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Divisional Morphogenesis in *Bakuella pampinaria* nov. spec. and Reevaluation of the Classification of the Urostylids (Ciliophora, Hypotrichida)

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SUMMARY

A new hypotrichous ciliate, *Bakuella pampinaria* nov. spec., colonizing vineleaf and pear-tree litter, is described. *Bakuella pampinaria* differs from the other species of the genus by having distinct rows of yellowish cortical granules. Several morphogenetic differences separate *Bakuella pampinaria* from *Bakuella edaphoni* and other congeners, especially in that the transverse cirri do not participate in the formation of the oral primordium. The type population of *Pseudourostyla cristata* was reinvestigated. Two frontoterminal cirri are recognizable in dividing specimens indicating that this genus is valid, i.e. different from *Urostyla*, which very likely lacks such cirri. The urostyline hypotrichs are recognized as a monophyletic taxon by two apomorphies, viz. the midventral cirri and the partial or complete reorganization of the proter's adoral zone of membranelles during cell division. Phylogeny and evolution within the urostylids are much less clear since character states (apomorphies, plesiomorphies, convergencies) are uncertain and morphogenetic data are still too sparse or inaccurate. This is exemplified on a selected set of genera using Hennig's phylogenetic method.

Introduction

Species of the urostyline hypotrich *Bakuella* have been found in marine, limnetic and terrestrial biotopes [19]. In this paper we describe the morphology and morphogenesis of a new species of this genus occurring in the uppermost layer of decomposing leaves. Another species of this extreme biotope has been described earlier [7]. The investigations on *B. pampinaria* and literature data are used to evaluate recent classifications of urostyline hypotrichs.

Material and Methods

Bakuella pampinaria was collected on December 15th 1990 and on March 15th 1991 from fallen leaves of non-grafted vines and from a pear-tree grown on ecofarmed land.

The top leaf of at least 3 layers of dry leaves was taken. Several such leaves were put in a petri dish and a raw culture according to Foissner [8] was set up. The run off from the raw culture was cautiously centrifuged and put into a small petri dish containing local spring water and a crushed wheat grain to support growth of indigenous bacteria and small ciliates which served as food organisms. *Bakuella pampinaria* divided readily in this culture for some weeks. Body shapes of living specimens were drawn from slides without coverslip. Details were studied on slightly to heavily squeezed individuals using an oil immersion objective. The infraciliature was revealed by Foissner's [10] protargol protocol. Drawings were made with the help of a camera lucida.

To make plain the changes during morphogenetical processes, old (parental) cirri are depicted by contour, whereas new cirri are shaded black.

Terminology is according to [19]. Statistical procedures follow methods described in [17].

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Results

Description of Bakuella pampinaria nov. spec. (Figs. 1–5, Table 1)

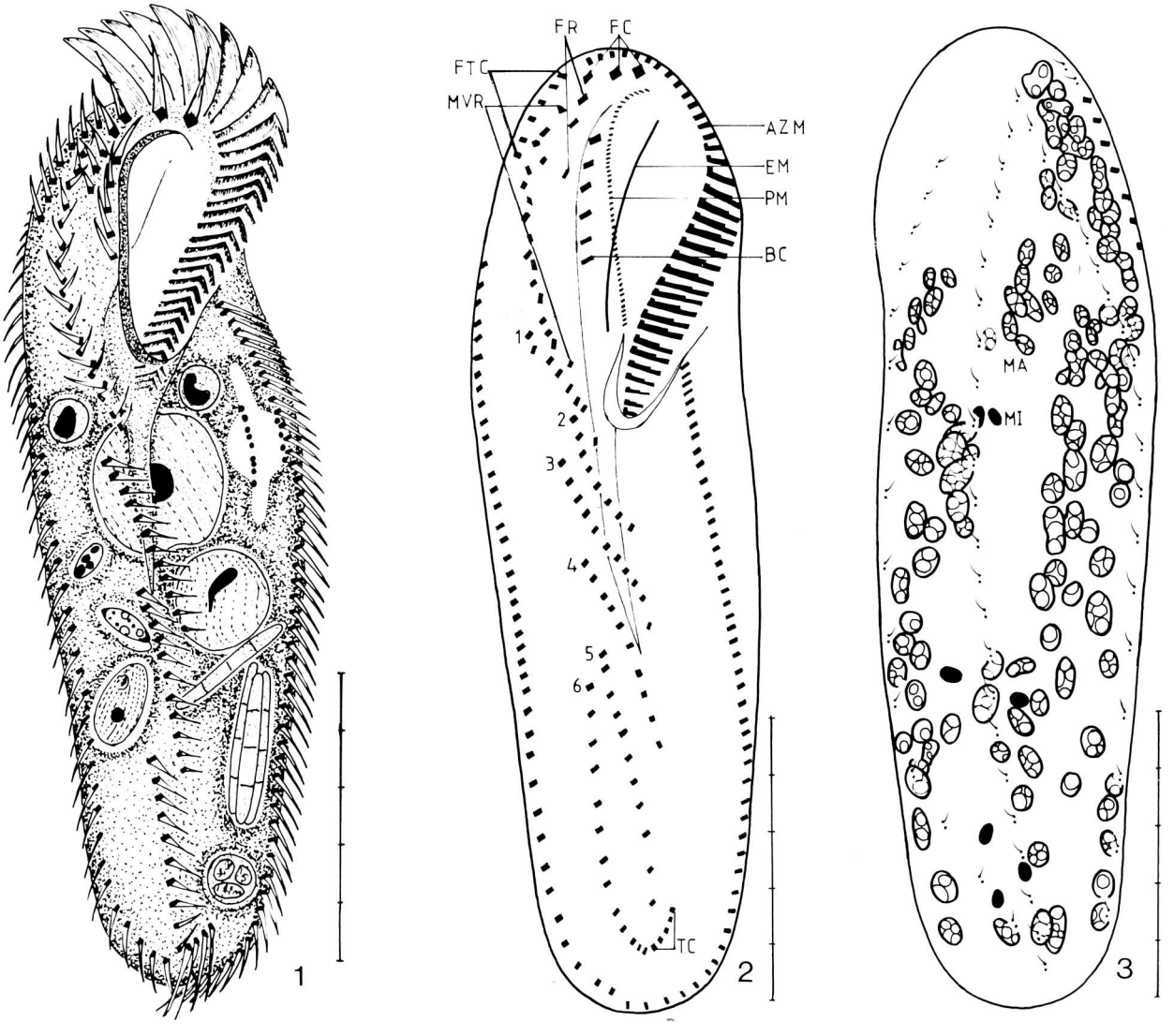
Diagnosis: Size in vivo 90–180 × 25–60 μm. Distinct rows of yellowish cortical granules. 31 adoral membranelles, 5 buccal cirri, 6 frontoterminal cirri, 9 pairs of midventral cirri, 3 ventral rows, 4 transverse cirri and 100 macronuclear segments on average. Posteriormost ventral row adjacent to right transverse cirrus. Transverse cirri not involved in stomatogenesis.

Derivatio nominis: "pampinus" (lat.), vineleaf.

Type location: Litter of vineleaves in the village Schrötten, Styria, Austria (E 15°49′, N 46°47′, alt. 320 m).

Type specimens: A holotype and a paratype of *Bakuella pampinaria* as 2 slides of protargol impregnated cells have been deposited in the collection of microscope slides of the Oberösterreichische Landesmuseum in Linz.

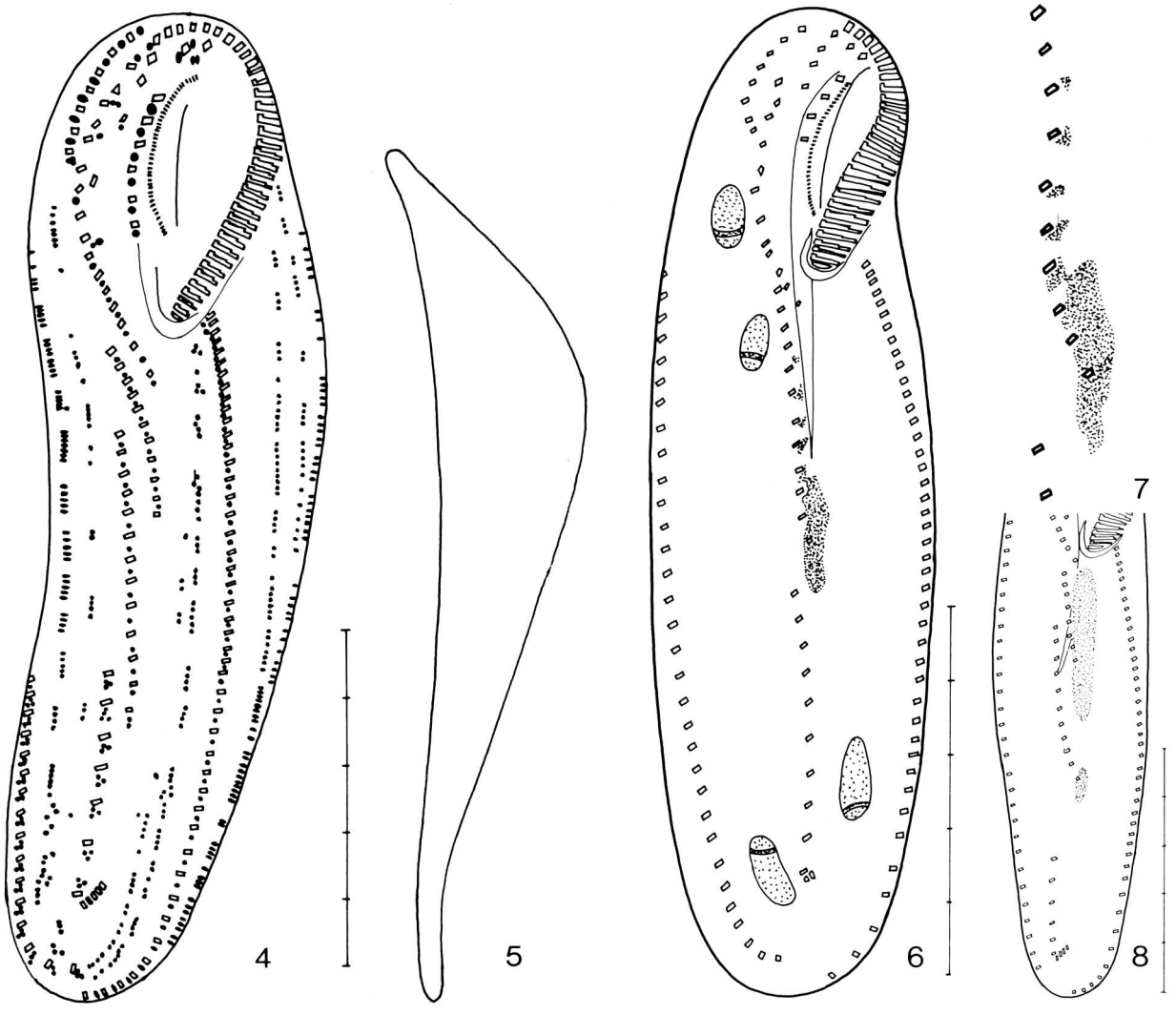
Description (see Table 1 for additional morphometric data): Long-elliptical, right body margin straight to slightly concave, left more or less convex. Both ends slightly narrowed and broadly rounded (Fig. 1). Dorso-ventrally flattened 2–3 : 1 (Fig. 5); highly flexible. Macronuclear segments ellipsoid, in vivo about 4–6 × 3–4 μm. 3–7 ellipsoid micronuclei, 1 to 2 usually near proximal end of adoral zone of membranelles (Fig. 3). Contractile vacuole on left border above mid-body, with inconspicuous collecting canals. Distinct rows of cortical granules within and between cirral and dorsal ciliary rows, recognizable in



Figs. 1–3. *Bakuella pampinaria* from life (Fig. 1) and after protargol impregnation (Figs. 2, 3). – Figs. 1, 2. Ventral views. – Fig. 3. Dorsal view. AZM = adoral zone of membranelles, BC = buccal row, EM = endoral membrane, FC = frontal cirri, FR = frontal row, FTC = frontoterminal row, MA = macronuclear segments, MI = micronuclei, MVR = midventral row, PM = paroral membrane, TC = transverse cirri, 1 to 6 = ventral rows. Scale bar division = 10 μm.

vivo at a magnification of ×100; granules yellowish, ellipsoid, about 1.5–2 × 1–1.5 µm, impregnate with protargol (Fig. 4). Cytoplasm brownish at low magnification, contains many large (up to 35 µm) food vacuoles in well-nourished specimens. Feeds on small ciliates, heterotrophic flagellates and fungal spores. Movement rather slow.

Buccal field large and deep, brightly shining. Adoral zone of membranelles 30–40% of body length. Paroral membrane conspicuous, anterior portion curved, composed of at least 3 rows of basal bodies. Endoral membrane crosses buccal cavity near dorsal inner surface of cell because of very deep buccal cavity; straight in anterior, curved in posterior portion, crosses or parallels paroral membrane depending on position of cell (Figs. 2, 4). Both membranes terminate at same level near proximal portion of adoral zone of membranelles. Pharyngeal fibres conspicuous, form curtain-like structure along entire paroral membrane. Cilia of adoral zone of membranelles in vivo 20 µm, transverse cirri 16 µm, other cirri 10–12 µm. Marginal rows almost confluent posteriorly, upper portion of right row extends onto dorsal side commencing with 2 dorsal bristles. Frontoterminal cirri form distinct row at anterior right margin. Midventral row short, usually terminating at level of adoral zone of membranelles. Distinction between midventral row and 1st ventral row may be difficult in large cells. 3 enlarged frontal cirri, right frontal cirrus at anterior end of short frontal row. Ventral rows extend more or less obliquely, last row adjacent to right transverse cirrus (Fig. 2). Dorsal cilia short, arranged in 3 rows almost as long as cell; no caudal cirri (Fig. 3).

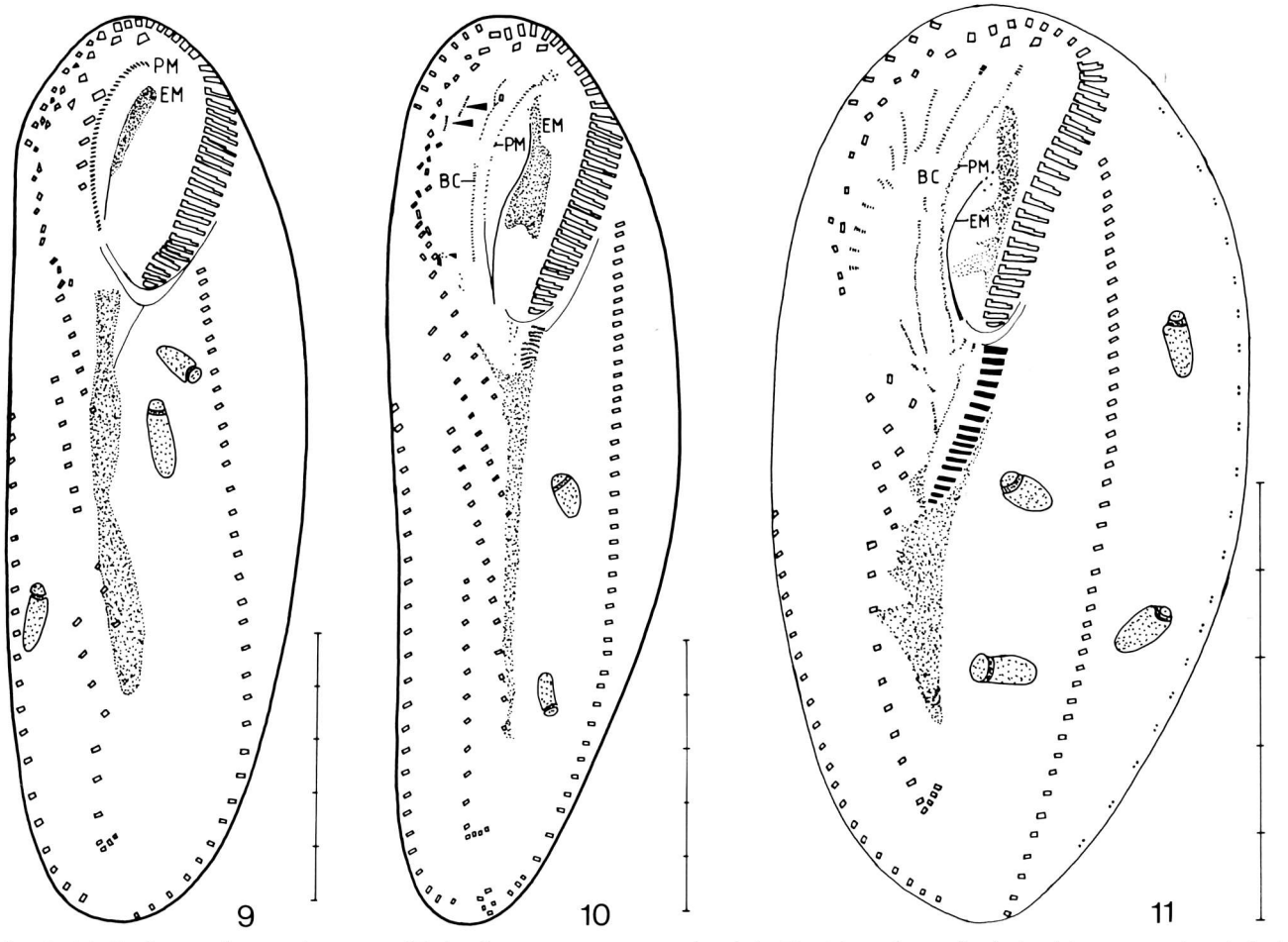


Figs. 4–8. *Bakuella pampinaria* from life (Fig. 5) and after protargol impregnation (Figs. 4, 6–8). – Fig. 4. Ventral view showing cortical granules (black dots) and cirral pattern (depicted by contour). – Fig. 5. Lateral view. – Figs. 6–8. Very early morphogenetic stages; Fig. 7 is an enlarged detail from Fig. 6. Scale bar division = 10 µm.

Table 1. Morphometric characterization of *Bakuella pampinaria*

Character[1]	$\bar{x}$	M	SD	V	Min	Max	n
Body, length	113.2	114.0	14.3	12.6	84.0	141.0	25
Body, width	36.1	36.0	5.4	15.0	28.0	48.0	25
Adoral zone of membranelles, length	41.1	42.0	5.5	13.4	30.0	57.0	25
Adoral membranelles, number	31.0	31.0	3.6	11.6	22.0	39.0	25
Frontoterminal cirri, number	5.8	6.0	1.0	17.2	5.0	8.0	25
Buccal cirri, number	4.9	5.0	0.8	16.0	3.0	6.4	25
Midventral row, number of pairs of cirri	9.2	9.0	1.6	17.7	6.0	13.0	25
Frontal row, number of cirri	2.6	2.0	0.6	25.4	2.0	4.0	25
Ventral rows, number	3.5	3.0	1.0	29.9	2.0	6.0	25
Transverse cirri, number	3.8	4.0	0.7	19.5	2.0	5.0	25
Right marginal row, number of cirri	39.7	41.0	6.3	15.9	23.0	51.0	25
Left marginal row, number of cirri	39.5	42.0	5.6	14.2	24.0	47.0	25
Dorsal kineties, number	3.0	3.0	0.0	0.0	3.0	3.0	25
Macronuclear segment, length	5.5	6.2	1.6	0.3	2.5	7.4	25
Macronuclear segment, width	2.3	2.5	0.4	0.2	1.2	2.5	25
Micronucleus, largest diameter	2.4	2.5	0.2	0.1	2.0	2.5	25
First ventral row, number of cirri	9.1	9.0	2.2	24.0	4.0	14.0	25
Second ventral row, number of cirri	9.6	9.0	3.2	33.0	4.0	17.0	25
Third ventral row, number of cirri	9.6	9.0	2.3	24.2	5.0	16.0	21
Fourth ventral row, number of cirri	7.1	7.0	1.2	25.5	5.0	11.0	11
Fifth ventral row, number of cirri	8.7	9.0	3.4	38.9	4.0	12.0	4
Sixth ventral row, number of cirri	13.0	13.0	0.0	0.0	13.0	13.0	1

[1] Data are based on protargol impregnated specimens from a raw culture. Measurements in µm. $\bar{x}$ = arithmetic mean; M = median; SD = standard deviation; V = coefficient of variation in %; Min = minimum value; Max = maximum value; n = sample size.



Figs. 9–11. Early morphogenetic stages of *Bakuella pampinaria;* arrowheads in Fig. 10 mark streaks derived from posterior cirri of frontal row. BC = buccal row, EM = endoral membrane, PM = paroral membrane. Scale bar division = 10 µm.

Divisional Morphogenesis (Figs. 6–15)

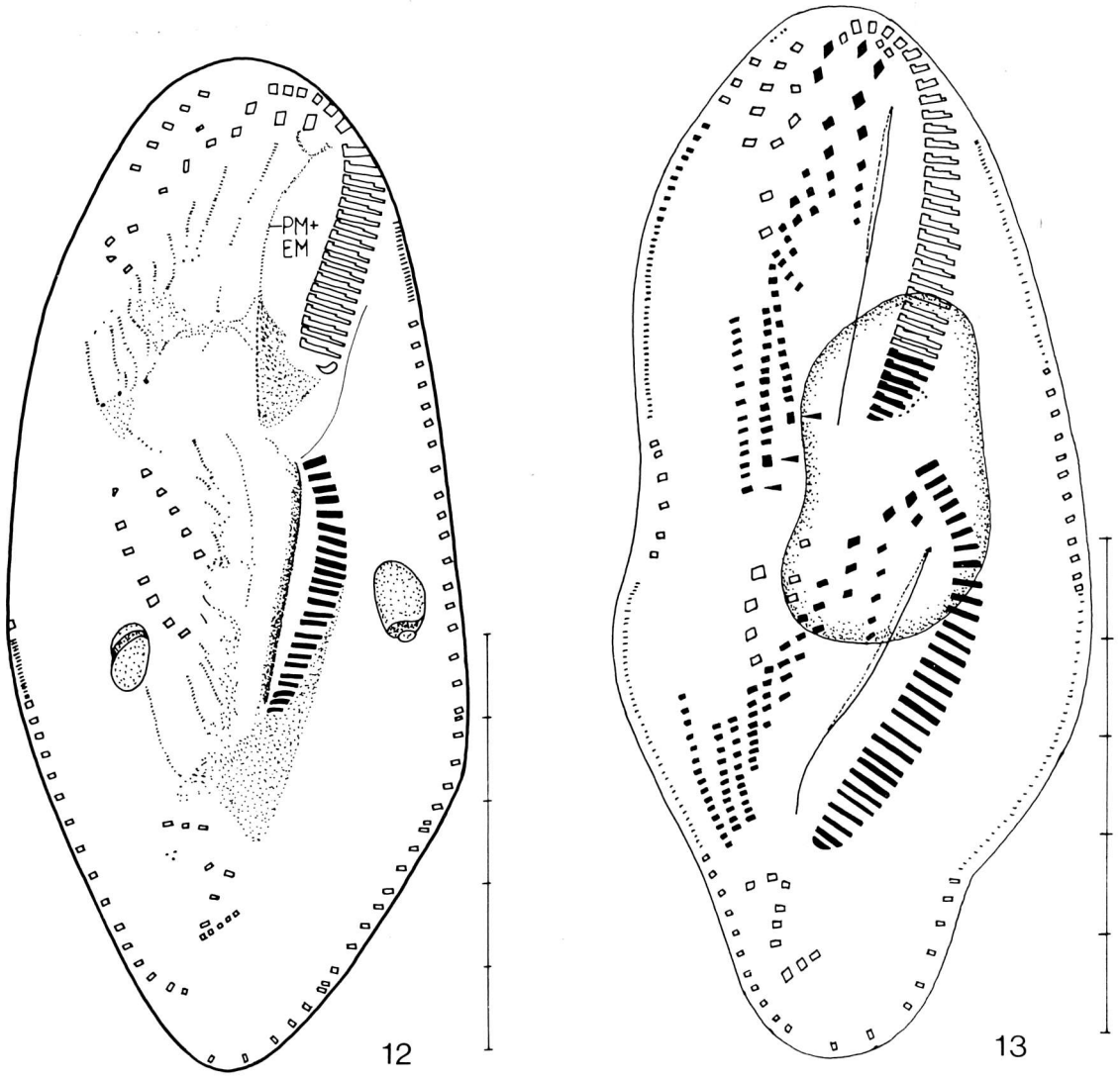
The nuclear apparatus and the marginal rows divide in the usual way (Fig. 13). The dorsal infraciliature develops according to type 1 [11]. No caudal cirri are formed (Fig. 15). These processes are thus not further commented.

Stage 1 (Figs. 6–8): Stomatogenesis commences with the formation of small groups of basal bodies close to the posteriormost cirri of the ventral rows. The transverse cirri and the adjacent (posteriormost) ventral row do not organize primordia. All parental cirri, even those with primordia nearby, appear intact.

Stage 2 (Fig. 9): By proliferation of basal bodies the primordial fields join, but never extend to the transverse cirri, which are thus not involved in the formation of the oral primordium. The distal half of the endoral membrane proliferates an elliptical field of basal bodies along its left side. The pharyngeal fibres are resorbed gradually (Figs. 9–13).

Stage 3 (Fig. 10): The anterior end of the oral primordium bifurcates and adoral membranelles differentiate in the left fork. The anlage to the left of the endoral membrane has developed to a substantial field of basal bodies. The paroral membrane disintegrates. The buccal cirri disorganize completely and form a long streak of basal bodies. The 3rd and 4th cirrus of the frontal row dissolve and form short streaks (Fig. 10, arrowheads). Some of the left cirri of the midventral row commence to proliferate basal bodies.

Stage 4 (Fig. 11): The formation of adoral membranelles within the oral primordium proceeds posteriad. A bifurcated streak organizes to the right of the developing adoral zone. Its left fork generates the undulating membranes and the left frontal cirrus (anlage 1 of the opisthe; cp. Fig. 12); the right fork organizes the buccal cirri and the middle frontal cirrus (anlage 2 of the opisthe). The anterior half of the parental endoral membrane is resorbed



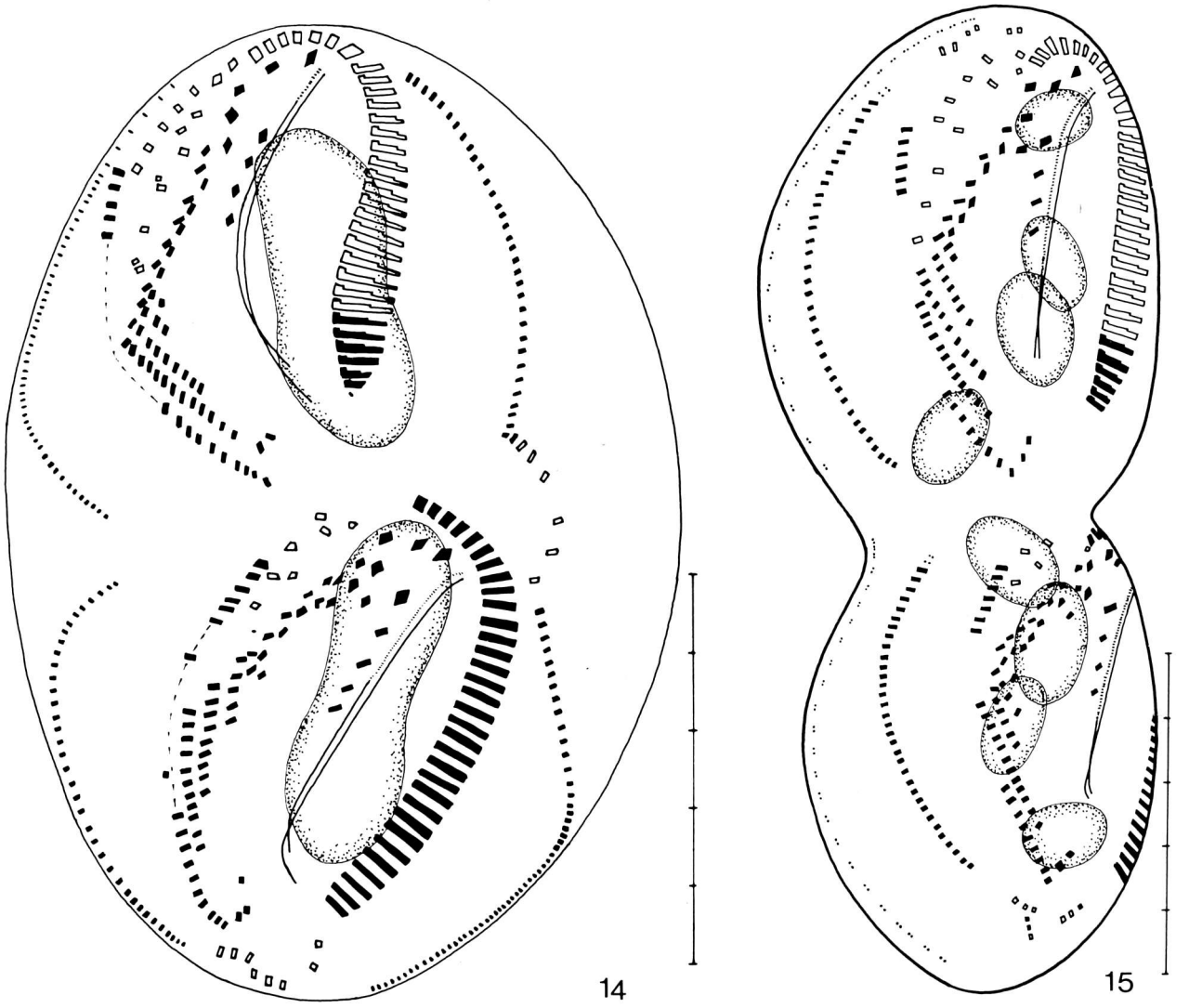
Figs. 12–13. Middle morphogenetic stages of *Bakuella pampinaria;* arrowheads in Fig. 13 mark enlarged transverse cirri. EM = endoral membrane, PM = paroral membrane. Scale bar division = 10 μm.

or incorporated in the anarchic field described above; the field elongates to the proximal portion of adoral zone of membranelles. The paroral membrane has become a long, distinct streak of anarchic basal bodies (anlage 1 for the undulating membrane and the left frontal cirrus of the proter). The streaks formed by the buccal cirri and the posterior cirri of the frontal row lengthen (anlage 2 for the buccal cirri and the middle frontal cirrus and anlage 3 for the frontal row and the right frontal cirrus of the proter, respectively). Oblique streaks develop from disaggregated left cirri of the midventral row (anlagen 4-n for midventral, frontoterminal and ventral rows and transverse cirri of the proter).

Stage 5 (Fig. 12): The anlage for the undulating membranes is a large streak of anarchic basal bodies in both daughter cells; it is forked at the anterior end where the left frontal cirrus is generated. The proximal portion of the parental adoral zone of membranelles and the endoral membrane dissolve and form a large field of scattered basal bodies. About 10 fronto-ventral anlagen are recognizable in either filial product; very likely, these develop from (or at least in contact with) the left cirri of the midventral row (proter) and from the ventral cirri (opisthe).

Stage 6 (Fig. 13): The anlage for the undulating membranes splits in both proter and opisthe, giving rise to the paroral and endoral membrane. The proximal membranelles of the parental adoral zone are reorganized from the anarchic field of basal bodies located between the paroral membrane and the proximal portion of the membranellar zone. Cirri organize within the streaks in both daughters; the cirrus at the posterior end of the 2–5 leftmost anlagen is slightly enlarged and separates to form the transverse cirral row (Fig. 13, arrowheads).

Stage 7 (Fig. 14): Endoral and paroral membrane are separate and their posterior portions are crossed. The rightmost ventral row splits in both filial products: the



Figs. 14, 15. Late morphogenetic stages of *Bakuella pampinaria;* dotted lines in Fig. 14 mark migrating frontoterminal cirri. Scale bar division = 10 μm.

anterior portion migrates anteriad becoming the frontoterminal row, the posterior portion is immobile, remaining attached to the right transverse cirrus (Fig. 14, dotted lines). The sequence of splitting and migration is clearly recognizable in Figs. 12, 13, 14.

Stage 8 (Fig. 15): Cytokinesis commences and cirri arrange in the species-specific pattern. Those parental cirri which did not participate in the formation of primordia are resorbed gradually; some even remain in post-dividers.

Reorganization (Physiological Regeneration)

Processes in reorganizers are very much like those in dividers (Figs. 16–18). A complete sequence, however, has not been observed. From the data available it appears that, like in cell division, only the proximal portion of the adoral zone is reorganized; cp. [15].

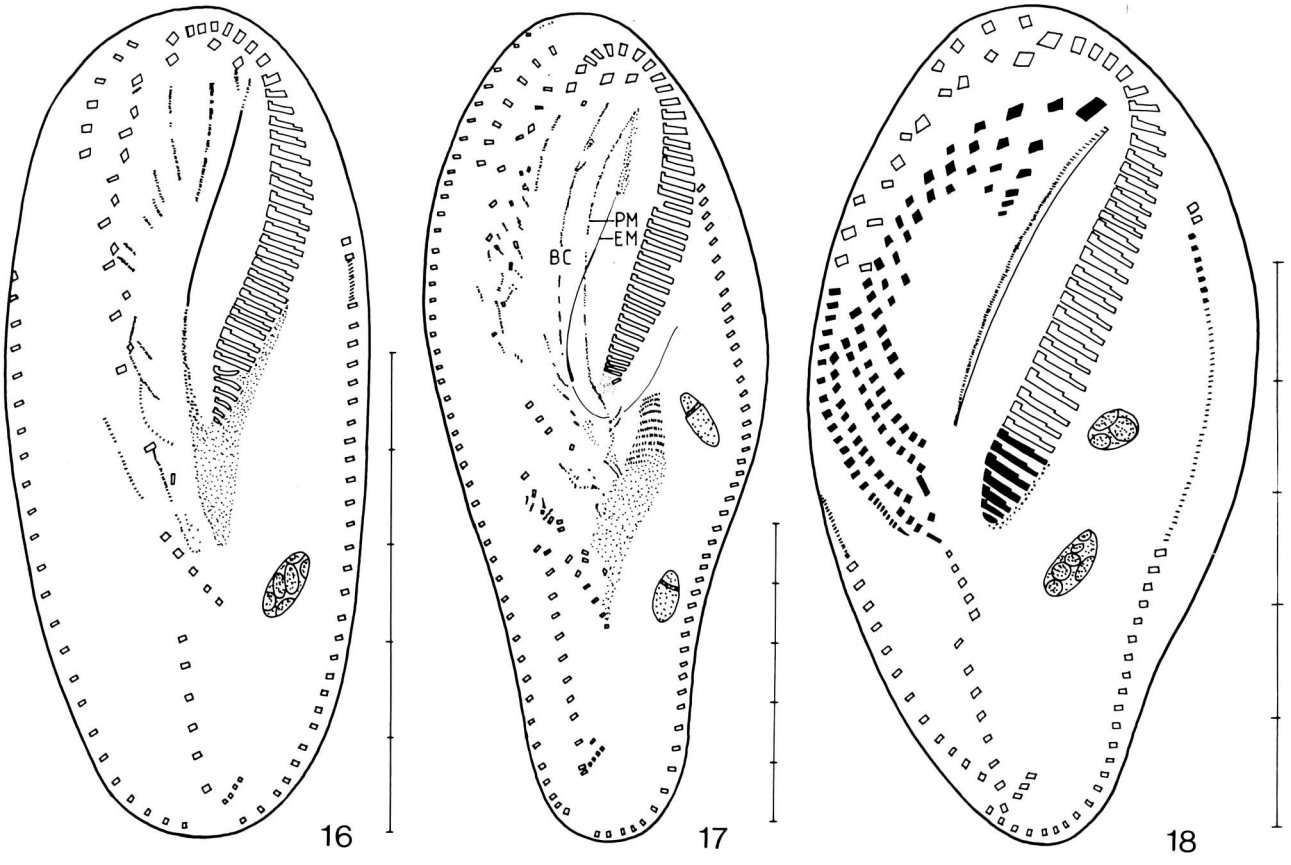
Discussion

Comparison with Related Species

Bakuella pampinaria is different from all species reviewed in Song, Wilbert and Berger [19] by having distinct cortical granules. The infraciliature is very similar to that of *B. edaphoni* [19] which differs primarily in the number of frontoterminal (2–5) and transverse (6–10) cirri and in some morphogenetic characters (see below). The second species reported from soil, *B. pulchra* (Buitkamp) Song, Wilbert and Berger, lacks midventral cirri and therefore belongs to another genus. The species reported from limnetic and marine biotopes also lack cortical granules (see [19] for detailed data): *B. agamalievi* Borror and Wicklow (posteriormost ventral row distinctly separate from transverse cirri, ventral rows very short); *B. crenata* Agamaliev and Alekperov (2 macronuclear segments); *B. imbricata* Alekperov (posteriormost ventral row distinctly separate from right transverse cirrus, 5–9 transverse cirri); *B. kreuzkampii* and *B. walibonensis* Mihailowitsch and Wilbert (2 frontoterminal cirri, ventral rows very short); *B. marina* Agamaliev and Alekperov (10 transverse cirri, 10 ventral rows; 5–11 transverse cirri, 3–4 dorsal kineties, body length 230–310 μm, according to Wilbert); *B. salinarium* Mihailowitsch and Wilbert (22–38 pairs of midventral cirri, 2 frontoterminal cirri, 13–21 ventral rows, 7–12 transverse cirri).

Morphogenesis

Morphogenetic data are available for three *Bakuella* species [1, 16, 19]. The most detailed accounts are those on



Figs. 16–18. Reorganizers of *Bakuella pampinaria*. BC = buccal row, EM = endoral membrane, PM = paroral membrane. Scale bar division = 10 μm.

B. salinarium [16] and those on *B. edaphoni* [19]. Our results largely confirm those of Song et al. [19], who also rectified some misinterpretations in other studies [1, 16]. Given our data, the morphogenesis of *B. pampinaria* differs in two important details from that of *B. salinarium* and *B. edaphoni:* The transverse cirri of *B. pampinaria* are not involved in the formation of the oral primordium or of cirral streaks, and the conspicuous anarchic field recognizable to the left of the endoral membrane, participating in the reorganization of the proximal portion of the adoral zone of membranelles, is apparently absent or inconspicuous in *B. edaphoni;* although it is similar to that found in *B. salinarium* [16]. Furthermore, Song et al. [19] suggest that the frontoterminal cirri of *B. edaphoni* originate from a very short streak between the 2 rightmost anlagen. Our data show convincingly that the frontoterminal row develops by splitting of the rightmost anlage. This is in accordance with the observations on *B. salinarium* [16]. Song et al. [19] thus very likely misinterpreted their data.

Reevaluation of the Classification of Urostyline Hypotrichs

The recent classifications of the urostylids are at least partially based on morphogenetic characters and have extensively discussed earlier efforts and nomenclatural problems [5, 6, 12, 13, 20, 23, 24]. The most recent and detailed revision proposes the following relationships [6]:

Suborder Urostylina Jankowski, 1979
Superfamily Urostyloidea Bütschli, 1889
Family Urostylidae Bütschli, 1889
Subfamily Urostylinae Bütschli, 1889
Subfamily Holostichinae Fauré-Fremiet, 1961
Family Pseudokeronopsidae Borror and Wicklow, 1983
Subfamily Pseudokeronopsinae Borror and Wicklow, 1983
Subfamily Thigmokeronopsinae Wicklow, 1981
Superfamily Pseudourostyloidea Jankowski, 1979
Family Pseudourostylidae Jankowski, 1979

We agree with most of the above cited authors that urostyline hypotrichs should be restricted to taxa having midventral cirri. This character defines the urostylids as a monophyletic assemblage and sets them off clearly from, e.g. the oxytrichids, spirofilids and kahliellids. Tuffrau [20], however, still maintains the suborder Stichotrichina Fauré-Fremiet including hypotrichs with and without midventral cirri. A second, possibly less important, apomorphy is the proter's adoral zone of membranelles which is partially (e.g. *Bakuella,* this paper) or completely (e.g. *Pseudokeronopsis* [24]) renewed during morphogenesis in all "midventral hypotrichs".

Phylogeny and evolution within the urostylids are much less clear. We could not find a reliable synapomorphy for either the Urostylidae or the Pseudokeronopsidae (in the sense of [6, 21]), indicating misclassification and inappropriate data. This is surprising and frustrating considering that a lot of morphotypes are well investigated. In spite of this, we include a scheme of argumentation containing some ideas which might stimulate discussion (Fig. 19). Only a few chief features will be discussed since the scheme is self-explanatory and very tentative; furthermore, only such morphotypes have been included which might be representative of higher categories (family, superfamily ...).

Wicklow [23] and Borror and Wicklow [6] emphasize the different origin of the marginal cirri in *Urostyla* (within parental rows) and *Pseudourostyla* (groups of marginal cirri arise from a common primordium [14]). Although

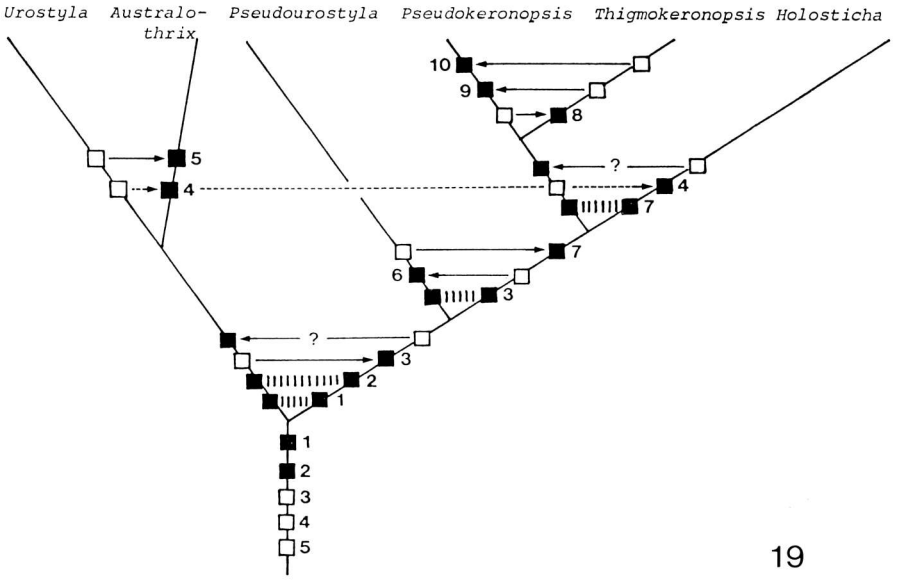
Table 2. Morphometric characterization of *Pseudourostyla cristata*

Character[1]	$\bar{x}$	M	SD	V	Min	Max	n
Body, length	246.3	243.0	46.9	19.0	171.0	361.0	25
Body, width	81.3	76.0	15.2	18.7	63.0	114.0	25
Distance from posteriormost transverse cirrus to posterior end of body	33.4	32.0	9.1	27.4	19.0	48.0	18
Distance from anterior end of body to posterior end of midventral row	201.6	195.0	39.2	19.5	152.0	266.0	16
Adoral zone of membranelles, length	97.3	101.0	11.2	11.5	72.0	114.0	25
Macronuclear segment, length	13.7	13.0	3.4	25.0	8.0	21.0	25
Macronuclear segment, width	5.2	6.0	1.0	19.2	4.0	6.0	25
Micronucleus, largest diameter	5.4	6.0	1.3	24.8	4.0	8.0	18
Macronuclear segment, number	58.4	55.0	11.2	19.1	44.0	83.0	23
Adoral membranelles, number	98.9	100.0	12.4	12.5	75.0	115.0	18
Right midventral row, number of cirri	34.5	35.0	5.1	14.9	27.0	44.0	8
Left midventral row, number of cirri	31.6	31.0	4.9	15.6	25.0	41.0	9
Frontoterminal cirri, number	2.0	2.0	0.0	0.0	2.0	2.0	8
Buccal cirri, number	1.0	1.0	0.2	21.3	1.0	2.0	22
Transverse cirri, number	9.7	10.0	1.6	16.1	6.0	12.0	21

[1] Data are based on protargol impregnated specimens made available by Prof. Jerka-Dziadosz. Measurements in μm. $\bar{x}$ = arithmetic mean; M = median; SD = standard deviation; V = coefficient of variation in %; Min = minimum value; Max = maximum value; n = sample size.

this is certainly a significant difference, we consider it as family character only since it is an apomorphy of a single genus. Like Wicklow [23], we suggest splitting the urostylids into two major groups using, however, the presence/absence of the highly distinct frontoterminal (migratory) cirri as a major character (Fig. 19). "Midventral hypotrichs" with frontoterminal cirri are united in an unranked taxon "holostichids" and such without migratory cirri in a likewise unranked taxon "urostylids".

Urostyla and *Australothrix* are possibly the only urostylids lacking frontoterminal cirri [4, 14]. Convincing morphogenetic evidence is, however, still not available. *Pseudourostyla* has migratory cirri [9, 22]. A reinvestigation of the type population of *P. cristata* (Table 2, slides



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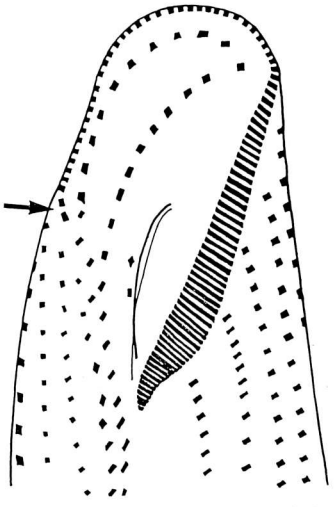
	Character state	
	Apomorph ■	Plesiomorph □
1	Midventral cirri	Without
2	Adoralzone of membranelles reorganized during cell division	Not reorganized
3	Frontoterminal (migratory) cirri	Without
4	Many frontal cirri forming bicorona	3-4 frontal cirri
5	Without transverse cirri	With
6	Marginal rows originate from common primordium	From individual primordia
7	Two marginal rows	More than two
8	Field of thigmotactic cirri	Without
9	Macronuclear segments divide individually during cell division	Fuse during cell division
10	Parental basal bodies not involved in formation of ciliary structures of daughters	Involved in formation of ciliary structures



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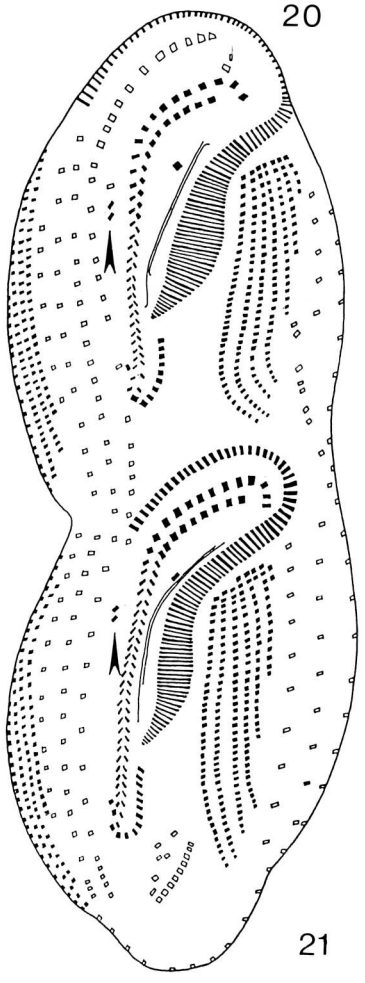

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Fig. 19. Tentative phylogenetic relationship within selected urostyline hypotrichs (see discussion for explanation).

Figs. 20, 21. *Pseudourostyla cristata* (drawn from protargol impregnated type slides kindly supplied by Prof. M. Jerka-Dziadosz). Infraciliature of ventral anterior portion and of a late divider. Arrow in Fig. 20 marks those cirri which could be the frontoterminal cirri recognizable in late dividers (arrowheads in Fig. 21).

kindly supplied by Prof. Jerka-Dziadosz) showed 2 frontoterminal cirri in dividing specimens (Fig. 21); they are, however, barely distinguishable from the other somatic cirri in interphasic individuals (Fig. 20), which might explain why Jerka-Dziadosz missed them. The infraciliature of *Australothrix* strongly resembles *Urostyla* spp.; however, a frontal bicorona is absent, as in the holostichids. We thus suggest that the reduction of the bicorona to a few enlarged frontal cirri in *Australothrix* and in holostichids have evolved convergently.

Three taxa can be distinguished within the holostichids which have frontoterminal cirri as major synapomorphy. The pseudourostylids have a unique character, viz. at least two marginal rows develop from a single anlage ([14]; confirmed by reinvestigation of the type slides); Wiackowski [22] claims, however, that he has seen this also in a strain of *Urostyla grandis*. A rather close relationship of *Urostyla* and *Pseudourostyla* is also indicated by the multiple marginal rows.

The reduction of the marginal cirri to two lateral rows might be considered as synapomorphy for the pseudokeronopsids and holostichids. The pseudokeronopsids retained the ancestral bicorona of frontal cirri, whereas the holostichids reduced it to a few enlarged cirri. It is, however, very uncertain whether *Pseudokeronopsis* and *Thigmokeronopsis* have a common ancestor as suggested by Borror and Wicklow [6] and in our scheme. *Pseudokeronopsis* has two outstanding features (the macronuclear segments divide individually during cell division and parental basal bodies do not participate in the formation of ciliary structures of daughter cells [24]) which might justify a more distinct separation.

Considering these obstacles, which dramatically increase if more genera are included in the argumentation scheme, it appears without heuristic value to rank and define higher categories definitely. Presently, at best species and genera can be defined and grouped to more or less practical assemblages to prepare identification keys. This pessimistic view is caused by many problems not solved during this study. To mention only a few: do *Keronella* and *Tricoronella* belong to the pseudokeronopsids as suggested by Blatterer and Foissner [4], Tuffrau [20] and Wiackowski [21] or to a family Bakuellidae as assumed by Wirnsberger [24]? Is *Bakuella* related to *Australothrix* as indicated by the short, indistinctly separated midventral rows? Has the conspicuous field of thigmotactic cirri in *Thigmokeronopsis* evolved from the sparse ventral rows of *Bakuella?* Or is *Bakuella* a reduced *Thigmokeronopsis* as indicated by the lack of a frontal bicorona? What is the phylogenetic significance of caudal cirri which occur in some *Holosticha* species, in *Keronella*, *Tricoronella* and even in *Australothrix*, but are absent in *Urostyla*, *Pseudokeronopsis*, *Thigmokeronopsis* and *Bakuella?* Are many marginal rows really plesiomorph? If so, have several evolutionary lines probably reduced them independently to two rows? This assumption would allow uniting *Australothrix* and several classical *(Holosticha, Uroleptus, Paruroleptus, Bakuella)* and recently described holostichids (e.g. *Territricha* [2], *Birojima* [3], *Holostichides* [9] and *Parabakuella* [18]) in a monophyletic taxon having as main apomorphy the reduction of the coronal frontal ciliature to few enlarged cirri.

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