the oxytrichids (Fig. 18); 3) *Stylonychia mytilus* is very likely more closely related to *Coniculostomum* (KAMRA et al. 1994) than to *S. pustulata*, because of the identical origin of the FVT cirri primordia (Table 3 and Figs. 38, 43). This is sustained by their almost identical interphasic FVT cirral patterns (Figs. 61, 62). Thus, the classification of *Coniculostomum* in the Kahliellidae (EIGNER 1995), based solely on the retention of some parental ciliature after division, is very likely artificial. It is highly unlikely that the distinctive 18 cirral pattern

and morphogenesis found in *Stylonychia mytilus* and *Coniculostomum* evolved convergently. Autapomorphies of *Coniculostomum* are the moniliform macronucleus and an increased number of marginal rows and dorsal kineties due to retention of parental cirri (characters 10, 22) and dorsomarginal kineties after division (characters 12, 23; KAMRA et al. 1994).

Computer analysis using successive weighting yields 72 most parsimonious trees, which is high and largely due to the great number of parallelisms in combination with a rather low number of characters. However, the 50% majority consensus tree (Fig. 49b) is rather similar to that constructed by hand (Fig. 49a), especially concerning the basic branching into the monophyla Oxytrichinae and Stylonychinae. Furthermore, the branching sequence within the Stylonychinae is identical. Only character 17 is differently used, viz. state 17-3 is considered as further apomorphy of the Stylonychinae and state 17-0 as apomorphy of the *Stylonychia pustulata/vorax* group.

The branching sequence in the Oxytrichinae is slightly different from the hand-generated tree, mainly due to the different use of characters 16, 17, and 23. However, this is not surprising because we were unable to define conclusively the plesiomorphic and apomorphic states of these characters. The program assumes that fragmentation of dorsal kinety (character 23) was reduced only once, thus forming a *Gonostomum-Urosoma-Tachysoma-Urosomoida* group. However, this implies that fragmentation occurred again in *Tachysoma*. Conversely, we preferred the hypothesis that fragmentation of dorsal kineties evolved only once, assuming that loss of fragmentation occurred twice, namely in *Urosomoida* and in the *Gonostomum-Urosoma* group. As in the Stylonychinae, character 17 is also differently used in the Oxytrichinae, viz. de novo formation (state 17-1) is assumed as plesiomorphic within the oxytrichids.

Characterization of the family Oxytrichidae, its subfamilies and genera

In this section traditional diagnoses are provided for the 18 FVT cirri oxytrichids we assign to the family. Still, some genera are not defined by a unique (autapomorphic) character but by a specific combination of plesiomorphies, i.e. their monophyly and/or genus status are questionable. Thus, and because we did not name and characterize the sister groups of the two main branches obtained in the cladograms, the characterization of a genus includes all features necessary to separate it from the other genera of the subfamily it belongs to. Consequently, genus comparison is restricted to similar genera from the other subfamily with which it can be confused by non-specialists. Genera are arranged alphabetically within the subfamilies.

Family Oxytrichidae EHRENBERG, 1838

Characterization: Euhypotrichina with flexible or rigid body and usually 18 FVT cirri clustered to six distinct groups. The FVT cirri originate from six longitudinal primordia segregating 1, 3, 3, 3, 4, 4 cirri. Six or less parental FVT cirri participate in primordia formation. At least one fragmenting dorsal kinety.

Type genus (original designation): *Oxytricha* BORY DE SAINT-VINCENT in LAMOUROUX, BORY DE SAINT-VINCENT & DESLONGCHAMPS, 1824.

Remarks: JANKOWSKI (1979) split the Oxytrichidae into three subfamilies, viz. Oxytrichinae (type *Oxytricha*), Ancystropodiinae (type *Ancystropodium*), and Psammomitriinae (type *Psammomitra*). The Oxytrichinae include all 18 FVT cirri oxytrichids, the Ancystropodiinae are monotypic, and the Psammomitriinae are an artificial assemblage including poorly known genera, some of which have been assigned to other families. Thus, we establish a new subfamily for the oxytrichids of the *Stylonychia* branch.

Subfamily Oxytrichinae JANKOWSKI, 1979

Characterization: Oxytrichidae with flexible body. Cirrus V/3 participates in primordia formation. Often with distinct cortical granules.

Type genus (original designation): *Oxytricha* BORY DE SAINT-VINCENT in LAMOUROUX, BORY DE SAINT-VINCENT & DESLONGCHAMPS, 1824.

Remarks: This subfamily contains the genera *Cyrtohymena*, *Gonostomum*, *Notohymena*, *Onychodromopsis*, *Oxytricha*, *Tachysoma*, *Urosoma*, and *Urosomoida*. Very likely, *Paruosoma*, *Pseudostrombidium*, and *Australocirrus oscitans* also belong to this assemblage, because they have a flexible body. However, this has to be confirmed by morphogenetic studies.

- *Australocirrus* BLATTERER & FOISSNER, 1988 (Fig. 50)

Improved characterization: Adoral zone of membranelles formed like a question mark. Undulating membranes in *Oxytricha* pattern. Frontoventral cirri form V-shaped pattern. Postoral ventral cirri underneath buccal vertex. Two pretransverse ventral and five transverse cirri. One right and one left row of marginal cirri. More than six dorsal kineties. Caudal cirri present. Dorsal morphogenesis in *Oxytricha* pattern, however, kinety 3 not with simple but with multiple fragmentation.

Type species (original designation): *Australocirrus oscitans* BLATTERER & FOISSNER, 1988.

Remarks: The two species known show multiple fragmentation of dorsal kinety 3, but differ significantly in body flexibility. In the very flexible *A. oscitans* cirrus V/3 is involved in primordia formation (W. F., unpubl.

data), supporting the classification in the *Oxytricha* branch. By contrast, the body of *A. octonucleatus* is rigid, indicating some relationship with *Sterkiella*; however, *Sterkiella* has simple fragmentation of dorsal kinety 3.

- *Cyrtohymena* FOISSNER, 1989 (Fig. 51)

Improved characterization: Adoral zone of membranelles formed like a question mark. Undulating membranes in *Cyrtohymena* pattern. Frontoventral cirri form V-shaped pattern. Postoral ventral cirri in dense cluster underneath buccal vertex. Two pretransverse and five (rarely four) transverse cirri. One right and one left row of marginal cirri. Usually six dorsal kineties. Caudal cirri present. Primordia V and VI of proter originate de novo. Dorsal morphogenesis in *Oxytricha* pattern.

Type species (original designation): *Oxytricha (Steinia) muscorum* KAHL, 1932.

Remarks: This genus is well defined and easily identified by the wide, deep and thus very transparent buccal cavity. However, some species (e.g., *C. quadrinucleata*, *C. tetracirrata*, *C. primicirrata*) deviate from the majority in that the body is rather inflexible, the relative length of the adoral zone is 40–50% of body length, and postoral ventral cirrus V/3 is distinctly displaced posteriorly, indicating that it is not involved in primordia formation. Thus, *Cyrtohymena* is very likely not monophyletic. By non-specialists in vivo easily confused with *Steinia* which has, however, a very rigid body and a peculiar pit in the buccal cavity (Fig. 27, arrow).

- *Gonostomum* STERKI, 1878 (Fig. 52)

Synonymy: *Plagiotricha* KENT, 1882 (type species by original designation): *Oxytricha strenua* ENGELMANN, 1862.

Improved characterization: Adoral zone of membranelles and undulating membranes in *Gonostomum* pattern. Frontoventral cirri in V-shaped pattern. Postoral ventral cirri right of adoral zone. Fewer than four transverse cirri. One right and one left row of marginal cirri. Three dorsal kineties. Caudal cirri present. Primary primordia. Dorsal morphogenesis in *Gonostomum* pattern.

Type species (original designation): *Oxytricha affinis* STEIN, 1859.

Remarks: *Gonostomum* is sometimes classified outside the oxytrichids, viz. in the Holostichidae (CORLISS 1979; TUFFRAU 1987) or Gonostomatidae (SMALL & LYNN 1985). However, ventral morphogenesis shows that *Gonostomum* evolved very likely from 18 FVT cirri oxytrichids (BORROR 1972; FOISSNER 1982; HEMBERGER 1982; SONG 1990; TUFFRAU & FLEURY 1994). In vivo easily distinguished from almost all genera (except the sister group *Urosoma*) of the oxytrichids by the dis-

tinctive shape of the adoral zone of membranelles and the widely spaced cilia of the paroral (Figs. 16, 22, 23). These characters are strongly reminiscent of *Kahliella* and *Wallackia* (BERGER & FOISSNER 1989a), which have, however, many more cirral rows. The type species, *Gonostomum affine*, is the most common hypotrich in soil (FOISSNER 1987c).

- *Notohymena* BLATTERER & FOISSNER, 1988 (Fig. 53)

Improved characterization: Adoral zone of membranelles formed like a question mark. Undulating membranes in *Notohymena* pattern. Frontoventral cirri in V-shaped pattern. Postoral ventral cirri in dense cluster underneath buccal vertex. Two pretransverse ventral and five transverse cirri. One right and one left row of marginal cirri. Six dorsal kineties. Caudal cirri present. Primordia V and VI of proter originate de novo. Dorsal morphogenesis in *Oxytricha* pattern.

Type species (original designation): *Notohymena rubescens* BLATTERER & FOISSNER, 1988.

Remarks: The cladistically significant character, viz. the hook-shaped distal end of the paroral, is recognizable only after protargol impregnation (Fig. 14). *Sterkiella* and *Steinia* have a broader and more rigid body. In addition, *Notohymena* species possess distinct cortical granules, organelles lacking in all genera of the subfamily Stylonychinae.

- *Onychodromopsis* STOKES, 1887 (Fig. 54)

Improved characterization: Adoral zone of membranelles formed like a question mark. Undulating membranes rather straight and arranged side by side or in *Oxytricha* pattern. Frontoventral cirri in V-shaped pattern. Postoral ventral cirri in dense cluster underneath buccal vertex. Two pretransverse ventral and five transverse cirri. Two or more right and one or more left rows of marginal cirri. Caudal cirri present. Primordia V and VI of the proter originate from cirrus V/4 and V/3, respectively. No parental marginal rows retained after division. Dorsal morphogenesis in *Oxytricha* pattern.

Type species (by monotypy): *Onychodromopsis flexilis* STOKES, 1887.

Remarks: *Onychodromopsis* has been rather differently classified, e.g. as incertae sedis in the Sporadotrichina (CORLISS 1979), in the Holostichidae (TUFFRAU 1987), in the Amphisiellidae (SMALL & LYNN 1985; TUFFRAU & FLEURY 1994), or as synonym of *Pleurotricha* (BORROR 1972), which has, however, a rigid body and lacks caudal cirri. The reinvestigation of the type species revealed that *Onychodromopsis* is very likely the sister group of *Oxytricha* (PETZ & FOISSNER 1996). *Onychodromopsis flexilis* has undulating membranes arranged almost in parallel (Fig. 54), indicating that a *Stylonychia*-like pattern evolved also in the

Oxytrichinae. However, other *Onychodromopsis* species have the plesiomorphic *Oxytricha* pattern. *Onychodromopsis* is easily confused with *Paraurostyla*, because of the increased number of cirral rows (FOISSNER et al. 1991).

- *Oxytricha* BORY DE SAINT-VINCENT in LAMOUROUX, BORY DE SAINT-VINCENT & DESLONGCHAMPS, 1824 (Fig. 55)

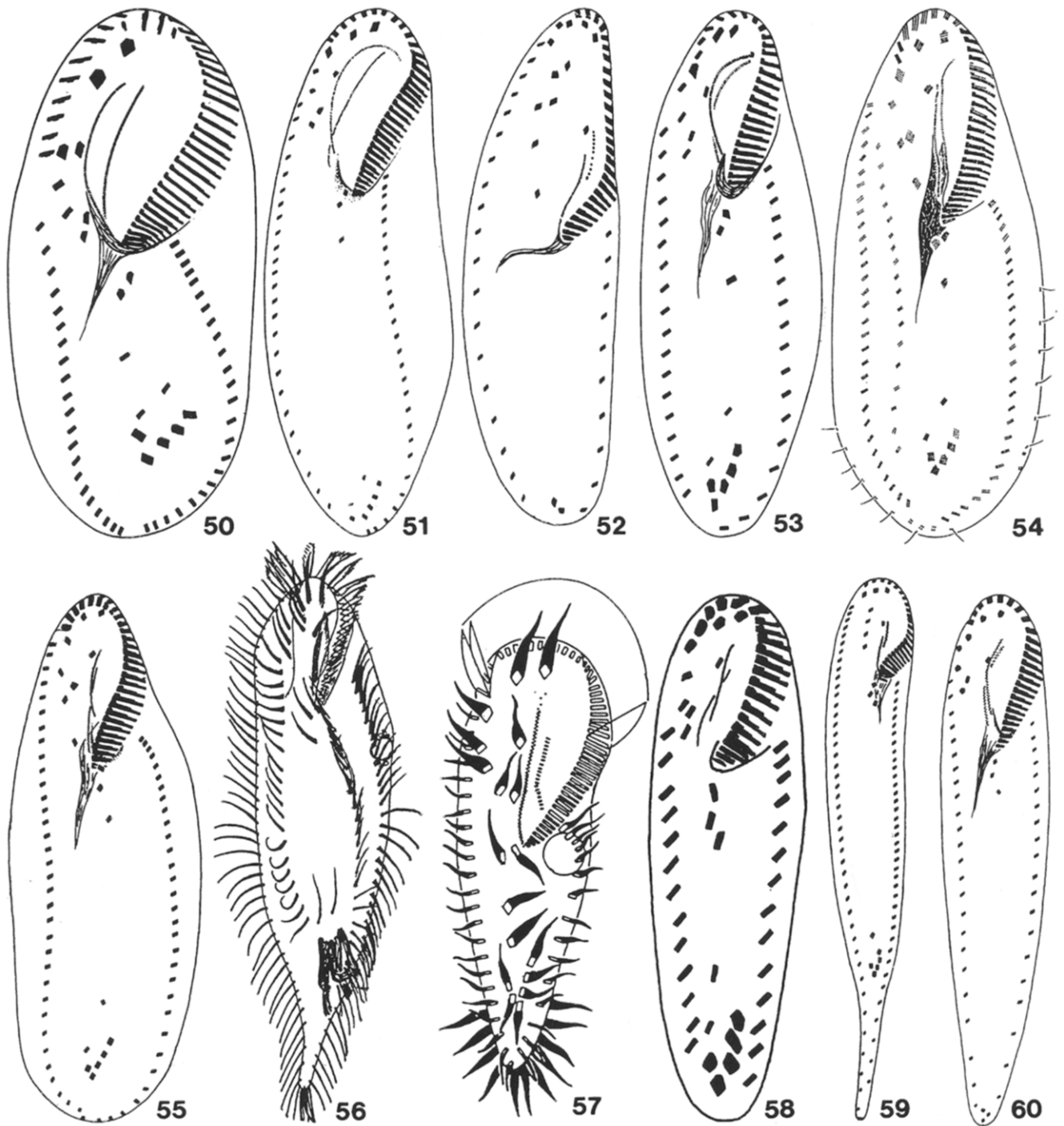
Synonymy: *Oxitricha* BORY DE SAINT-VINCENT in LAMOUROUX et al., 1824 (no type species fixed, see remarks); *Actinotricha* COHN, 1866 (type species by monotypy: *Actinotricha saltans* COHN, 1866); *Opisthotricha* KENT, 1882 (type species by original designation: *Oxytricha parallela* ENGELMANN, 1862).

Improved characterization: Adoral zone of membranelles formed like a question mark. Undulating membranes in *Oxytricha* pattern. Frontoventral cirri in V-shaped pattern. Postoral ventral cirri in dense cluster underneath buccal vertex. Two pretransverse ventral and five, rarely four transverse cirri. One right and one left row of marginal cirri. Usually five or six, rarely four dorsal kineties. Caudal cirri present. Primordia V and VI of the proter originate from cirrus V/4 and V/3, respectively. Dorsal morphogenesis in *Oxytricha* or *Urosomoida* pattern.

Type species (subsequent designation by FOISSNER 1989): *Oxytricha granulifera* FOISSNER & ADAM, 1983b.

Remarks: BORY DE SAINT-VINCENT in LAMOUROUX et al. (1824) used the spelling *Oxitricha* when establishing the genus. The first reviser (EHRENBERG 1838) changed it to *Oxytricha*, subsequently accepted by all revisers (KAHL 1932; BORROR 1972; CORLISS 1979). For a detailed discussion of the rather complicated type species problem, see FOISSNER (1989).

Oxytricha is the most voluminous genus within the oxytrichids, comprising about 50 valid species and about 60 species indeterminata (H. B., unpubl. data). Only a quarter of the valid species has been described in detail. *Actinotricha* is a little known genus which has been synonymized with *Tachysoma* (BORROR 1972) and *Oxytricha* (SONG et al. 1991). Very likely, it is closely related to the *O. setigera* group because the frontoventral cirri are distinctly displaced posteriorly. *Opisthotricha* was established for *Oxytricha* species with long caudal cirri (KENT 1880–1882). However, this feature is valuable for species distinction only. Non-specialists easily confuse *Oxytricha* with the stylonychid genera *Sterkiella* (body only slightly flexible, posterior postoral ventral cirrus V/3 distinctly separated from cirri V/4 and IV/2; see the "*Oxytricha nova*" problem mentioned in the introduction), *Histriculus* (body very rigid, confluent marginal rows, no caudal cirri) and *Stylonychia* (body very rigid, undulating



Figs. 50–60. Ventral infraciliature (protargol impregnation unless otherwise indicated) of type species of genera assigned to subfamily Oxytrichinae. **50.** *Australocirrus oscitans*, 205 μm . From BLATTERER & FOISSNER (1988). **51.** *Cyrtohymena muscorum*, 145 μm . From BERGER & FOISSNER (1989a). **52.** *Gonostomum affine*, 70 μm . From FOISSNER (1982). **53.** *Notohymena rubescens*, 90 μm . From BLATTERER & FOISSNER (1988). **54.** *Onychodromopsis flexilis*, 155 μm . From PETZ & FOISSNER (1996). **55.** *Oxytricha granulifera*, 85 μm . From FOISSNER & ADAM (1983b). **56.** *Parurosoma dubium*, 215 μm ; mercuric chlorid fixation. From GELEI (1954). **57.** *Pseudostrombidium planctonicum*, 200 μm . From WILBERT (1986). **58.** *Tachysoma pellionellum*, 50 μm . Original. **59.** *Urosoma cienkowskii*, 105 μm . From FOISSNER (1982). **60.** *Urosomoida agilis*, 90 μm . From BERGER & FOISSNER (1987).

membranes side by side) where cirrus V/3 is, however, not involved in primordia formation.

• *Parurosoma* GELEI, 1954 (Fig. 56)

Improved characterization: Adoral zone of membranelles, undulating membranes, and frontoventral cirri similar to in *Urosoma*. Postoral ventral cirri in dense cluster underneath buccal vertex. Two pretransverse ventral and five transverse cirri. Two right and two left rows of marginal cirri. Four, sometimes five dorsal kineties. Caudal cirri present. Dorsal morphogenesis very likely in *Urosomoida* pattern.

Type species (by monotypy): *Holosticha* (*Parurosoma*) *dubium* GELEI, 1954.

Remarks: Monotypic, i.e. includes only the type species, which has to be redescribed in detail. GELEI (1954) classified *Parurosoma* as subgenus of *Holosticha*. Thus, CORLISS (1979) and TUFFRAU (1987) included it in the family Holostichidae. BORROR (1972) synonymized it with *Pleurotricha*, which has, however, a rigid body and lacks caudal cirri.

• *Pseudostrombidium* HORVÁTH, 1933 (Fig. 57)

Improved characterization: Adoral zone of membranelles formed like a question mark. Undulating membranes almost straight and side by side. Frontoventral cirri in V-shaped pattern. Postoral ventral cirri underneath buccal vertex. Two pretransverse ventral and five transverse cirri. One right and one left row of marginal cirri. Six dorsal kineties. Number of caudal cirri distinctly increased (>4). Dorsal morphogenesis in *Oxytricha* pattern.

Type species (by monotypy): *Pseudostrombidium planctonicum* HORVÁTH, 1933.

Remarks: Monotypic, i. e. includes only the euplanktonic type species. KAHL (1932) obviously confused *Pseudostrombidium* with *Parastrombidium* (FRAURÉ-FREMIET 1924), an oligotrich. BORROR (1972) synonymized *P. planctonicum* with *Urosoma acuminata* which is clearly different (FOISSNER 1982; BERGER & FOISSNER 1987). According to the original description and a recent redescription (WILBERT 1986), the undulating membranes are rather straight and do not intersect, similarly to in *Stylonychia* (Fig. 57). However, the micrographs of a protargol impregnated specimen in SKIBBE (1994) indicate an oral apparatus of the *Oxytricha* pattern. Differs from *Stylonychia* spp. not only by the supple body but also by the significantly higher number of caudal cirri. Morphogenetic studies are necessary to clarify the systematic position of this curious oxytrichid.

• *Tachysoma* STOKES, 1887 (Fig. 58)

Improved characterization: Adoral zone of membranelles formed like a question mark. Undulating

membranes in *Oxytricha* pattern. Frontoventral cirri in V-shaped pattern. Postoral ventral cirri in dense cluster underneath buccal vertex. Two pretransverse ventral and five transverse cirri. One right and one left row of marginal cirri. Four to six dorsal kineties. Caudal cirri absent. FVT-cirri originate from primary primordia or separate anlagen. Dorsal morphogenesis in *Tachysoma*, *Oxytricha*, or *Urosomoida* pattern.

Type species (subsequent designation by BORROR 1972): *Trichoda pellationella* MÜLLER, 1773.

Remarks: Very likely an artificial assemblage of flexibleoxytrichids without caudal cirri. The type species is one of the most common oxytrichids in freshwater (FOISSNER et al. 1991). *Histiculus* also lacks caudal cirri, but is broader and much more rigid.

• *Urosoma* KOWALEWSKIEGO, 1882 (Fig. 59)

Improved characterization: Adoral zone of membranelles and undulating membranes in *Gonostomum* pattern. Frontoventral cirri arranged in a row with anterior cirrus usually slightly displaced to left. Postoral ventral cirri in dense cluster underneath buccal vertex. Two pretransverse ventral and five transverse cirri. One right and one left row of marginal cirri. Four dorsal kineties. Caudal cirri present. Primary primordia. Dorsal morphogenesis in *Urosomoida* pattern.

Type species (by monotypy): *Urosoma cienkowskii* KOWALEWSKIEGO, 1882.

Remarks: Most species assigned to this genus are slender and posteriorly more or less distinctly narrowed. However, the only autapomorphy we could find is the arrangement of the frontoventral cirri (Fig. 2). The same pattern occurs in some species originally assigned to the genera *Perisincirra* (*P. similis* FOISSNER, 1982) and *Hemisincirra* (*H. polynucleata* FOISSNER, 1984). This character and the agreements in the oral apparatus and dorsal infraciliature indicate that they might belong to *Urosoma*, although the FVT cirri underneath the adoral zone are partially or completely reduced. Very likely, *P. similis* and *H. polynucleata* form a distinct clade in *Urosoma*. Alive and in protargol slides, *Urosoma* is easily distinguished from all genera of the subfamily Stylonychinae by the short (<30% of body length) adoral zone of membranelles and the slender body.

• *Urosomoida* HEMBERGER in FOISSNER, 1982 (Fig. 60)

Improved characterization: Adoral zone of membranelles formed like a question mark. Undulating membranes in *Oxytricha* pattern. Frontoventral cirri in V-shaped pattern. Postoral ventral cirri in dense cluster underneath buccal vertex. One pretransverse ventral cirrus and less than four transverse cirri. One right and one left row of marginal cirri. Four dorsal kineties. Caudal cirri present. Primordia V and VI of the proter origi-

nate de novo. Dorsal morphogenesis in *Urosomoida* pattern.

Type species (original designation): *Uroleptus agilis* ENGELMANN, 1862.

Remarks: FOISSNER (1982) published the diagnosis proposed by HEMBERGER (1982) verbatim. Thus, the appropriate citation of the genus is "HEMBERGER in FOISSNER 1982" (article 50a of the ICZN 1985). Some species can be confused with *Sterkiella* spp., which have, however, a broader and less flexible body. Often difficult to separate from *Oxytricha*.

Subfamily Stylonychinae n. subfam.

Characterization: Oxytrichidae with rigid body. Cirrus V/3 not involved in primordia formation.

Type genus: *Stylonychia* EHRENBERG, 1830.

Remarks: This subfamily includes the genera of the *Stylonychia* branch in our cladograms (Figs. 49a, b), viz. *Coniculostomum*, *Histriculus*, *Steinia*, *Sterkiella*, and *Stylonychia*. Furthermore, *Parastylonychia* and *Pleurotricha* are assigned to this subfamily because they have a rigid body, a rather unique character within the euhypotrichs. The other two autapomorphies shown in the cladogram, the relative length ($\geq 40\%$) of the adoral zone and the lack of cortical granules are rather weak and were thus not used in the characterization. Very likely, *Onychodromus*, *Laurentiella*, and *Pattersoniella* belong to this subfamily, too (see section genera not considered). Their exact position within the cladogram is, however, beyond the scope of the present paper.

- *Coniculostomum* NJINE, 1979 (Fig. 61)

Synonymy: *Laurentiella* (*Laurosticha*) JANKOWSKI, 1979 (type species by original designation: *Laurentia monilata* DRAGESCO & NJINE, 1971).

Improved characterization: Undulating membranes in *Stylonychia* pattern. Two or more right and one or more left marginal rows, distinctly separate posteriorly. More than six dorsal kineties. Caudal cirri present and usually distinctly elongated. Primordium II of the proter originates from oral primordium. Primordia V and VI of the proter and primordium IV of the opisthe originate from postoral ventral cirrus V/4. Parental marginal cirri partially retained after division. Dorsal morphogenesis in *Coniculostomum* pattern.

Type species (by monotypy): *Laurentia monilata* DRAGESCO & NJINE, 1971.

Remarks: The subgenus *Laurosticha* JANKOWSKI, 1979 was published in the same year as *Coniculostomum* which prevailed. The oxytrichid lineage of this peculiar genus was recognized only recently by detailed morphogenetic studies (KAMRA & SAPRA 1990; KAMRA et al. 1994) showing several conspicuous synapomorphies

with the *Stylonychia mytilus*-complex. Thus, a classification within the kahliellids (EIGNER 1995), based solely on the retention of parental marginal rows and dorsal kineties, is very likely artificial.

- *Histriculus* CORLISS, 1960 (Fig. 31)

Synonymy: *Histrio* STERKI, 1878 (type species by original designation: *Histrio steinii* STERKI, 1878, a junior synonym of *Histriculus histrio*); (?) *Parahistriculus* GROLIÈRE, 1975 (type species by monotypy: *Parahistriculus minimus* GROLIÈRE, 1975).

Improved characterization: Undulating membranes in *Oxytricha* pattern. One right and one left row of marginal cirri, posteriorly confluent. Six dorsal kineties. Caudal cirri absent. Dorsal morphogenesis in *Oxytricha* pattern.

Type species (original designation): *Paramaecium histrio* MÜLLER, 1773.

Remarks: *Histrio* STERKI is a junior homonym replaced by CORLISS (1960). *Parahistriculus minimus* GROLIÈRE, 1975 differs in the dorsal pattern (four kineties only), so that the synonymy is questionable. *Oxytricha* and related genera have a very supple and slender body, open marginal rows, and caudal cirri.

- *Parastylonychia* DRAGESCO, 1963 (Fig. 63)

Improved characterization: Undulating membranes in *Stylonychia* pattern. One right and one left row of marginal cirri, distinctly separate posteriorly. Caudal cirri absent.

Type species (by monotypy): *Parastylonychia plouneouri* DRAGESCO, 1963.

Remarks: Monotypic i.e. includes only the type species. A detailed redescription and morphogenetic data are required for a more exact classification of this marine species.

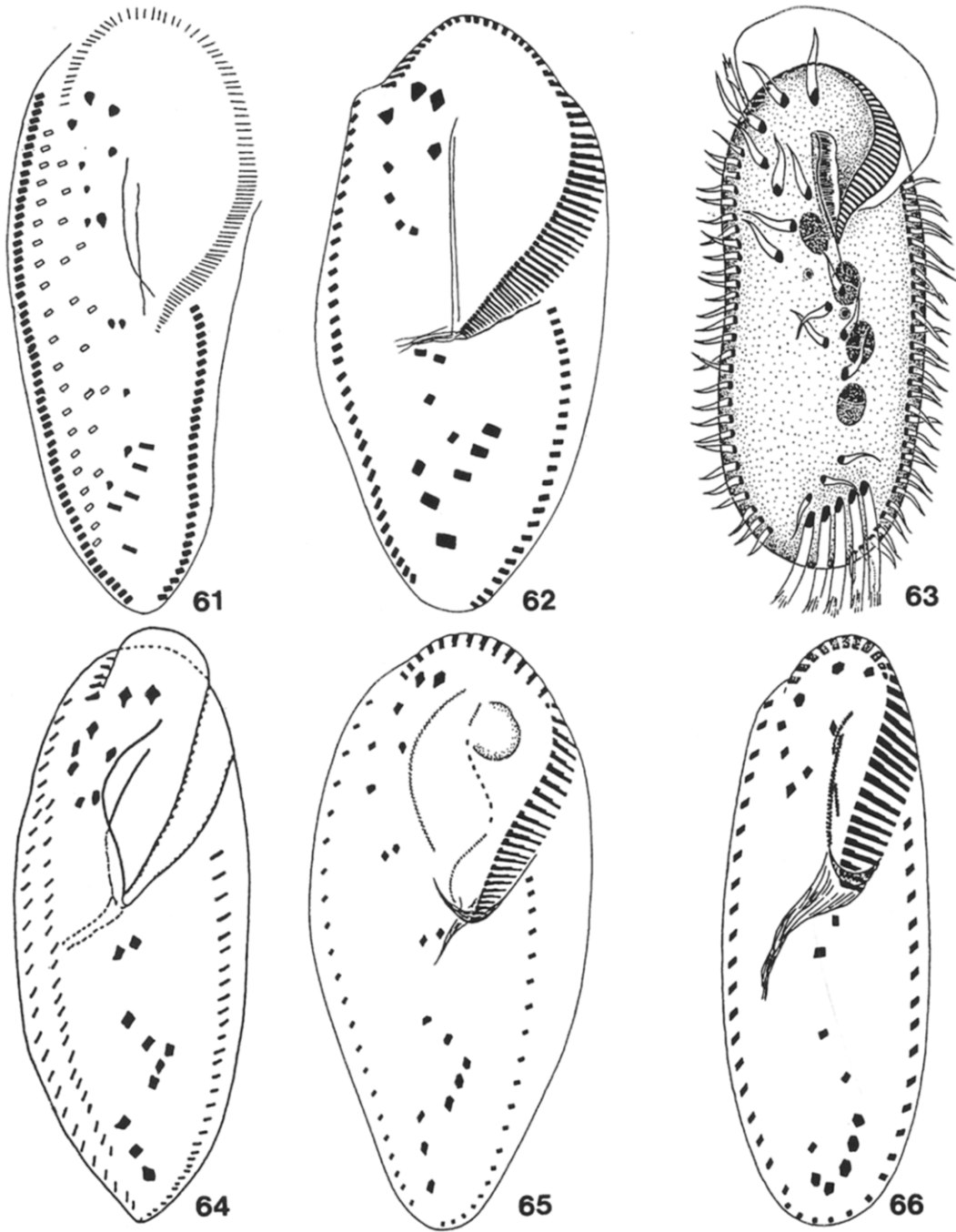
- *Pleurotricha* STEIN, 1859 (Fig. 64)

Synonymy: *Allotricha* STERKI, 1878 (type species by original designation: *Allotricha mollis* STERKI, 1878, a nomen nudum species).

Improved characterization: Undulating membranes in *Oxytricha* pattern. Two or more right and one or more left rows of marginal cirri. Caudal cirri absent. No parental marginal cirri retained after division. Dorsal morphogenesis in *Oxytricha* pattern.

Type species (original designation): *Stylonychia lanceolata* EHRENBERG, 1835.

Remarks: The inner right marginal row of the type species develops according to character state 22-1 (Table 1; BORROR & WICKLOW 1982). In contrast, in *Coniculostomum* parental right marginal cirri are retained and form some inner right marginal rows (KAMRA & SAPRA 1990). Detailed morphogenetic studies are necessary to clarify the position of *Pleurotricha*



Figs. 61–66. Ventral infraciliature (protargol impregnation) of type species (except of Figs. 65, 66) of genera assigned to subfamily Stylonychinae. *Histiculus histrio* see Fig. 31. **61.** *Coniculostomum monilata*, 285 μm . From KAMRA & SAPRA (1990). Marginal cirri retained from previous generations are depicted by contour. **62.** *Stylonychia mytilus*-complex, 180 μm . From WIRNSBERGER et al. (1986). **63.** *Parastylonychia plouneouri*, 200 μm . From DRAGESCO (1963). **64.** *Pleurotricha lanceolata*, 105 μm . From JEFFRIES & MELLOTT (1968). **65.** *Steinia sphagnicola*, 140 μm . From FOISSNER (1989). **66.** *Sterkiella histriomuscorum*, 65 μm . From FOISSNER (1982). The type of this genus, *S. cavicola*, is shown in Fig. 1.

within the cladogram. Possibly, it is closely related to *Histiculus* because of the lack of caudal cirri. *Onychodromopsis* and *Parurosoma* have a more slender and supple body and caudal cirri.

- *Steinia* DIESING, 1866 (Fig. 65)

Improved characterization: Undulating membranes in *Steinia* pattern. One right and one left row of

marginal cirri, distinctly separate posteriorly. Caudal cirri present. Six dorsal kineties. Primordia V and VI of the proter and opisthe originate from postoral ventral cirrus V/4. Dorsal morphogenesis in *Oxytricha* pattern.

Type species (subsequent designation by FOISSNER 1989): *Oxytricha platystoma* EHRENBERG, 1831.

Remarks: By non-specialists in vivo easily confused with *Cyrtohymena* because the large buccal cavity is transparent in both genera. However, *Cyrtohymena* lacks the small pit in the buccal cavity (Fig. 27, arrow) and usually has a more flexible body.

- *Sterkiella* FOISSNER, BLATTERER, BERGER & KOHMANN, 1991 (Figs. 1, 66)

Improved characterization: Undulating membranes in *Oxytricha* pattern. One right and one left row of marginal cirri, distinctly separate posteriorly. Six dorsal kineties. Caudal cirri present. Primordia V and VI of the opisthe originate de novo. Dorsal morphogenesis in *Oxytricha* pattern.

Type species (original designation): *Oxytricha cavicola* KAHL, 1935.

Remarks: *Sterkiella histriomuscorum* is very common in freshwater and soil (FOISSNER et al. 1991) and has often been misidentified as *Oxytricha* sp. because it is not as rigid as the other members of the Stylonychinae. The autapomorphy (character 18) has been confirmed in the type species only (W. F., unpubl. data).

- *Stylonychia* EHRENBERG, 1830 (Fig. 62)

Improved characterization: Undulating membranes in *Stylonychia* pattern. One right and one left row of marginal cirri, distinctly separate posteriorly. Six dorsal kineties. Caudal cirri present and often distinctly elongated. Primordium II of the proter originates from oral primordium. Primordia V and VI of the proter originate from frontoventral cirrus IV/3 or from postoral ventral cirrus V/4. Primordium IV of the opisthe originates from postoral ventral cirrus V/4. Dorsal morphogenesis in *Oxytricha* pattern.

Type species (subsequent designation by FROMENTEL 1875): *Trichoda mytilus* MÜLLER, 1773.

Remarks: Morphogenetic (characters 17, 20, 21) and molecular biological data (SCHLEGEL & STEINBRÜCK 1986) suggest that *Stylonychia* is not monophyletic (Figs. 49a, b). However, molecular biological data on the closely related genera *Steinia* and *Coniculostomum* should be awaited before splitting. In vivo, small species, for instance the very common *S. pustulata*, are easily confused with *Oxytricha* spp., which have, however, a more slender and flexible body and intersecting undulating membranes.

Key to oxytrichid genera

For definition of term see section characters and Figs. 1, 6. Many characters can be recognized by careful examination of living specimens with differential interference contrast. However, this requires a lot of experience. Thus, we base the key mainly on characters recognizable after protargol impregnation, a well-known and widely used technique for identifying ciliates (FOISSNER 1991). Keys for the most common freshwater oxytrichid species are found in KAHL (1932), FOISSNER et al. (1991, 1995), and FOISSNER & BERGER (1996). Species with distinct cortical granules (Fig. 28) belong to the subfamily Oxytrichinae.

1. One right and one left row of marginal cirri (Fig. 1) . . . 5
 - Two or more right and one or more left rows of marginal cirri 2
2. Caudal cirri¹⁾ present 3
 - Caudal cirri¹⁾ absent *Pleurotricha* (Fig. 64)
3. Body tailed *Parurosoma* (Fig. 56)
 - Body not tailed 4
4. Adoral zone of membranelles about 50 % of body length. Macronucleus moniliform. Body rigid
 - *Coniculostomum* (Fig. 61)
 - Adoral zone of membranelles <35% of body length. Two macronuclear nodules. Body supple
 - *Onychodromopsis* (Fig. 54)
5. Undulating membranes in *Steinia* pattern (Figs. 12, 18, 25) *Steinia* (Fig. 65)
 - Undulating membranes not as above 6
6. Undulating membranes in *Cyrtohymena* pattern (Figs. 9, 15, 21) *Cyrtohymena* (Fig. 51)
 - Undulating membranes not as above 7
7. Undulating membranes in *Notohymena* pattern (Figs. 8, 14) *Notohymena* (Fig. 53)
 - Undulating membranes not as above 8
8. Undulating membranes and adoral zone of membranelles in *Gonostomum* pattern (Figs. 4, 10, 16, 22) 9
 - Undulating membranes and adoral zone not as above 10
9. Adoral zone of membranelles <30% of body length. Four dorsal kineties *Urosoma* (Fig. 59)
 - Adoral zone of membranelles 40–50% of body length. Three dorsal kineties *Gonostomum* (Fig. 52)
10. Undulating membranes in *Stylonychia* pattern (Figs. 11, 17, 24) 11
 - Undulating membranes in *Oxytricha* pattern (Figs. 1, 7, 13, 19) 12
11. Caudal cirri¹⁾ present (Fig. 6) *Stylonychia* (Fig. 62)
 - Caudal cirri¹⁾ absent *Parastylonychia* (Fig. 63)
12. Caudal cirri¹⁾ present (Fig. 6) 14
 - Caudal cirri¹⁾ absent 13

¹⁾ Sometimes difficult to distinguish from marginal cirri, which usually insert more ventrally than caudal cirri (Fig. 6). Most easily recognizable in late dividers having the caudal cirri still attached to certain dorsal kineties (Fig. 44).

13. Marginal rows distinctly separate posteriorly. Body supple *Tachysoma* (Fig. 58)
 - Marginal rows confluent posteriorly (Figs. 29, 31). Body rigid *Histiculus* (Fig. 31)
14. Number of pretransverse ventral and transverse cirri usually <6 (Fig. 5). Four dorsal kineties *Urosomoida* (Fig. 60)
 - Two pretransverse ventral and four or five transverse cirri (Fig. 1). Usually five or more dorsal kineties .. 15
15. Number of caudal cirri¹) distinctly increased (10–20) forming rather dense corona at rounded posterior end of organism *Pseudostrombidium* (Fig. 57)
 - Usually three caudal cirri¹) 16
16. Dorsal kinety 3 with multiple fragmentation, i.e. more than six dorsal kineties *Australocirrus* (Fig. 50)
 - Five (rarely four) to six dorsal kineties 17
17. Adoral zone of membranelles ≤35% of body length. Postoral ventral cirri form narrow group close beneath buccal vertex. Ratio of body width to length <40%, usually about 30%. Body supple .. *Oxytricha* (Fig. 55)
 - Adoral zone of membranelles ≥40% of body length. Postoral ventral cirrus V/3 distinctly set off from the other two postoral cirri (Figs. 1, 66). Ratio of body width to length ≥40%. Body rigid or slightly flexible *Sterkiella* (Figs. 1, 66)

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