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Evolution of ciliary patterns in the Oligotrichida (Ciliophora, Spirotricha) and its taxonomic implications

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Abstract

Although the somatic ciliature of the Oligotrichida typically comprises only a girdle and ventral kinety, a considerable diversity of ciliary patterns occurs. The four main girdle kinety patterns are identically found in tailed and tail-less species. The contractile tail has a complicated and unique ultrastructure and is potentially useful for the cell's movement and/or stabilization during feeding. Accordingly, I assume that this structure has evolved only once, namely, in the Tontoniidae nov. fam., and that the different girdle kinety patterns developed convergently in the tailed and tail-less taxa. Further distinct features suggest the establishment of the families Cyrtostrombidiidae nov. fam. (with cyrtos-like pharyngeal fibres and lack of ventral membranelles and endoral) and Pelagostrombidiidae nov. fam. (with neoformation organelle). An attempt is made to reconstruct the evolution of the kinety patterns based on morphologic, ontogenetic, and ultrastructural data. Some genera of tail-less Oligotrichida base on differences in the ciliary pattern;

Omegastrombidium nov. gen. is erected for a further girdle kinety pattern. Likewise, the tailed genus *Tontonia* is split, resulting in two new genera, viz., *Pseudotontonia* nov. gen. and *Spirotontonia* nov. gen. Furthermore, the genus *Spirostrombidium* is split due to the different origin of the parallel course of girdle and ventral kinety, and *Parallelostrombidium* nov. gen. is established. However, the genus *Thigmostrombidium* is rejected because its enlarged thigmotactic membranelles are interpreted as an adaptation to the benthic lifestyle, which occurred several times within different girdle kinety patterns.

Keywords

Oligotrichida; Ciliophora; Protozoa; Ciliary patterns; New genera; New families

Introduction

The Oligotrichida are usually assigned to the Spirotricha. In contrast to the related hypotrichs and stichotrichs, the somatic ciliature of the Oligotrichida is highly reduced, typically comprising only two ciliary rows with short cilia: the girdle kinety and the ventral kinety. Nevertheless, the diversity of ciliary patterns created by these two rows is considerable. Identical girdle kinety patterns occur in species with and without a tail, enlarged membranelles, a cyrtos, or a neoformation organelle. This raises questions of how these patterns evolved and whether the girdle kinety patterns or the other features developed convergently. In the present paper, an attempt is made to reconstruct the evolution of the girdle kinety patterns based on morphologic, ontogenetic, and ultrastructural data from ~120 oligotrichid species. Furthermore, the significance of the tail, the enlarged membranelles, the

cyrtos, the neoformation organelle, and the ciliary patterns for the classification of the Oligotrichida is evaluated.

At the present state of knowledge, the phylogeny of oligotrichid ciliates can only poorly be inferred from gene sequences due to the lack of sufficient data (Modeo et al., 2003; Agatha et al., 2004). Therefore, the proposed evolution of the ciliary patterns might significantly contribute to the elucidation of the oligotrichid evolution.

Materials and methods

Data acquisition

Since (i) the most recent review of the Oligotrichida by Maeda and Carey (1985) does not include all data provided in the original descriptions and (ii) a monograph comprising the many recent descriptions and redescrptions of oligotrichid ciliates is lacking, the original literature was used (Fauré-Fremiet, 1912, 1950; Penard, 1922; Kahl, 1933; Alekperov, 1985; Corliss and Snyder, 1986; Dragesco and Dragesco-Kernéis, 1986; Lynn et al., 1988; Montagnes and Lynn, 1988; Montagnes et al., 1988, 1990; Foissner et al., 1991; Krainer, 1991; Alekperov and Mamajeva, 1992; Petz and Foissner, 1992; Lynn and Gilron, 1993; Martin and Montagnes, 1993; Montagnes and Taylor, 1994; Petz, 1994; Song et al., 1994; Krainer, 1995; Petz et al., 1995; Agatha and Riedel-Lorjé, 1997; Alekperov and Asadullayeva, 1997; Song and Packroff, 1997; Montagnes and Humphrey, 1998; Song and Bradbury, 1998; Foissner et al., 1999; Lei et al., 1999a, b; Song et al., 2000; Suzuki and Han, 2000; Suzuki and Song, 2001; Kim et al., 2002; Montagnes et al., 2002; Agatha, 2003; Granda and Montagnes, 2003; Modeo et al., 2003; Agatha et al., 2004; and references in Maeda and Carey, 1985). However, only sufficiently known genera were considered, i.e., *Cyrtostrombidium* Lynn and Gilron, 1993, *Laboea* Lohmann, 1908, *Limnostrombidium* Krainer, 1995, *Novistrombidium* Song and Bradbury, 1998, *Pelagostrombidium* Krainer, 1991, *Spirostrombidium* Jankowski, 1978, *Strombidium* Claparède and Lachmann, 1859, *Thigmotrombidium* Jankowski, 1978, and *Tontonia* Fauré-Fremiet, 1914. Other genera, such as *Echinostrombidium* Jankowski, 1978, *Lissostrombidium* Jankowski, 1978, *Metastrombidium* Fauré-Fremiet, 1924, *Peristrombidium* Jankowski, 1978, and *Seravinella* Alekperov and Mamajeva, 1992, were excluded as their type species are insufficiently known. Data on oligotrichid ontogenesis are comparatively rare (Fauré-Fremiet, 1912; Anigstein, 1913; Penard, 1916, 1920, 1922; Buddenbrock, 1922; Yagiu, 1933; Fauré-Fremiet, 1953; Kormos and Kormos, 1958; Deroux, 1974; Petz, 1994; Song and Wang, 1996; Agatha and Riedel-Lorjé, 1997; Montagnes and Humphrey, 1998; Suzuki and Song, 2001; Agatha, 2003; Agatha et al., 2004). Likewise, electron microscopical observations are available only for *Laboea* (Agatha et al., 2004), *Limnostrombidium*, *Pelagostrombidium* (Foissner et al., 1991, 1994, 1999), *Novistrombidium* (Agatha, 2003; Modeo et al., 2003), *Strombidium* (Fauré-Fremiet and Ganier, 1970; Montagnes et al., 1988; Montagnes and Humphrey, 1998; Modeo et al., 2001, 2003; Agatha, 2003), *Spirostrombidium* (Montagnes and Taylor, 1994), and *Tontonia* (Greuet et al., 1986; Laval-Peuto et al., 1986).

Terminology

The lack of a uniform terminology in oligotrichid ciliates causes some confusion; therefore, the ciliary structures are shown in Fig. 1. Anterior membranelles (paramembranelles adorales externes, collar membranelles, adoral membranelles) and ventral membranelles (membranelles orales, buccal membranelles, ventral adoral membranelles, inner adoral membranelles), together with their polykinetids, form a conspicuous, C-shaped zone apically. In halteriids, the oral ciliature additionally comprises two undulating membranes: one on the inner wall of the buccal lip called endoral and one on the outer wall named paroral; both are assumed to correspond to the endoral and paroral of the Stichotrichida

(Szabó, 1935; Figs. 5b–d and 6a–c). In long-term cultures of halteriids, the paroral is occasionally reduced (Foissner, unpubl.), a process which probably happened also in the evolution of the Oligotrichia (Agatha, 2004). The homology of the inner membrane of halteriids and oligotrichids is indicated not only by the same position, but also by the de novo origin, monostichomonad structure, and perilemma cover (Petz and Foissner, 1992; Petz, 1994; Song and Wang, 1996; Agatha, 2003, 2004; Agatha et al., 2004). Thus, the inner membrane of the Oligotrichida should likewise be called endoral.

The somatic ciliature is highly reduced, typically comprising only a girdle and a ventral kinety. The girdle kinety is variously referred to as circumferential ciliary row, circle kinety, equatorial kinety or sillon circulaire; occasionally, it is also incorrectly named “paratene”, which means kinetids of adjacent ciliary rows giving the impression of a kinety (Corliss, 1979; Small and Lynn, 1985; Corliss and Snyder, 1986; Krainer, 1991, 1995). Ontogenetic data, however, clearly show that the girdle kinety is a “true” kinety, i.e., the ciliary row lengthens by intrakinetal proliferation of basal bodies and simply divides, like the longitudinal ventral kinety (Petz, 1994; Song and Wang, 1996; Agatha, 2003). In “typical” morphostatic oligotrichids, the girdle kinety is horizontally orientated and ostensibly continuous, while a ventral gap is recognizable during ontogenesis. The left kinety portion becomes the opisthe’s girdle kinety, while the right forms the proter’s (Figs. 4a–c). Due to a similar ontogenetic behaviour, that part of the girdle kinety, which extends horizontally from the ventral membranellar zone to the middle of the dorsal side in *Laboea strobila*, is named left portion, while the remaining sinistrally spiralled part is designated as right portion (Figs. 4g–i, 7i and 8g; Agatha et al., 2004). The direction of the kinety spiral is determined following Montagnes and Taylor (1994). The ventral kinety (Kaudalreihe, post-equatorial kinety) extends longitudinally between the girdle kinety and the posterior cell end. Frequently, it is shortened anteriorly, occasionally partially or entirely shifted onto the dorsal side, and occasionally lacking.

The classification of the taxa here follows Agatha (2004), i.e., the class Hypotrichea comprises the orders Hypotrichida and Stichotrichida, while the class Oligotrichea contains the subclasses Halteriia and Oligotrichia; the latter consists of the orders Choreotrichida and Oligotrichida.

Results and discussion

Montagnes and Taylor (1994) suggested that the oligotrichid kineties originated from longitudinal ciliary rows. Hence, the ancestor of the oligotrichids is assumed to have several longitudinal, dikinetidal somatic kineties with only anterior basal bodies distinctly ciliated, as in the dorsal kineties of the outgroup Hypotrichea and the bristle complexes of at least some Halteriia (Figs. 2a, 5a and d; Grain, 1972; Grim, 1974; Ruffolo, 1976; Petz and Foissner, 1992; Berger, 1999). The following steps in the evolution of the oligotrichid ciliary patterns are inferred from the orientation of the somatic dikinetids, namely, whether the anterior or the posterior basal body is distinctly ciliated. First, a reduction in the kinety number to two occurred (the origin of the tail cilia in tontoniids is uncertain and requires ontogenetic investigation). Probably, these two kineties were originally situated on the dorsal side, but their posterior portions were shifted ventrally by a dextral torsion of the proximal end of the membranellar zone and the cell proper, which is recapitulated during ontogenesis (Figs. 3j–r). The right ciliary row became the girdle kinety and the left ciliary row became the ventral kinety, which was distinctly shortened anteriorly and remained parallel to the girdle kinety; these processes generated the most ancestral Type I pattern found, for instance, in *Spirostrombidium rhyticollare* (Figs. 2b, 7b and c). This idea is supported by a dextrally spiralled third kinety, occurring in some *Strombidium elegans* specimens (Fig. 5j). Type II originated from Type I by the longitudinal orientation of the

ventral kinety, as in *Novistrombidium* species (Figs. 2c, 7a and 8a). Type III was produced by a posterior migration of the right girdle kinety portion; both kinety ends are thus close to the posterior end of the ventral side, as in *Strombidium elegans* (tail-less; Figs. 2d, 5i and j) and *Tontonia gracillima* (tailed; Fig. 5e). Type IV originated because the posterior portion of the girdle kinety partially surrounded the posterior cell end, curving anteriorly and parallel to the left of the ventral kinety; therefore, it is inversely orientated to the ventral kinety, as in *Spirostrombidium urceolare* (Figs. 2e, 7d and e). Type V was produced by an anterior migration of the left kinety portion (Fig. 2f); the girdle kinety is thus horizontal, as in the tail-less genera *Strombidium* (Figs. 7f and 8b), *Pelagostrombidium* (Figs. 7g and 8d), *Limnostrombidium* (Figs. 7h, 8c and f), *Cyrtostrombidium* (Fig. 7j), and the tailed *Tontonia cornuta* (Fig. 5g). Type VI derived from the horizontal girdle kinety: the right kinety portion spiralled sinistrally to the posterior cell end, as in the tail-less *Laboea strobila* (Figs. 2g, 7i and 8g) and the tailed *Tontonia grandis* (Fig. 5h). It cannot be excluded that this girdle kinety pattern developed from Type III (Fig. 2d); however, late dividers of *L. strobila* indicate a lengthening and spiralling of the right kinety end and thus a derivation from Type V (Figs. 2f and 4g–i; Agatha et al., 2004).

The ontogenetic results on *Strombidium*, *Laboea*, and *Novistrombidium* support this concept of ciliary pattern evolution: (i) the dextral torsion of the proximal end of the oral apparatus along with the cell proper is apparently repeated by the curvature of the oral primordium in the Oligotrichia, while the Hypotrichia and Halteria show an anticlockwise rotation of the new oral apparatus (Fig. 3); and (ii) *Strombidium* and *Laboea* apparently recapitulate the dextrally spiralled course of the girdle kinety in *Novistrombidium*; they are thus probably more derived (Fig. 4; Agatha et al., 2004).

The proposed evolution of the girdle kinety patterns is mainly based on the orientation of the somatic dikinetids. Deviating data, such as monokinetidal somatic kineties, ciliated posterior basal bodies in ventral dikinetids and/or ciliated right basal bodies in girdle dikinetids as well as changes of polarity within a kinety, are interpreted as misobservations, especially as protargol preparations of high quality are difficult to obtain and often only the ciliated basal body sufficiently impregnates. Other argumentations are also less parsimonious.

The orientation of the dikinetids shows that the parallel course of the ventral kinety and the posterior portion of the girdle kinety is achieved in two ways (Figs. 2b and e). Accordingly, the genus *Spirostrombidium*, which was defined mainly by this feature, has to be split into *Spirostrombidium* for the Type IV pattern and *Parallelostrombidium* nov. gen. for the Type I pattern of the girdle kinety (see *Diagnosis of taxa*). Species with a dextrally spiralled girdle kinety but without a ventral kinety cannot be definitely assigned to the Type I or II pattern (Figs. 2b and c) corresponding to the tail-less genera *Parallelostrombidium* nov. gen. and *Novistrombidium*, respectively. Thus, other distinguishing features are required. The arrangement of extrusomes is a potentially useful character (attached along the girdle kinety in *Parallelostrombidium* vs. directly underneath the membranellar zone in *Novistrombidium*; Figs. 7a and b), and this feature can easily be examined by additional live observations.

Identical girdle kinety patterns occur in the tailed and tail-less oligotrichids. Three explanations are possible: (i) the ancestor with the dextrally spiralled girdle and longitudinal ventral kinety had a tail, which disappeared in Types II, IV, V, and VI (four convergences); (ii) the tail developed convergently within Types II, III, V, and VI (four convergences); (iii) the girdle kinety patterns evolved convergently in the tailed and tail-less taxa (three convergences). The last argumentation is the most parsimonious one, not only because it assumes merely three convergences, but also because (i) there is no evidence for the recapitulation of a tail in the ontogenesis of the tail-less taxa, (ii) the ingroup comparison shows a majority of tail-less species (~140 vs. 10), (iii) the loss of a potentially useful tail [a

contribution to the cell's movement and/or the stabilization of the cell during feeding are speculated by Kahl (1932) and Fauré-Fremiet (1924)] would be surprising, and (iv) it seems less probable that such a complex and contractile structure has been generated independently several times. Furthermore, the assumption of a convergent evolution of the girdle kinety patterns is more plausible considering the restricted diversity of courses producible by a single kinety (cp. cingulum patterns in dinoflagellates).

On the other hand, it is assumed that the genera *Strombidium*, *Cyrtostrombidium*, *Limnostrombidium*, and *Pelagostrombidium* have a common tail-less ancestor with a horizontal girdle kinety. The latter three genera are characterized by strong features, justifying the erection of distinct families: the Cyrtostrombidiidae nov. fam. for species with cyrtos-like pharyngeal fibres, but without ventral membranelles and endoral (Fig. 7j), and the Pelagostrombidiidae nov. fam. for the genera *Limnostrombidium* and *Pelagostrombidium*, which have a neoformation organelle (permanent tube in which stomatogenesis takes place; Figs. 7g and h, 8c and f).

Jankowski (1978) and Song (1999) used the thigmotactic membranelles of *Strombidium calkinsi* Fauré-Fremiet, 1932 to establish the genera *Thigmostrombidium* and *Heterostrombidium*. Such enlarged membranelles are combined with different ciliary patterns (Figs. 2d–f), viz., with Type III in *Strombidium elegans* Florentin, 1901 (Fig. 5i); Type IV in *Spirostrombidium urceolare* (Stein, 1867) Lei et al., 1999a (Fig. 7d) and probably in *S. sauerbreyae* (Kahl, 1932) Petz et al., 1995, as redescribed by Fauré-Fremiet (1950); and Type V in *Heterostrombidium paracalkinsi* Lei et al., 1999b and probably *Thigmostrombidium calkinsi* (Fauré-Fremiet, 1932) Jankowski, 1978. The girdle kinety patterns of *Strombidium corsicum* (Gourret and Roeser, 1888) Kahl, 1932, *Peristrombidium latum* (Kahl, 1932) Jankowski, 1978, as redescribed by Fauré-Fremiet (1950), and *Strombidium clavellinae* Buddenbrock, 1922 are unknown. Kahl (1932) and Fauré-Fremiet (1950) interpreted these specialized thigmotactic anterior or ventral membranelles as an adaptation to the benthic lifestyle, which appears to have evolved convergently within the different girdle kinety patterns. This conclusion seems reasonable, as the enlarged membranelles occur in different positions and are usually combined with a dorsoventrally flattened cell shape. Accordingly, *Thigmostrombidium* and its junior synonym *Heterostrombidium* are rejected and the type species *Strombidium calkinsi* is (again) affiliated with *Strombidium* because the arrangement of extrusomes and the upper margin of the distended cell surface indicate a horizontal girdle kinety. Likewise, *H. paracalkinsi* is assigned to *Strombidium*: *S. paracalkinsi* (Lei et al., 1999b) nov. comb.

Within the tail-less oligotrichids, the girdle kinety patterns were used to define the genera *Laboea* Lohmann, 1908 (Agatha et al., 2004), *Spirostrombidium* Jankowski, 1978 (Petz et al., 1995), and *Novistrombidium* Song and Bradbury, 1998 (Agatha, 2003). Consequently, the tailed genus *Tontonia*, where similar patterns occur, has to be split accordingly (see *Diagnosis of taxa*). The absence of the ventral kinety in *Pelagostrombidium* and some *Strombidium* species is difficult to interpret at the present state of knowledge. Since it tends to be reduced, its absence is regarded only as a species-specific feature.

Are new genera and families necessary?

In oligotrichid ciliates, somatic ciliary patterns were rarely used for generic distinction, likely because the main patterns of the girdle kinety seemed to be not restricted to a distinct genus. Thus, several authors regarded a subdivision of the ~120 described oligotrichid species as not substantiated and proposed to await further molecular and morphological data before new taxa are established (Modeo et al., 2003). However, only half of the oligotrichid species used for gene sequence analyses have been identified on species level (Modeo et al., 2003; Agatha et al., 2004). The paraphyly of the genus *Strombidium* (Strüder-Kypke,

unpubl.) and the great genetic distances (Snoeyenbos-West et al., 2002) shown by the gene trees indicate that the sequenced oligotrichids belong to a wide variety of genera and possibly families. Even the ~50 choreotrichid species were subdivided into four suborders and three families (Small and Lynn, 1985; Montagnes and Lynn, 1991; Laval-Peuto et al., 1994; Lynn and Small, 2002). Although the course of the somatic ciliary rows used in the Oligotrichida is less conservative than the structure of the somatic kinetids used in the Choreotrichida, this is not true for the ontogenetic data. Another argument, namely, that the new genera will comprise only few (usually two) species each and thus will not contribute to a far-reaching subdivision of the Oligotrichida is also valid for the Choreotrichida, where several genera also comprise only one to three species. On the other hand, the number of tontoniid species doubled and that of the other oligotrichids increased by about 50% since 1988, when silver impregnation techniques were applied to oligotrichid taxonomy. Moreover, these investigations were almost exclusively conducted in neritic regions, while the oceanic areas are still fresh ground. Further studies in these areas and the reinvestigation of poorly known species will thus certainly greatly increase not only the known overall oligotrichid diversity, but also enlarge the number of species in the small genera.

The evolution of the ciliary patterns and the evaluation of the morphologic and ontogenetic data provide good evidences for the revision of the oligotrichids (Agatha, 2004). The observed great morphologic and genetic diversity is thus expressed by the erection of new families and genera.

Diagnosis of taxa

Strombidiidae Fauré-Fremiet, 1970

Improved diagnosis—Oral ciliature with anterior and ventral membranelles and endoral. Stomatogenesis in transient tube.

Type genus—*Strombidium* Claparède and Lachmann, 1859.

Comparison with related families—The order Oligotrichida comprises three further families: the Cyrtostrombidiidae nov. fam. (with cyrtos-like pharyngeal fibres, without ventral membranelles and endoral), the Pelagostrombidiidae nov. fam. (with neof ormation organelle), and the Tontoniidae nov. fam. (with contractile tail).

Strombidium Claparede and Lachmann, 1859

Improved diagnosis—Girdle kinety horizontal. Ventral kinety longitudinal, occasionally reduced or lacking. Oral primordium develops at or below level of girdle kinety.

Type species—*Strombidium sulcatum* Claparède and Lachmann, 1859.

Comparison with related genera—According to the authoritative redescriptions by Fauré-Fremiet (1912), Fauré-Fremiet and Ganier (1970), and Granda and Montagnes (2003), *S. sulcatum* has a horizontal girdle kinety (Type V; Fig. 2f). This course separates *Strombidium* (Figs. 7f and 8b) from *Laboea* (sinistrally spiralled; Type VI; Figs. 2g, 7i and 8g; Montagnes et al., 1988; Agatha et al., 2004), *Omegastrombidium* nov. gen. (both ends near the posterior end of ventral side; Type III; Figs. 2d, 5i and j), as well as from *Parallelostrombidium* nov. gen., *Novistrombidium*, and *Spirostrombidium* where it is dextrally spiralled (Types I, II, IV; Figs. 2b, c, e, 7a–e and 8a; Montagnes and Taylor, 1994; Petz et al., 1995; Song and Bradbury, 1998; Lei et al., 1999a; Agatha, 2003; Modeo et al., 2003). Observations on early dividers of *Strombidium* show the oral primordium at or below the level of the girdle kinety (Fauré-Fremiet, 1953; Deroux, 1974; Petz, 1994; Song and

Wang, 1996; Montagnes and Humphrey, 1998; Agatha, 2003). In *Laboea*, the new oral apparatus originates below the left girdle kinety portion (Figs. 4g–h; Agatha et al., 2004), while appearing above it in *Novistrombidium* (Figs. 4d–f; Agatha, 2003). The horizontal girdle kinety in *S. constrictum* (Meunier, 1910) Wulff, 1919 is near the rear end, probably due to a secondary posterior shift. Since its ontogenesis is unknown, an affiliation of the species with *Strombidium* is uncertain.

***Spirostrombidium* Jankowski, 1978**

Improved diagnosis—Girdle kinety dextrally spiralled, posterior portion inversely orientated and parallel to longitudinal ventral kinety.

Type species—*Strombidium sauerbreyae* Kahl, 1932 [replacement name established by Kahl (1932) due to homonymy of the originally designated type *Strombidium coronatum* Sauerbrey, 1928 with *Strombidium coronatum* (Leegaard, 1915) Kahl, 1932].

Comparison with related genera—Jankowski (1978) established the genus using the spiralled “cytoskeleton” (probably the arrangement of extrusomes) as distinguishing feature. Petz et al. (1995) improved the diagnosis mainly by including the course of the somatic kineties, which are parallel to each other in the posterior cell portion. This feature is, however, achieved in two ways: (i) the ventral kinety follows the course of the girdle kinety (Type I; Fig. 2b) or (ii) the posterior portion of the girdle kinety is curved anteriorly and parallel to the longitudinal ventral kinety (Type IV; Fig. 2e). Both types are distinguished by the orientation of the posterior girdle kinety portion in relation to the ventral kinety (equally vs. inversely orientated). This difference necessitates a split of the genus *Spirostrombidium*. Unfortunately, the ciliary pattern of the type species *S. sauerbreyae* (Kahl, 1932) Petz et al., 1995 is unknown. The arrangement of the extrusomes, however, indicates an affiliation with Type IV rather than with Type I (girdle kinety inversely vs. equally orientated; Figs. 2b and e). Furthermore, the course of the girdle kinety causes a broadly rounded posterior cell end in Type IV, while specimens of the Type I pattern are posteriorly pointed (pers. observ.; Montagnes and Taylor, 1994; Petz et al., 1995); the latter belong to the new genus *Parallelostrombidium* nov. gen. (see below). Two further broadly obconical species, i.e., *Spirostrombidium pseudocinctum* (Wang, 1934), as redescribed by Petz et al. (1995), and *S. urceolare* (Stein, 1867), as redescribed by Lei et al. (1999a; Figs. 7d and e), belong to Type IV and thus remain in the genus *Spirostrombidium*.

***Parallelostrombidium* nov. gen.**

Diagnosis—Ventral kinety follows posterior portion of dextrally spiralled girdle kinety; thus, both with same orientation.

Type species—*Strombidium rhyticollare* Corliss and Snyder, 1986.

Remarks—*Strombidium rhyticollare* is selected as type because its description is based not only on protargol impregnations, but also on live observations (Figs. 7b and c; Corliss and Snyder, 1986; Petz et al., 1995).

Etymology—Composite of the Greek preposition “para” (corresponding to), the Greek reciprocal pronoun “allel” (each other), and *Strombidium*, referring to the parallel course of the somatic kineties and the similarity to the genus *Strombidium*. Neuter gender.

Comparison with related genera—There are two genera with a parallel course of the girdle and ventral kinety: *Parallelostrombidium* (Figs. 7b and c) and *Spirostrombidium*

(Figs. 7d and e). Both differ in the orientation of the posterior girdle kinety portion relative to the ventral kinety (with same vs. inverse orientation, corresponding to Type I vs. Type IV; Figs. 2b and e) and, consequently, in their cell shape (pointed vs. broadly rounded posteriorly). *Strombidium siculum* is a further member of *Parallelostrombidium*: *P. siculum* (Montagnes and Taylor, 1994) nov. comb.

***Omegastrombidium* nov. gen.**

Diagnosis—Girdle kinety horizontally orientated on dorsal side, while kinety ends extend to posterior end of ventral side.

Type species—*Strombidium elegans* Florentin, 1901.

Remarks—*Strombidium elegans* is selected as type because its description is based not only on silver impregnations, but also on live observations (Figs. 5i and j; Florentin, 1901; Lei et al., 1999a; Song et al., 2000).

Etymology—Composite of the last letter of the Greek alphabet and the generic name *Strombidium*, referring to the roughly Ω -shaped girdle kinety and the similarity to the genus *Strombidium*. Neuter gender.

Comparison with related genera—According to the redescrptions of the type species by Lei et al. (1999a) and Song et al. (2000), *Omegastrombidium* (Figs. 5i and j) differs in the girdle kinety pattern from the other genera of the family Strombidiidae (for details, see discussion of *Strombidium*). In field material and cultures, a fragment-like third kinety occurs in *O. elegans* nov. comb. More data, especially ontogenetic investigations, are required to interpret this structure, which might be an atavism, indicating an oligotrichid ancestor with more than just two somatic kineties. Since the lack of the ventral kinety in *Strombidium elatum* is assumed to be only a species-specific feature, this species is affiliated with *Omegastrombidium*: *O. elatum* (Aleksperov, 1985) nov. comb.

Cyrtostrombidiidae nov. fam

Diagnosis—Oral ciliature with anterior membranelles only. Pharyngeal fibres thick and cyrtos-like after protargol impregnation. Stomatogenesis in transient tube.

Type genus—*Cyrtostrombidium* Lynn and Gilron, 1993.

Comparison with related families—The Cyrtostrombidiidae have a unique oral organization, i.e., the ventral membranelles and the endoral are lacking (Fig. 7j). Furthermore, the protargol-impregnated pharyngeal fibres are cyrtos-like and distinctly thicker than those of the other Oligotrichida. Stomatogenesis takes place within a transient tube, as live and protargol-impregnated morphostatic specimens do not show a neoformation organelle (own observ.; Lynn and Gilron, 1993).

Pelagostrombidiidae nov. fam.

Diagnosis—Stomatogenesis in permanent tube (=neoformation organelle). Oral ciliature with anterior and ventral membranelles and endoral.

Type genus—*Pelagostrombidium* Krainer, 1991.

Comparison with related families—The family Pelagostrombidiidae is apparently restricted to freshwater. The family differs from the other oligotrichid families by the

neoformation organelle, a permanent tube in which the oral primordium develops (Penard, 1916, 1920, 1922; Krainer, 1991; Petz and Foissner, 1992; Krainer, 1995). Although all Oligotrichia have a hypoapokinetal stomatogenesis (Foissner, 1996), the neoformation organelle only occurs in *Pelagostrombidium* and *Limnostrombidium* (Figs. 7g and h, 8c and f). Thus, the erection of a new family, as suggested by Petz (1994), seems justified.

Tontoniidae nov. fam

Diagnosis—With contractile, usually ciliated tail. Oral ciliature with anterior and ventral membranelles and endoral. Stomatogenesis in transient tube.

Type genus—*Tontonia* Fauré-Fremiet, 1914.

Remarks—Jankowski (1975) merely mentioned a family Tontoniidae without providing a diagnosis; thus, the family name is not available.

Comparison with related families—The tail (=caudal appendix, peduncle) has a highly complex ultrastructure, which differs distinctly from other contractile systems in protozoa (Greuet et al., 1986). Kahl (1932), Fauré-Fremiet (1914, 1924), and Greuet et al. (1986) assumed that its centrally located microfilaments manage the contraction of the tail. The tail's function is uncertain; Kahl (1932) and Fauré-Fremiet (1924) speculated that it contributes to the cell's movement and/or stabilizes the cell during feeding. Nevertheless, it represents a strong feature suitable for characterizing the new family, which comprises four genera, differing in their girdle kinety patterns. Ontogenetic data are required to ascertain the origin of the tail cilia, which might represent either a fragment of the ventral kinety or an independent third ciliary row.

***Tontonia* Fauré-Fremiet, 1914**

Improved diagnosis—Girdle kinety dextrally spiralled.

Type species—*Tontonia appendiculariformis* Fauré-Fremiet, 1914.

Comparison with related genera—According to the arrangement of the extrusomes, *T. appendiculariformis* Fauré-Fremiet, 1914 has a dextrally spiralled girdle kinety like *Tontonia antarctica* Petz et al., 1995 (Fig. 5f). *Tontonia* differs from the other tontoniid genera in the girdle kinety pattern: both ends are near the posterior end of the ventral side in *Paratontonia* Jankowski, 1978 (Type III; Figs. 2d and 5e); horizontally orientated in *Pseudotontonia* nov. gen. (Type V; Figs. 2f and 5g); and sinistrally spiralled in *Spirotontonia* nov. gen. (Type VI; Figs. 2g and 5h).

***Paratontonia* Jankowski, 1978**

Improved diagnosis—Girdle kinety horizontally orientated on dorsal side, while kinety ends extend to posterior end of ventral side.

Type species—*Tontonia gracillima* Fauré-Fremiet, 1924.

Remarks—Jankowski (1978) established the genus for *T. gracillima* and defined it by the lack of a “cytoskeleton”, which was interpreted as the absence of extrusomes by Petz et al. (1995). Since such structures were mentioned in its redescription (Fig. 5e; Lynn et al., 1988), *Paratontonia* was regarded as synonym of *Tontonia* (Petz et al., 1995; Aescht, 2001). My new results, however, justify its maintenance, although with a different diagnosis.

Comparison with related genera—For differences between the tontoniid genera, see genus *Tontonia*. *Paratontonia* matches *Omegastrombidium* in the pattern of the girdle kinety (Type III; Fig. 2d), but has a ciliated tail. *Tontonia poopsia* is also assigned to *Paratontonia*: *P. poopsia* (Montagnes and Lynn, 1988) nov. comb.

***Pseudotontonia* nov. gen**

Diagnosis—Girdle kinety horizontally orientated. Oral primordium develops at or underneath level of girdle kinety.

Type species—*Laboea cornuta* Leegaard, 1915.

Remarks—*Laboea cornuta* is selected as type because it has been redescribed from live and protargol-impregnated specimens; moreover, some ontogenetic data are available (Fig. 5g; Suzuki and Song, 2001).

Etymology—Composite of the Greek prefix “pseudo-” (false) and the generic name *Tontonia*. Feminine gender.

Comparison with related genera—For differences between the tontoniid genera, see genus *Tontonia*. The genus is characterized by a girdle kinety pattern typical of the tail-less genera *Strombidium*, *Cyrtostrombidium*, *Limnostrombidium*, and *Pelagostrombidium*, in which it probably developed convergently (Agatha, 2004). In tail-less Oligotrichida, the site where the oral primordium originates differs in relation to the left portion of the girdle kinety (see genus *Strombidium*). Since such differences probably occur between the tontoniid genera as well, this feature is included into the diagnosis. Because of its similar girdle kinety pattern, *Tontonia simplicidens* is affiliated with *Pseudotontonia*: *P. simplicidens* (Lynn and Gilron, 1993) nov. comb.

***Spirotontonia* nov. gen**

Diagnosis—Girdle kinety performs more than one sinistral turn around cell. Oral primordium underneath left ventral portion of girdle kinety.

Type species—*Tontonia grandis* Suzuki and Han, 2000.

Etymology—Composite of the Latin noun “spira” (whorl) and *Tontonia*, referring to the sinistrally spiralled girdle kinety and the similarity to the genus *Tontonia*. Feminine gender.

Comparison with related genera—For differences between the tontoniid genera, see genus *Tontonia*. A sinistrally spiralled girdle kinety characterizes not only the tailed genus *Spirotontonia* (Fig. 5h), but developed probably convergently in the tail-less genus *Laboea* (Figs. 7i and 8g; Montagnes et al., 1988; Agatha, 2004; Agatha et al., 2004). *Tontonia turbinata* is also affiliated with *Spirotontonia*: *S. turbinata* (Song and Bradbury, 1998) nov. comb.

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Fig. 1.

Ventral view of a generalized oligotrichid ciliate, illustrating some diagnostic features.

Large anterior membranelles (AM) and small ventral membranelles (VM) along with their polykinetids form the membranellar zone. The endoral (EM) extends on the inner wall of the buccal lip. The somatic ciliature typically comprises a girdle kinety (GK) and a ventral kinety (VK). The distended cell surface (DC) occupies the cell portion underneath the girdle kinety in fixed and impregnated cells.

Fig. 2.

Evolution of oligotrichid ciliary patterns. (a) The ancestor had many longitudinal somatic kineties, whose dikinetids bore a distinct cilium at each anterior basal body only (see detail). (b) Type I pattern. The kinecy number was reduced to two. The rightwards torsion of the proximal end of the membranellar zone and the cell proper caused the dextrally spiralled pattern of the girdle kinety (GK; red in web version) and ventral kinety (VK; blue in web version). (c) Type II pattern. The ventral kinety orientated longitudinally. (d) Type III pattern. The right portion of the girdle kinety migrated posteriorly; both kinecy ends are thus close to the cell's posterior end. (e) Type IV pattern. The posterior portion of the girdle kinety curved anteriorly and is thus inversely orientated to the parallel ventral kinety. (f) Type V pattern. The left portion of the dextrally spiralled girdle kinety migrated anteriorly, causing a horizontal orientation. (g) Type VI pattern. The right portion of the horizontal girdle kinety spiralled sinistrally to the rear end. Arrows indicate the orientation of the kineties.

Fig. 3.

Ventral (a–h, j–l, p–r) and dorsal (i, m, n) views and oral primordium (o) of early (a, d, g, j, m, p), middle (b, e, h, k, n, q), and late (c, f, i, l, o, r) dividers after protargol impregnation. The hypotrichs (a–c; *Diophrys scutum* from Song and Packroff, 1993), stichotrichs (d–f; *Lamostyla halophila* from Foissner et al., 2002), and halteriids (g–i; *Halteria grandinella* from Song, 1993) show a pronounced rightwards rotation of the anterior end of the oral primordium (arrows), whereas the oligotrichids (j–l; *Strombidium arenicola* from Agatha, 2003) and choreotrichids, including the strobilidiids (m–o; *Strombidinopsis spiniferum* from Dale and Lynn, 1998) and tintinnids (p–r; *Tintinnopsis cylindrata* from Petz and Foissner, 1993), show a pronounced rightwards rotation of the posterior end of the oral primordium (arrows).

Fig. 4.

Schematized illustrations of the main ontogenetic events in *Strombidium* (a–c), *Novistrombidium* (d–f), and *Laboea strobila* (g–i). During ontogenesis, the dextrally spiralled course of the girdle kinety found in *Novistrombidium* is apparently recapitulated in *Strombidium* and *Laboea* (for details, see Agatha et al., 2004). Thus, the latter taxa are assumed to be more derived. These observations support the proposed evolution of the ciliary patterns (cp. Fig. 2). The oral primordia are symbolized by dashed circles. GK/GK', proter's/opisthe's girdle kinety (red and yellow in web version); VK/VK', proter's/opisthe's ventral kinety (blue and light blue in web version).

Fig. 5.

Halteriid and oligotrichid genera from live (b, f, g) and after protargol impregnation (a, c–e, h–j). (a, c) *Halteria grandinella*. Schema of bristles (from Grim, 1974) and oral cavity (from Grain, 1972). (b, d) *Meseres corlissi*. Arrows denote paroral (from Petz and Foissner, 1992). (e, i, j) *Paratontonia gracillima* (e) and *Omegastrombidium elegans* (i, j). Both ends of the girdle kinety are near the rear end (e from Lynn et al., 1988; i, j from Song et al., 2000). (f) *Tontonia appendiculariformis* has a dextrally spiralled girdle kinety (from Fauré-Fremiet, 1924). (g) *Pseudotontonia cornuta* has a horizontal girdle kinety (from Suzuki and Song, 2001). (h) *Spirotontonia grandis* has a sinistrally spiralled girdle kinety (from Suzuki and Han, 2000). AM, anterior membranellae; DK, dikinetids; EK, extra kinety; EM, endoral; F, fibres; GK, girdle kinety; PM, paroral; SK, somatic kineties; TC, tail cilia; TM, thigmotactic membranellae; VK, ventral kinety; VM, ventral membranellae.

Fig. 6. Halteriid genera in the scanning electron microscope. The minute paroral is marked by arrowheads. (a, b) *Halteria grandinella*, ventral view of a morphostatic specimen and posterior polar view of a middle divider (from Petz and Foissner, 1992). (c) Ventral view of *Meseres corlissi* (from Petz and Foissner, 1992). AM, anterior membranellae; B, bristles; OB, opisthe's bristle; OP, oral primordium; SK, somatic kineties; VM, ventral membranellae.

Fig. 7.

Strombidiid genera after protargol impregnation. (a) Ventral view of *Novistrombidium apsheronicum* (from Agatha, 2003). The girdle kinety is dextrally spiralled, the ventral kinety longitudinal. (b, c) Ventral and dorsal view of *Parallelostrombidium rhyticollare*. The posterior portion of the girdle kinety and the ventral kinety have the same orientation (from Petz et al., 1995). (d, e) Ventral and dorsal view of *Spirostrombidium urceolare* (from Lei et al., 1999a). The posterior portion of the girdle kinety is parallel to the ventral kinety, but inversely orientated. (f–h, j) Ventral views of genera with a horizontal girdle kinety: *Strombidium* (*S. arenicola* from Agatha, 2003), *Pelagostrombidium* (*P. mirabile* from Krainer, 1991), *Limnostrombidium* (*L. pelagicum* from Krainer, 1991), and *Cyrtostrombidium* (*C. longisomum* from Lynn and Gilron, 1993). Instead of ventral membranelles and an endoral, *Cyrtostrombidium* species have cyrtos-like pharyngeal fibres (arrow). (i) Ventral view of *Laboea strobila*, showing sinistrally spiralled girdle kinety (from Montagnes et al., 1988). AM, anterior membranelles/polykinetids; E, extrusomes/extrusome attachment sites; GK, girdle kinety; NF, neoformation organelle; TM, thigmotactic membranelles; VK, ventral kinety; VM, ventral membranelles/polykinetids.

Fig. 8. Strombidiid genera in the scanning electron microscope. (a) Ventral view of *Novistrombidium*, showing dextrally spiralled course of the girdle kinety (*N. apsheronicum* from Agatha, 2003). (b, e) Ventral view of *Strombidium* and detail of its horizontal girdle kinety (*S. arenicola* from Agatha, 2003). (c, f) Ventral view of *Limnostrombidium* and detail of its horizontally orientated girdle kinety (*L. viride*; c from Foissner et al., 1999; f kindly supplied by W. Foissner). Arrowheads denote opening of neoformation organelle (tube in which the oral primordium develops). (d) Ventral view of *Pelagostrombidium* (*P. mirabile* from Foissner et al., 1999). Note that no somatic ciliature is recognizable. (g) Ventral view of *L. strobila*, showing the sinistrally spiralled girdle kinety (from Agatha et al., 2004). AM, anterior membranelles; E, just ejected extrusomes; GK, girdle kinety; VK, ventral kinety; VM, ventral membranelles.