Morphogenesis, fine structure, and phylogenetic relationships of the «heterotrich» ciliate *Bryometopus atypicus* (Protozoa, Colpodea)*

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**SUMMARY**

The stomatogenetic of *Bryometopus atypicus* is parakinetical. Ecto- and endoplasm are separated by *a lamina corticalis* at the proximal ends of the basal bodies. The somatic cinetodesms are composed of ciliated dikinetids, which are joined by 3 proximal desmoses and possess 2 parasomal sacs. The anterior basal body bears 5-7 transverse microtubules and 1-7 postciliary microtubules. The fibrillar associates of the posterior basal body are a cinetodesmal fibril, 5-7 transverse microtubules, and 1-7 postciliary microtubules. In the frontal region there are some triads with an unciliated and unjoined anterior basal body. The posterior basal body of the «paroral in pairs» shows postciliary microtubules which are arranged parallel to the longitudinal axis of the membrane; the anterior basal body has transverse microtubules. Both fibrillar systems extend to the oral ribs of the right buccal wall. Underneath and parallel to the longitudinal axis of the paroral membrane a nematodesmal bundle extends to the cytopharynx, where a cross-striated filamentous material and a cytoplasmic lip are situated. The adoral organelles are composed of 2 longer rows arranged in a zigzag-pattern and a shorter right row of basal bodies, which show convergent postciliary fusions.
microtubules, interkinetosomal links, parasomal sacs, nematodesmata, and a filamentous reticulum at their basis. The morphogenesis and the fine structure of the somatic dikinetids, of the mucocysts, and of the adoral organelles of *B. atypicus* justify its inclusion in the colpodid ciliates. However, *B. atypicus* has characters of diverse taxa: the *lamina corticalis* of haptozoids; 3 proximal desmoses of karyorelictids and spirotrichs; paroral transverse microtubules of gymnostomes and spirotrichs; oral ribs, cross-striated filamentous material, and a filamentous reticulum at the basis of the adoral organelles like hymenostomes. This special constellation of characters confirms the establishment of the subclass *Bryometopia* (Foissner, 1985) within the Colpodea and points to the possibility of a convergent evolution of certain types of the colpodid oral apparatus.

### Abstract

Les processus morphogénétiques et les caractères ultrastructuraux corticaux généraux de *Bryometopus atypicus* sont ceux des Colpodea. Cependant des caractères particuliers (*lamina corticalis*, 3 desmoses proximales, microtubules transverses à la parorale, crêtes orales, système microfibrillaire sous-paroral) nécessitent la distinction d'une sous-classe des *Bryometopia dans les Colpodea*.

### Synopsis

Morphogenetical processes and general cortical fine structural characters of *Bryometopus atypicus* are those of colpodea. However, peculiar characters (*lamina corticalis*, 3 proximal desmoses, paroral transverse microtubules, oral ribs, sub-paroral microfibrillar system) lead to the distinction of a subclass *Bryometopia* within the Colpodea.

### INTRODUCTION

For a long time *Bryometopus* was considered to be a typical heterotrich genus, mainly on account of its oral region (Kahl, 1932; Corliss, 1979; Foissner, 1980). Recently, the light microscopical re-examination of Foissner (1984) pointed to a colpodid nature of *Bryometopus atypicus*. However, this suggestion must be proved by the investigation of the morphogenesis and the fine structure of the somatic kinetids, which are probably very conservative during evolution (Lynn, 1976a, 1981; Puytorac and Perez-Paniagua, 1979; Foissner, 1985). On the basis of a convergent evolution of the oral apparatus and partly of the silverline system, Foissner (1985) divided the Colpodea into the subclasses *Bryometopia* and *Colpoda*. This proposal requires examination too, since the diverse oral structures of numerous colpodid taxa were shown to be homologous in their origin, position, and structure (Puytorac et al., 1979; Grain et al., 1979; Didier et al., 1980). Puytorac et al. (1984) suggested a different classification of the colpodid group based on a numerical phenetic analysis.

### MATERIAL AND METHODS

*Bryometopus atypicus* was collected from the top soil (0-5 cm) of a meadow in Salzburg (Austria). Detailed information about the sampling place is given in Foissner (1984). We could not establish pure cultures. Thus, we used material grown in the raw cultures described in Foissner (1982). To reveal the infraciliature, the silver carbonate method was used (cf. Foissner, 1984). The frequently employed fixation in 0.25-4% glutaraldehyde was inappropriate for transmission electron microscopy, because all extrusomes were discharged destroying the pellicula. The structures were only preserved fairly well in 12% (w/v) glutaraldehyde in 0.05 M Na-cacodylat buffer, pH 7.0. The procedures that followed were the same as described in Foissner and Foissner (1985).

### RESULTS

**MORPHOLOGY OF THE NON-DIVIDING SPECIMEN**

(fig. 1)

The morphological and biometric characters of the investigated population of *Bryometopus atypicus* are in accordance with those described in Foissner (1980, 1984). Therefore, we only give a photo-

**MORPHOGENESIS**

(fig. 2-9)

The stomatogenesis begins with a proliferation of basal bodies within about 7-10 right lateral somatic
kineties near the posterior end of the body (fig. 2, 5). If the number of basal bodies increases, the anlagen separate in the middle. The posterior basal bodies form the adoral organelles and the anterior kinetids form the paroral membrane (fig. 3, 6-8). During the cytokinesis the new oral apparatus turns about 45° to the right. This causes the paroral membrane to be placed along the longitudinal axis of the cell (fig. 9).

In the early morphogenetic stages the basal bodies of the parental paroral membrane are narrowly arranged (fig. 2, 5). Later the pairs of basal bodies appear to be separated and disordered (fig. 3, 4, 6-8). The pharyngeal fibers are not stained with silver carbonate in the last stages of the morphogenesis. These observations indicate that some parts of the parental oral apparatus are reorganized during the divisional events.

The proliferation of basal bodies within the somatic kineties occurs as follows: at first, the pairs separate and anteriad of each anterior basal body a new kinetid develops. In this way typical triades are formed (fig. 2, 4, 5). Later more or less distinct quadrilles originate, when a new kinetid is generated anteriad of the posterior basal body of the former pair. They become separated during the stretching of the cell (fig. 3, 7-9).

The division of the nuclear apparatus is without peculiarities (fig. 3, 6, 7). Likewise, the silverline system remains unchanged.

FINE STRUCTURE

OF THE SOMATIC CORTEX
(fig. 10-17)

The pellicula is composed of a three-layered cell membrane, flat alveoli, and a fine epiplasm. Ectoplasm and endoplasm are separated by a filamentous layer, about 150 nm in thickness, which is designated as lamina corticalis (Corliss, 1979). This microfilamentous material adjoins the proximal ends of the basal bodies (fig. 10, 17).

The somatic kineties consist of paired, ciliated basal bodies, which are orientated obliquely to the longitudinal axis of the kinety (fig. 10-12). The basal bodies are 437-529 nm in length (x = 479, n = 7) and 161-184 nm in diameter (x = 176, n = 7). Their proximal ends are surrounded by electron-dense material, where the fibrillar derivatives of the somatic kinetids and the 3 interkinetosomal linkages are anchored (fig. 10, 14). Desmose 1 extends between the triplet 9 (which bears the postciliary microtubules) and the posterior basal body (fig. 10, 14). Desmose 2 joins the triplets 2, 3 of the anterior basal body and the triplets 3, 4 of the posterior one. At the same level desmose 3 extends between the triplet 1 of the anterior kinetid and the triplet 5 of the posterior basal body (fig. 10, 14). Serial sections show that the more distal proceeding medial desmose of typical colpodid taxa is missing. The anterior basal body has 5-7 (x = 5, n = 7) transverse microtubules above the triplets 3-5 and 1-7 (x = 4, n = 11) postciliary microtubules. Fibrillar associates of the posterior basal body include about 5-7 transverse microtubules beside the triplets 2-4, which are usually sectioned very obliquely, 4-7 (x = 5, n = 11) postciliary microtubules, and a kinetodesmal fibril at the triplets 6, 7 having a major periodicity of 826-920 nm (x = 879, n = 4). Two parasomal sacs, about 46-80 nm in diameter (x = 66, n = 6) occur, one anteriad of the kinetodesmal fibril and the other posteriad of the posterior transverse ribbon (fig. 10-13, 34, 35c). In the anterior region of the body a third basal body frequently occurs anteriad of the dikenetids showing transverse and postciliary microtubules. It is neither ciliated nor joined to the neighbouring pair of basal bodies (fig. 14-16).

FINE STRUCTURE

OF THE ORAL REGION
(fig. 18-29)

The paroral membrane is aligned with the somatic kinety 1 (fig. 1), but its dikenetids are more narrowly spaced and have a different structure. The paroral pairs are only joined by 2 desmoses at the triplets 9 and 1, 2 of the anterior basal body and at the triplets 5 and 3 of the posterior kinetid (fig. 18). Only one parasomal sac is placed beside the posterior basal body on the right side (fig. 25). They lack a kinetodesmal fibril as well as the postciliary microtubules of the anterior basal body and the posterior transverse microtubules. The characteristic zigzag-pattern of the paroral membrane results from the narrow and oblique arrangement of the dikenetids. By that means the 5 postciliary microtubules of the posterior basal body are situated just beside the 5 transverse fibrils of the anterior basal body of the neighbouring pair (fig. 21). Furthermore, the postciliary microtubules are orientated parallel to the longitudinal axis of the paroral membrane (fig. 18). Nematodesmata originate at the proximal ends of the paroral basal bodies (fig. 19). They
unite to a bundle which extends to the cytopharynx underneath and parallel to the longitudinal axis of the membrane (fig. 20). The oral ribs of the right buccal wall, which has a characteristic alveolar layer, contain the postciliary and transverse ribbons of the paroral membrane and numerous single microtubules surrounded by electron-dense material (fig. 23, 24, 26). The origin of the last mentioned elements was not clarified. In the posterior part of the buccal wall a cross-striated filamentous material and a cytoplasmic lip are situated (fig. 23, 24, 26). Some sections indicate that this lip bends over the cytopharyngeal region and forms a cavity-like structure.

The adoral organelles consist of 2 longer rows of 5-7 basal bodies and a shorter, right row of 2-3 kinetids. The basal bodies of each organelle are arranged in a zigzag-pattern and linked by longitudinal and oblique electron-dense material in their proximal third (fig. 27). At their basis a filamentous reticulum occurs separating the bright ectoplasm from the dark endoplasm (fig. 29). We discriminate this structure from the somatic lamina corticalis according to Peck (1978). In addition nematodesmata originate at the proximal ends of the basal bodies and extend to the cytopharynx (fig. 28). At least the external kinetids of each adoral organelle bear 3-7 convergent postciliary microtubules (k = 5, n = 29), which extend to the paroral (fig. 26, 28). Parasomal sacs are irregularly distributed between the rows of basal bodies.

INTERNAL ORGANIZATION (fig. 30-33)

In the somatic region irregularly distributed mitochondria are found in both the ectoplasm and the endoplasm (fig. 17). Many extrusomes occur underneath the pellicula (fig. 12, 13, 33). Their content may be concentrated, thread-like or para-crystalline. Structures undistinguishable from these extrusomes are frequently in the endoplasm too. Some pictures suggest that their content is discharged into the food vacuoles (fig. 31). Food vacuoles can coalesce to a big, single vacuole (fig. 30). They are full of bacteria, spores of fungi, myelin structures, and vesicles. The micronucleus is situated close to the macronucleus and has its own membrane (fig. 32). Nucleolar organizing centers are discernible in the macronucleus. Such centers are known to exist in many species of very different taxonomical categories (Frenkel, 1980; Raikov, 1978). The nuclear apparatus is rich in chromatin. The expulsion porus of the contractile vacuole is tubular and bordered by a single row of microtubules, similar to those described for other ciliates (Lynn, 1976a, d, 1978, 1979; Peck, 1977; Lynn and Didier, 1978).

DISCUSSION

IS BRYOMETOPUS A COLPODID TAXON?

1. The morphogenesis is on the whole fairly similar in all colpodid taxa. Thus, Foissner (1985) considered it to be a conservative character. However, with respect to the stomatogenesis there are two distinct groups. The genera Cyrtolophosis, Platyprya, Woodruffia, Sorogenia, Bursaria, and Microdiaphanosoma generate the new oral apparatus within the somatic kineties and divide in the free-moving condition (grölère, 1975, buittkamp, 1977; mc coy, 1977; dragescu et al., 1977; bardele, foissner, and blanton (unpub.); perez-paniagua et al., 1980; foissner, 1981). In contrast, the Colpodidae and Grossglockneridae rearrange the somatic kineties radially and symmetrically in the division cyst and proliferate new basal bodies at the anterior ends of the kineties (perez-paniagua and Perez-Silva, 1978; Perez-Paniagua et al., 1979; Garcia-Rodriguez et al., 1981; foissner and didier, 1983). This complica-

Fig. 1-4. – Morphology and morphogenesis of Bryometopus atypicus. Light micrographs after silver carbonat impregnation. Fig. 1. – Infraclature of a non-dividing specimen in ventral view. The paroral membrane (P) is aligned with the somatic kinety 1 (SK 1). aO, adoral organelles; Ma, macronucleus; Mi, micronucleus. Fig. 2. – The stomatogenesis begins with a proliferation of basal bodies (A) within several right lateral somatic kineties near the posterior end of the body. Fig. 3. – Intermediate morphogenetic stage. Arrow, slightly disorganized parental paroral membrane. Fig. 4. – Late divisional stage. Conspicuous zigzag- pattern of the paroral membrane of the proton. It is not appropriate to give magnifications to this kind of preparation, because the specimens become very inflated. Additionally, they are strongly squeezed for observation.
Fig. 5-9. – Morphogenesis of *Bryometopus atypicus* drawn after silver carbonat impregnation. Fig. 5. – Early divisional stage. Note the triades (arrows) of basal bodies within the somatic kineties. Fig. 6-8. – Intermediate morphogenetic stages. The anlagen of the opisthe arrange to the oral structures. Note the slightly disordered paroral membrane of the proter. Fig. 9. – Late divisional stage.
Transmission electron micrographs of the somatic cortex of *Bryometopus atypicus*. Fig. 10-12. – Transverse sections of somatic dikinetids. Fig. 10. – At the proximal ends of the basal bodies three desmoses extend between the pair. Postciliary microtubules are associated with each basal body. At this level the *lamina corticalis* is situated. 67 000 : 1. Fig. 11. – At the medial level of a pair the transverse microtubules of the anterior and the posterior basal body and the kinetodesmal fibril are sectioned. 67 000 : 1. Fig. 12. – The distal section shows one of the parasomal sacs and a discharged mucocyst. 64 000 : 1. Fig. 13. – Longitudinal section of an anterior basal body of a pair. 52 000 : 1. Fig. 14-16. – Transverse sections of somatic triades in the anterior part of the body. Fig. 14. – The third anterior basal body has transverse and postciliary microtubules, but it is unjoined to the « typical » dikinetid. 64 000 : 1. Fig. 15-16. – The additional basal body is unciliated (arrow). 64 000 : 1. Fig. 17 – Longitudinal section of a somatic kinety. The *lamina corticalis* is adjoined to the proximal ends of the basal bodies. 52 000 : 1. D 1-3, desmoses; Kd, kinetodesmal fibril; Lc, *lamina corticalis*; Mu, mucocyst; Pca, anterior postciliary ribbon; Pcp, posterior postciliary microtubules; Ps, parasomal sac; Ta, anterior transverse ribbon; Tp, posterior transverse microtubules.
ted mode of morphogenesis is probably the derived state of the more frequently occurring situation, which is represented by the first group and shared by Bryometopus (fig. 2, 5, 6).

Another remarkable aspect is the varying degree of dedifferentiation of the parental oral structures during the divisional events. At least four types, which presumably are phylogenetic sequence, are distinguishable. The oral apparatus of Platophrya, Sorogena, and Microdiaphanosoma seems to remain unchanged (Grolière, 1975; Bardele, Foissner and Blanton (unpubl.); Foissner, 1981). In Woodruffia only the right buccal area is disorganized and rebuilt by the paroral primordium (Puytorac et al., 1979). The rearrangement of the paroral membrane of Bryometopus is less striking, however, there is probably an interkinetosomal reorganization (fig. 6-8). Furthermore, the pharyngeal fibers of Bryometopus and Platophrya (Dragesco et al., 1977) are not provable during the last morphogenetical stages, but it is not known whether they are resorbed and rebuilt or only unimpressable. The right as well as the left buccal structures are partly reorganized in Cytolophosis and Bursaria and completely dedifferentiated in Colpoda, Tilia, Bresslaua, and Pseudoplathyrya (Buitkamp, 1977; McCoy, 1977; Perez-Paniagua et al., 1979, 1980; Perez-Paniagua and Perez-Silva, 1978; Garcia-Rodriguez et al., 1981; Foissner and Didier, 1983).

2. The position of the fibrillar derivatives and the parasomal sacs of the somatic dikinetids of Bryometopus atypicus resemble the colpodid pattern (compare fig. 35 b, c).

3. The left buccal structures of B. atypicus show convergent postciliary microtubules, interkinetosomal linkages, nematodesmata, and parasomal sacs like those of typical colpods (Lynn, 1976a-d, 1978; Njine, 1979; Grain et al., 1979; Puytorac et al., 1979; Perez-Paniagua et al., 1979, 1980; Didier et al., 1980; Goldner and Lynn, 1980; Garcia-Rodriguez et al., 1981).

4. The fine structure of the extrusomes of B. atypicus is very similar to that known in Bryophrya, Platophrya, Enigmastoma (syn. Kuikikophrya, see Foissner and Adam, 1981), Woodruffia, Cytolophosis, and Pseudoplathyrya (Grain et al., 1979; Dragesco et al., 1977; Njine, 1979; Puytorac et al., 1979, 1983; Didier et al., 1980).

These four reasons indicate a colpodid nature of the « heterotrich » genus Bryometopus, but there are some contradictory findings:

1. The structure and the position of the lamina corticalis of B. atypicus resemble those known in haptorid and buetschlid ciliates (fig. 17: Wessenberg and Antipa, 1968; Grain and Golinska, 1969; Grain, 1970; Holt et al., 1973; Foissner and Foissner, 1983). Furthermore, the prostomial gymnostomes usually have oral dikinetids, whose transverse ribbons extend from the anterior kinetosomes to support the cytopharynx (Holt et al., 1973; Lynn, 1981; Small and Lynn, 1981). This is also true of the right buccal ciliature of Bryometopus and Bursaria (fig. 18, 21, 23, 36 g, h; Perez-Paniagua et al., 1980). These fine structural characters indicate a haptorid ancestor of the colpodids. Likewise, Corliss (1979) pointed to some quite primitive features of the Colpodida, such as a single RNA-nucleolus in the macronucleus, common absence of conjugation, and lack of toxicysts and trichocysts. Foissner (1985) mentioned similarities in the silverline system and the course of the somatic kineties of haptorids and bryometopids.

2. Generally colpodid taxa show a medial linkage slightly distal to the two proximal desmoses of the somatic dikinetids (Didier and Chessa, 1970; Lynn, 1976 a-d, 1979, 1980; Grain et al., 1979; Goldner and Lynn, 1980; Didier et al., 1980;...
Fig. 26-29. – Fine structure of the left buccal area of *Bryometopus atypicus*. Fig. 26. – Longitudinal section of the oral ribs (*Or*) with its microtubules (*Mt*) and the cytoplasmic lip (*Cl*). The postciliary microtubules (*Pc*) of the adoral organelles extend to the left buccal wall. 42 000 : 1. Fig. 27. – Transverse section of the adoral organelles. At least the external basal bodies bear convergent postciliary microtubules (*Pcc*). The kinetids are arranged in a zigzag-pattern (lines) and joined by oblique and longitudinal links (arrowheads). 52 000 : 1. Fig. 28. – Nematodesmata (*Nd*) and postciliary microtubules (*Pc*) originate at the basis of the adoral organelles. 70 000 : 1. Fig. 29. – Longitudinal section of adoral organelles. The filamentous reticulum (*Fr*) at the basis of the left buccal structures separates the dark endoplasm and the bright ectoplasm. 31 000 : 1.
Fig. 30-33. – Transmission electron micrographs of the internal organization of *Bryometopus atypicus*. Fig. 30. – Food vacuoles often unite to a large single vacuole. 13 000 : 1. Fig. 31. – The content of an extrusome-like organelle discharges into a food vacuole (FV). 56 000 : 1. Fig. 32. – The macronucleus (Ma) has large nucleoli (N), where nucleolar organizing centers (arrows) are discernible. It is accompanied by a single micronucleus (Mi). 12 000 : 1. Fig. 33. – Mucocyst (Mu) in the somatic cortex. 72 000 : 1.
Garcia-Rodriguez et al., 1981). However, Bryometopus atypicus has three proximal desmoses like Stentor coeruleus (fig. 35 a, c) and Loxodes magnus (Huang and Pitelka, 1973; Puytorac and Ninje, 1970). The hypotrich Paraurostyla weissel shows this kind of linkage during the morphogenesis (Jerk-Dziadosz, 1980, 1981, 1982). Goldner and Lynn (1980) and Wicklow (1981, 1982) emphasized other similarities in the somatic kinetid pattern of these groups. For instance, Bursaria truncatella (described in Perez-Paniagua et al., 1980) has a colpodid «left» Km-fiber as well as a heterotrich «right» one. We suppose that the right Km-fiber has evolved independently twice in heterotrich and colpodid ciliates. In addition, fine structural characters of the oral apparatus relate colpodids and spirotrichs, besides the obvious similarities in the position of the paroral and oral organelles. Small and Lynn (1981) considered the oral transverse fibrillar system to be a special character of the Rhabdophora. Now it is also described in two colpodid taxa, hypotrichs and heterotrichs, although strongly reduced in Stentor or even lacking in Condylostoma (Perez-Paniagua et al., 1980; Bakowska and Jerk-Dziadosz, 1978; Wicklow, 1981, 1982; Bernard and Bohatier, 1981; Bohatier, 1978; see fig. 36 a, b, g, h, i, j, l, m). Oral transverse microtubules are also absent in hymenostomes and the most colpodid taxa (Didier and Chessa, 1970; Didier et al., 1980; Garcia-Rodriguez et al., 1981; Goldner and Lynn, 1980; Grain et al., 1979; Lynn, 1976a, 1979; Puytorac et al., 1979, 1983; Peck, 1977, 1978; Smith, 1982 a, b). Therefore, we accept the oral transverse fibrillar system to be ancestral, as suggested by Puytorac and Grain (1976) and Corliss (1979). Consequently, its absence is considered to be a derived character. A further reduction of oral fibrillar associates is shown by the colpodid Platophrya, whose adoral organelles even lack the postciliary microtubules (Dragesco et al., 1977).

3. Bryometopus atypicus is related to the hymenostomes by the oral ribs, the cross-striated filamentous material, and the filamentous reticulum at the basis of the adoral organelles. This constellation of characters and the special cytoplasmic lip are unknown in other colpodid taxa. However, Didier et al. (1980) described in Cyrtolophosis a marked alveolar layer in the region of the cytostome and compared it to the oral ribs of the hymenostomes, but their pictures are not very clear in this point. Moreover, in contrast to Bryometopus and the hymenostome ciliates, the «oral ribs» of Cyrtolophosis show microtubules originating from the basal bodies lying in the left oral area. Comparing hymenostomes and Bryometopus, the oral ribs of the first group are more conspicuous and perpendicular to the pellicula supported by a short and a longer row of microtubules (Peck, 1977, 1978; Corliss, 1979). Only one of these rows originates from the paroral structures, because they still show postciliary ribs (Sattler and Staehelin, 1979; Smith, 1982 a, b). In contrast, the two fibrillar systems of B. atypicus originate from the paroral membrane and the oral ribs are very flat. In addition, the postciliary and transverse ribs are situated almost parallel to the pellicula (fig. 23). These characters resemble somatic conditions and suggest that Bryometopus has an ancestral type of oral ribs.

Like B. atypicus, Tetrahymena pyriformis has a cross-striated filamentous material between the oral ribs and the paroral membrane (Sattler and Staehelin, 1979). This is true of the microstome form of T. vorax, whereas its macrostome variant shows a «simple» filamentous material (Smith, 1982 a, b).
STRUCTURE, PHYLOGENY OF BRYOMETOPUS ATYPICUS
b). Striated regions of microfilaments were also described in the right oral area of Nycctotherus, Dileptus, and Glaucoma (Paulin, 1967; Grain and Golinska, 1969; Lynn and Didier, 1978). In Frontonia and Avelia similar structures are in the left oral region (Gil, 1984; Nouzarede, 1976). Sattler and Stæhelin (1979) compared this material to muscles and supposed peristaltic functions.

This comparison indicates numerous new relations between the oral structures of colpodids, haptorids, sib promotrichids, and gymnolophids, but clear phylogenetic relationships are not recognizable. Therefore, like Lynn (1976 a, 1981), we emphasize the somatic kinetid pattern, which seems to be more conservative and suggest an inclusion of Bryometopus into the Colpodea, as already supposed by Foissner (1984, 1985).

THE POSITION OF BRYOMETOPUS WITHIN THE COLPODEA

The light microscopical findings, such as the kreyellid silverline system and the arched somatic kineties, indicate an ancestral position of Bryometopus within the class (Foissner, 1985). This is supported by our electron microscopical results. The somatic kineties of B. atypicus have no conspicuous colpodid «left» Km-fiber and lack nematodesmata (fig. 34). Likewise, the strange organization of the oral region points to an early separation from the typical colpodids.

A somatic filamentous layer is also described in Tillina magna, Bursaria truncatella, Enigmostoma dragescoi, and Bresslaua insidiatrix (Lynn, 1976 d, 1980; Nihm, 1979; Lynn, 1979 without figure). But their microfilaments are situated much deeper in the cytoplasm than those of Bryometopus. In addition, they are connected by nematodesmata (Tillina, Bursaria) or a thick micro-filament (Enigmostoma) to the somatic kineties. In Bursaria and Tillina the filamentous material forms a network like that known in some peniculins (Allen, 1971; Didier, 1971). Therefore, we suppose that the complex systems of Bursaria, Tillina, and Enigmostoma are evolved states of the «simple» lamina corticalis, which occurs in Bryometopus and is well known in haptorids.

Colpodid ciliates were characterized by oral postciliary ribbons extending to support the cypopharynx (Small and Lynn, 1981). Therefore, Bursaria and Bryometopus with their paroral transverse microtubules have an extraordinary position. Additionally both taxa were considered to be typical heterotrich ciliates for a long time and both species have somatic triades (Perez-Paniagua et al., 1980). Unfortunately, the French authors did not discuss the special aspect of the right buccal ciliation of Bursaria truncatella. In contrast, they compared it with the «stichodyades» of Cyrtolophosis (Didier et al., 1980), though Puytorac and Grain (1976) stated that this type does not show a transverse fibrillar system. Consequently, Bursaria and Bryometopus belong to the type of «paroral in pairs». If we accept the possession of the paroral transverse microtubules to be ancestral, we may suppose that the Cyrtolophosidida and the Bryophyrida descended from a Bryometopus-like taxon, whereas the Colpodida and the Grossglocknerida derived from a Bursaria-like taxon. The homogeneity of the first group is supported by the morphogenesis and the silverline systems (Foissner, 1985).

In addition, Bryometopus and Cyrtolophosis are similar in the orientation of the paroral postciliary microtubules parallel to the longitudinal axis of the membrane and the nematodesmal bundle (fig. 36 h, k; Didier et al., 1980). The Colpodida, Grossglocknerida, and Bursariomorpha are united by the colpodid silverline system (Foissner, 1985) and the most extensive participation of the parental oral structures during the division. Consequently, within the Colpodea the lack of transverse microtubules of the right buccal structures has evolved more than once. In addition, the broad variability of the paroral ciliature, for instance its arrangement, the orientation of the postciliary microtubules, and the interkinetosomal links (compare fig. 36 d-h, k), indicates that certain types of the colpodid oral ciliation have evolved by convergence (Bardele, 1981).

This suggests an artificial classification of some colpodid taxa in the recently proposed systems of Puytorac et al. (1984) and Foissner (1985). For example, we do not believe that the position of the micronucleus in the perinuclear area of the macro-nucleus has evolved twice in platyophryid and cyrtolophosid taxa, as the phenetic scheme of Puytorac et al. (1984) suggests. However, the monophyletic origin of the Colpodea is very likely, mainly because of the backward transverse ribbon of the posterior somatic basal body. Apart from these phylogenetic considerations, we must pay attention to the strange constellation of characters presented by Bryometopus: the lamina corticalis, the three proximal somatic desmoses, the paroral
transverse microtubules, the cross-striated filamentous material, the special cytoplasmic lip, the oral ribs, and the filamentous reticulum at the basis of the adoral organelles. In our opinion these peculiarities justify the division of the Colpodea in the subclasses Bryometopida and Colpodia, as proposed by FOISSNER (1985). Whether this separation is tenable must be clarified by the investigations of further bryometopid genera, especially of Microdia- phanosoma.

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