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

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Morphogenèse, ultrastructure et relations phylogénétiques du Cilié « Hétérotriche » *Bryometopus atypicus* (Protozoaire, Colpodea)

#### RÉSUMÉ

La stomatogenèse de Bryometopus atypicus est paracinétienne. L'ecto- et l'endoplasme sont séparés par une lamina corticalis. Les cinéties somatiques sont composées de dicinétides ciliées. Les cinétosomes appariés sont réunis par 3 desmoses proximales et ils sont associés à deux sacs parasomaux. Le cinétosome antérieur porte 5 - 7 fibres transverses et 1 à 7 fibres postciliaires, le cinétosome postérieur une fibre cinétodesmale, 5 - 7 fibres transverses, 1 - 7 fibres postciliaires. Dans la région antérieure, il y a quelques triades avec un cinétosome supplémentaire non cilié et non réuni au cinétosome antérieur. Le cinétosome postérieur des paires de la parorale a des fibres postciliaires parallèles à l'axe longitudinal de l'organelle ; le cinétosome antérieur a des fibres transverses. Les 2 systèmes fibrillaires s'étendent aux crêtes orales. Sous-jacent et parallèle à la parorale, un faisceau de némadesmes s'étend jusqu'au cytopharynx où un matériel fibrillaire et une lèvre cyto-

plasmique sont décelables. Les organelles adoraux sont composés de 3 rangées de cinétosomes dont une rangée droite plus courte qui porte des fibres postciliaires convergentes, des liaisons intercinétosomiennes, des sacs parasomaux, des némadesmes et un réticulum filamenteux à la base. La morphogenèse et l'ultrastructure des dicinétides, des mucocystes, des organelles adoraux de Bryometopus atypicus justifient son inclusion dans le groupe des Colpodes. Cependant, on relève aussi chez ce Cilié des caractères d'autres taxa : une lamina corticalis comme chez les Haptorida; 3 desmoses proximales comme chez les Karyorelictida et les Spirotriches ; des microtubules transverses à l'infraciliature parorale comme chez les Gymnostomes et Spirotriches ; des crêtes orales, du matériel fibrillaire à la base de la parorale comme chez les Hyménostomes. D'où la justification d'une sous-classe Bryometopia chez les Colpodea.

#### SUMMARY

The stomatogenesis of *Bryometopus atypicus* is parakinetal. Ecto- and endoplasm are separated by a *lamina corticalis* at the proximal ends of the basal bodies. The somatic kineties 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 kinetodesmal fibril, 5-7 transverse microtubules, and 1-7 postciliary microtubules. In the frontal region there are some triades 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

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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 haptorids; 3 proximal desmoses of karyorelictids and spirotrichs; paroral transverse

#### 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. 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.

#### Synopsis

Morphogenetical processes and general cortical fine structural characters of *Bryometopus atypicus* are those of colpodea. However, pecular characters (*lamina corticalis*, 3 proximal desmoses, paroral transverse microtubules, oral ribs, sub-paroral microfibrillary 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; PUY-TORAC 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 Colpodia. 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 % (!) 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 FOISS-NER (1980, 1984). Therefore, we only give a photograph of the interphase infraciliature for a better understanding of the divisional processes (fig. 1).

#### 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  $45^{\circ}$  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. Ectoand 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 ( $\bar{x} = 479$ , n = 7) and 161-184 nm in diameter ( $\bar{x} = 176$ , n = 7). Their proximal ends are surrounded by electron-dense material, where the fibrillar derivates 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 microtubu-

les according to the convention of PUYTORAC, 1970) of the anterior basal body and the triplets 5, 6 of the posterior kinetid. 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 ( $\bar{x} = 5$ , n = 7) transverse microtubules above the triplets 3-5 and 1-7 ( $\bar{x} = 4$ , 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 ( $\bar{x} = 5$ , n = 11) postciliary microtubules, and a kinetodesmal fibril at the triplets 6, 7 having a major periodicity of 826-920 nm ( $\bar{x} = 879$ , n = 4). Two parasomal sacs, about 46-80 nm in diameter ( $\bar{x} = 66$ , 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 dikinetids 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 dikinetids 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 dikinetids. 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 electrondense 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 ( $\bar{x} = 5$ , n = 29), which extend to the pellicula (*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 paracristalline. 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, Platyophrya, Woodruffia, Sorogena, Bursaria, and Microdiaphanosoma generate the new oral apparatus within the somatic kineties and divide in the free-moving condition (GROLIÈRE, 1975, BUIT-KAMP, 1977; MC COY, 1977; DRAGESCO *et al.*, 1977; BARDELE, FOISSNER, and BLANTON (unpubl.); 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-

<sup>FIG. 1-4. – Morphology and morphogenesis of</sup> *Bryometopus atypicus*. Light micrographs after silver carbonat impregnation.
FIG. 1. – Infraciliature 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 proter.

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.

## STRUCTURE, PHYLOGENY OF BRYOMETOPUS ATYPICUS

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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.



FIG. 10-17. – 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 occuring 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 a phylogenetic sequence, are distinguishable. The oral apparatus of *Platvophrva*. 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 Platyophrya (DRA-GESCO et al., 1977) are not provable during the last morphogenetical stages, but it is not known whether they are resorbed and rebuilt or only unimpregnable. The right as well as the left buccal structures are partly reorganized in Cyrtolophosis and Bursaria and completely dedifferentiated in Colpoda, Tillina, Bresslaua, and Pseudoplatyophrya (BUITKAMP, 1977; MC COY, 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 derivates and the parasomal sacs of the somatic dikinetids of *Bryome*-topus 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 colpodids (LYNN, 1976*a-d*, 1978; NJINE, 1979; GRAIN *et al.*, 1979; PUYTORAC *et al.*, 1979; PEREZ-PANIAGUA *et al.*, 1979, 1980;

DIDIER et al., 1980; GOLDER 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*, *Platyophrya*, *Enigmostoma* (syn. *Kuklikophrya*, see FOISSNER and ADAM, 1981), *Woodruffia*, *Cyrtolophosis*, and *Pseudoplatyophrya* (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; WESSEN-BERG and ANTIPA, 1968; GRAIN and GOLINSKA, 1969; GRAIN, 1970; HOLT et al., 1973; FOISSNER and FOISSNER, 1985). 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; GOLDER and LYNN, 1980; DIDIER *et al.*, 1980;

<sup>FIG. 18-25. – Fine structure of the right buccal area of</sup> *Bryometopus atypicus*. FIG. 18. – Proximal transverse section of the paroral pairs of basal bodies which are linked by two desmoses (D). The anterior kinetid shows transverse microtubules (Ta). The posterior basal body has a postciliary ribbon (Pcp). 52 000: 1. FIG. 19. – Nematodesmata (Nd) originate at the basis of the paroral kinetids. 56 000: 1. FIG. 20. – The nematodesmal bundle (Ndb) extends parallel to the longitudinal axis of the paroral membrane. 52 000: 1. FIG. 21. – The paroral basal bodies are arranged in a zigzag-pattern. Therefore, the transverse microtubules of the anterior kinetid (Ta) lay just beside the postciliary ribbon of the posterior basal body (Pcp) belonging to the neighbouring pair. 52 000: 1. FIG. 23. – Oblique section of the cytopharyngeal region showing the cytoplasmic lip (Cl). Arrowheads, single microtubules underneath the fibrillar derivates (Mt) of the paroral membrane. 48 000: 1. FIG. 24. – The posterior part of the buccal wall shows cross-striated filamentous material. Single microtubules (Mt) are recognizable underneath the alveoli of the oral ribs (Or). 52 000: 1. FIG. 25. – Parasomal sacs (Ps) are situated to the right of the paroral membrane. 52 000: 1. FIG. 2000: 1.





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 (*C1*). 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 (*Pcc*) 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, Brvometopus atypicus has three proximal desmoses like Stentor coeruleus (fig. 35 a, c) and Loxodes magnus (HUANG and PITELKA, 1973; PUYTORAC and NJINE, 1970). The hypotrich Paraurostyla weissei shows this kind of linkage during the morphogenesis (JER-KA-DZIADOSZ, 1980, 1981, 1982). GOLDER 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 spirotrich, besides the obvious similarities in the position of the paroral and adoral 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 JER-KA-DZIADOSZ, 1978; WICKLOW, 1981, 1982; BER-NARD 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: GOLDER 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 *Platyophrya*, 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 ribbons (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 ribbons 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 STAE-HELIN, 1979). This is true of the microstome form of *T. vorax*, whereas its macrostome variant shows a « simple » filamentous material (SMITH, 1982 *a*,

FIG. 34-36. – Diagrammatic drawings. Cell's right is to observer's left (except fig. 35). The anterior end of the cell is toward the top of the drawing. FIG. 34. - Reconstruction of the somatic cortex of Bryometopus atypicus. Fv, food vacuole; Kd, kinetodesmal fibril; Lc, lamina corticalis; M, mitochondrium; Mu, mucocyst: Pca, postciliary microtubules of the anterior basal body of a pair; Pcp, postciliary ribbon of the posterior basal body of a pair; Ps, parasomal sac; Ta, transverse microtubules of the anterior kinetid of a pair; Tp, transverse ribbon of the posterior basal body of a pair. FIG. 35. - Schemes of the somatic dikinetids of Stentor (a HUANG and PITELKA, 1973), Colpoda (b LYNN, 1981), and Bryometopus (c). Note the similar interkinetosomal links of the heterotrich (a) and the colpodid ciliate (c). FIG. 36. - Schematic representation of the buccal ciliature of haptorid (a), heterotrich (b, i, j), hymenostome (c), colpodid (d-h, k), and hypotrich (1, m) ciliates. The schemes (a-h, k) were drawn according to transmission electron micrographs. We did not change the terms used in the original papers. a: Perioral ciliature of Spathidum (BOHATIER et al., 1978). b: Haplokinety of Climacostomum (PECK et al., 1975). c: Paroral kinety of Glaucoma (PECK, 1978). d: Inverted paroral of Woodruffia (PUYTORAC et al., 1979). e: Right circumoral ciliature of Enigmostoma (NJINE, 1979). f: Paroral of Platyophrya (DRAGESCO et al., 1977). g: Stichodyades of Bursaria (PEREZ-PANIAGUA et al., 1980). h: Paroral in pairs of Bryometopus (fig. 18, 20, 21). i, j: Paroral complex of Stentor (from BERNARD and BOHATIER, 1981). i: Stichodyad at the level of the frontal field, *i*: Inverted pairs at the level of the cytopharynx. k: Stichodyad of Cyrtolophosis (DIDIER et al., 1980). l, m: Right buccal ciliature of Paraurostyla (from BAKOWSKA and JERKA-DZIADOSZ, 1978). l: Outer preoral membranelle. m: Inner preoral membranelle.

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b). Striated regions of microfilaments were also described in the right oral area of *Nyctotherous, 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 STAEHELIN (1979) compared this material to muscles and supposed peristaltic functions.

This comparison indicates numerous new relations between the oral structures of colpodids, haptorids, spirotrichs, and hymenostomes, 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 kinetids 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; NJINE, 1979; LYNN, 1979 without figure). But their microfilaments are situated much deeper in the cytoplasma than those of Bryometopus. In addition, they are connected by nematodesmata (Tillina, Bursaria) or a thick micro-filament (Enigmostoma) to the somatic kinetids. In Bursaria and Tilling 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 cytopharynx (SMALL and LYNN, 1981). Therefore, *Bur*-

saria 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 ciliature 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 Bryophryida 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 Bursariomorphida 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 ciliature 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 macronucleus has evolved twice in platyophryid and cyrtolophosidid taxa, as the phenetic scheme of PUY-TORAC *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 Bryometopia and Colpodia, as proposed by FOISSNER (1985). Whether this separation is tenable must be clarified by the investigations of

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further bryometopid genera, especially of *Microdia-phanosoma*.

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