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European Journal of Protistology 45 (2009) 87–97
European Journal of PROTISTOLOGY
www.elsevier.de/ejop

Morphology and ontogenesis of *Platyophrya bromelicola* nov. spec., a new macrostome-forming colpodid (Protists, Ciliophora) from tank bromeliads of Jamaica

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Received 15 February 2008; received in revised form 7 July 2008; accepted 11 July 2008

Abstract

Platyophrya bromelicola nov. spec. was discovered in tanks of bromeliads from Jamaica. Its morphology, ontogenesis, and small-subunit rDNA were studied using standard methods. *Platyophrya bromelicola* differs from its congeners mainly by the pyriform, unflattened body (vs. reniform and flattened); the free-swimming (planktonic) habit (vs. biofilm creepers); and the unique ability to form two distinct morphs, i.e., small, bacteriophagous microstomes and large, predaceous macrostomes. Microstomes and macrostomes can be distinguished not only by body size and feeding preferences but also by the postoral pseudomembrane composed of two vs. three to four dikinetids per kinety. The ability to form macrostomes is considered as an adaptation to the highly competitive habitat. Ontogenesis closely resembles that of other members of the family. *Platyophrya bromelicola* is distinct not only morphologically but also genetically (3.7% in the small-subunit rDNA) from *P. vorax*, a common, cosmopolitan moss and soil species.

Keywords: Biodiversity; Biogeography; Bromeliaceae; Colpodea; Hapantotypes; International Code of Zoological Nomenclature (ICZN)

Introduction

Bromeliads are rosette plants restricted to Central and South America. They have coalescing leaf axils, forming small cisterns or tanks that collect rain water (Foissner 2003a, b; Picado 1913). There are 2000 to 3000 bromeliad species, many of which have peculiar life-styles in a wide variety of environments, providing innumerable niches for protists and small metazoans. Thus, many species of organisms have evolved in tank bromeliads, ranging from protists to amphibians (Foissner 2003a, b; Foissner et al. 2003; Fried and Foissner 2007; Little and Hebert 1996; Martinelli 2000). When the cisterns desiccate during the dry seasons, space constraints and food shortages cause extreme competition among the organisms. Many of the bromeliad-specific ciliates react to the increased competition by switching from a bacteriophagous microstome morph to a predaceous macrostome morph (Foissner et al. 2003). Here, this is exemplified by a new species of *Platyophrya*, a genus in which macrostomes have not been described previously (Foissner 1993).

The protists of the bromeliad habitat are almost unexplored (for a brief review, see Foissner et al. 2003).

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doi:10.1016/j.ejop.2008.07.003

Foissner et al. (2003) and Foissner (2003a, b) discovered about 10 undescribed ciliate species in the tanks of bromeliads from the Dominican Republic, Ecuador, and Brazil. Since then, 20 more new species have been discovered in samples from Costa Rica, Jamaica, and Venezuela. Against this background, a diverse undescribed ciliate fauna may be anticipated in bromeliad cisterns. The nature and extent of this diversity are presently studied in Jamaica, where we discovered the new species described in this paper.

Material and methods, terminology

Platyophrya bromelicola was discovered in three tankwater samples from tree bromeliads in the parish of St. Thomas at the eastern tip of Jamaica, i.e., near the villages of Golden Grove and Rowlandsfield. The samples were collected in June 2005 and immediately sent to the Salzburg laboratory, where they were screened for the species present and then treated in the following way: the water was sieved through a 500 µm net to remove crustaceans and insect larvae. One portion of the samples was fixed for preparations, while the rest was used to establish raw cultures with 1–3 squashed wheat grains. *Platyophrya bromelicola* and some other ciliates occurred in the native tank water and grew well in the wheat grain cultures, where they fed on bacteria and heterotrophic flagellates. All trials to establish pure cultures failed; we even could not study the resting cyst because the specimens died when transferred from the raw sample to concave slides, which usually induces cyst formation. Thus, all data are based on material from two exponentially growing raw cultures containing both microstomes (90%) and macrostomes (10%).

Cells were studied in vivo using a high-power oil immersion objective and differential interference contrast optics. The infraciliature and various cytological structures were revealed by scanning electron microscopy and silver impregnation techniques described in Foissner (1991). Counts and measurements on prepared specimens were performed at a magnification of ×1000. In vivo measurements were conducted at magnifications of ×100–1000. Although these provide only rough estimates, it is worth giving such data as specimens may change in preparations. Illustrations of live specimens were based on free-hand sketches, while those of prepared cells were made with a drawing device.

The small-subunit rDNA of *P. bromelicola* has been analysed previously by Dunthorn et al. (2008), where the species was named "*Platyophrya* sp.". Thus, we refer to this study for details on amplification, sequencing, and genealogical analyses. To calculate the pairwise distance between *Platyophrya* sp. (= *bromelicola*) and *P. vorax* (GenBank # AF060454), we used the uncorrected "*p*" method in PAUP* v 4.0b (Swofford 2002).

Terminology is according to the monographs of Foissner (1993, 1996). In analogy to *Tetrahymena* (Corliss 1973), we use the terms microstome (small or ordinary mouthed) and macrostome (large mouthed). Like Corliss (1973), we use both terms as an adjective (e.g., microstome specimens) and as a noun (e.g., microstomes).

Results

Description of *Platyophrya bromelicola* nov. spec.

Diagnosis: *Platyophrya* with a bacteriophagous microstome (MI) and a predaceous macrostome (MA) morph. Size about 40 × 20 µm (MI) or 55 × 35 µm (MA) in vivo. Shape usually pyriform, rarely ellipsoidal or obovate with acute rear end; unflattened. Micronucleus in perinuclear space of macronucleus. On average 17 (MI) or 20 (MA) ciliary rows and 5 (MI) or 6 (MA) adoral organelles. Postoral pseudomembrane composed of kineties with 2 (MI) or 3–4 (MA) dikinetids.

Type locality: Arboricolous and terrestrial tank bromeliads near the road to Rowlandsfield (76° 29′ W, 18° N), i.e., about 5 km north of the village of Golden Grove, eastern Jamaica.

Type material: 3 hapantotype slides (2 with protargol-impregnated microstomes and macrostomes, Figs 2, 8, 9; 1 with silver nitrate-impregnated macrostomes showing the right and left side silverline pattern, Figs 14, 16) and 10 paratype slides have been deposited in the Biology Centre of the Museum of Upper Austria, Linz (LI), accession numbers 57–69/2008. Relevant specimens are marked by black ink circles on the coverslip. The 18S rDNA sequence of *P. bromelicola* has been deposited in GenBank, accession number EU039906.

We apply the hapantotype regulation of the ICZN (article 73.3) because *P. bromelicola* has two distinct morphs, of which the microstomes are easily confused with several congeners. Two further hapantotype specimens show the right and left side silverline pattern, which is indispensable for the generic assignment. The last action is possibly not fully covered by article 73.3, which needs to be improved in this respect.

Etymology: Composite of *Bromeliaceae* (the plants in whose leaf-tanks it occurs) and the Latin verb *colere* (dwelling), referring to its typical habitat.

Description: In the environmental samples mainly microstome specimens occur (>95%). In laboratory raw cultures both microstomes (MI) and macrostomes (MA) develop, with the former strongly dominating (~93%, $n = 154$). For the sake of clarity, MI and MA

Table 1. Morphometric data on microstome (upper line) and macrostome (lower line) specimens of *Platyophrya bromelicola*.

Characteristics[a]	$\bar{x}$	*M*	SD	SE	CV	Min	Max	*n*	% Increase
Body, length	35.8	37.0	4.9	1.1	13.7	26.0	42.0	19	–
	50.6	50.0	5.0	1.1	9.8	40.0	60.0	19	41
Body, width	18.0	18.0	3.0	0.7	16.9	13.0	22.0	19	–
	29.6	29.0	3.9	0.9	13.3	23.0	38.0	19	64
Anterior body end to macronucleus	11.6	12.0	3.2	0.7	27.8	7.0	18.0	19	–
	13.8	13.0	3.4	0.8	24.7	8.0	20.0	19	19
Macronucleus, length	7.6	8.0	1.1	0.3	14.8	6.0	9.0	19	–
	9.8	10.0	1.4	0.3	14.5	7.0	13.0	19	29
Macronucleus, width	7.1	7.0	0.9	0.2	13.2	6.0	9.0	19	–
	9.1	9.0	1.1	0.2	11.5	7.0	11.0	19	28
Number of ciliary rows	17.2	17.0	1.3	0.3	7.6	15.0	19.0	19	–
	19.5	20.0	1.0	0.5	8.1	17.0	22.0	10	13
Number of dikinetids in a right side ciliary row	17.4	17.0	2.3	0.5	13.1	14.0	23.0	19	–
	23.1	23.0	2.6	0.7	11.3	19.0	27.0	19	33
Number of dikinetids in a left side ciliary row	10.8	10.0	1.6	0.4	15.0	8.0	14.0	19	–
(with postoral pseudomembrane)	14.6	14.5	2.0	0.5	13.5	10.0	18.0	18	35
Mouth entrance, length	5.6	6.0	–	–	–	5.0	6.0	19	–
	8.6	8.0	0.8	0.2	9.8	7.0	10.0	19	54
Mouth entrance, width	4.7	5.0	0.8	0.2	16.0	3.0	6.0	19	–
	5.9	6.0	0.6	0.1	9.6	5.0	7.0	19	26
Number of adoral organelles[b]	5.2	5.0	0.5	0.1	10.3	4.0	6.0	19	–
	5.9	6.0	–	–	–	5.0	6.0	19	13
Number of paroral dikinetids	27.0	27.5	1.2	0.2	4.4	25.0	28.0	8	–
	33.4	33.0	2.7	0.9	8.0	30.0	38.0	8	20
Number per kinety of dikinetids forming	2.0	2.0	0.0	0.0	0.0	2.0	2.0	19	–
postoral pseudomembrane	3.2	3.0	–	–	–	3.0	4.0	19	50
Number of kineties forming postoral	12.3	12.0	1.0	0.2	7.7	10.0	14.0	19	–
pseudomembrane	14.0	14.0	1.5	0.4	10.8	12.0	16.0	19	14
Number of proter adoral organelles[c]	5.8	6.0	–	–	–	5.0	6.0	11	–
Number of opisthe adoral organelles[c]	6.2	6.0	0.8	0.2	13.0	5.0	8.0	13	–

[a]Data based on mounted, protargol-impregnated, randomly selected specimens from a raw culture. Measurements in μm. CV – coefficient of variation in %, *M* – median, Max – maximum, Min – minimum, *n* – number of specimens investigated, SD – standard deviation, SE – standard error of mean, $\bar{x}$ – arithmetic mean, % Increase – the increase in the mean value for macrostomes relative to microstomes.

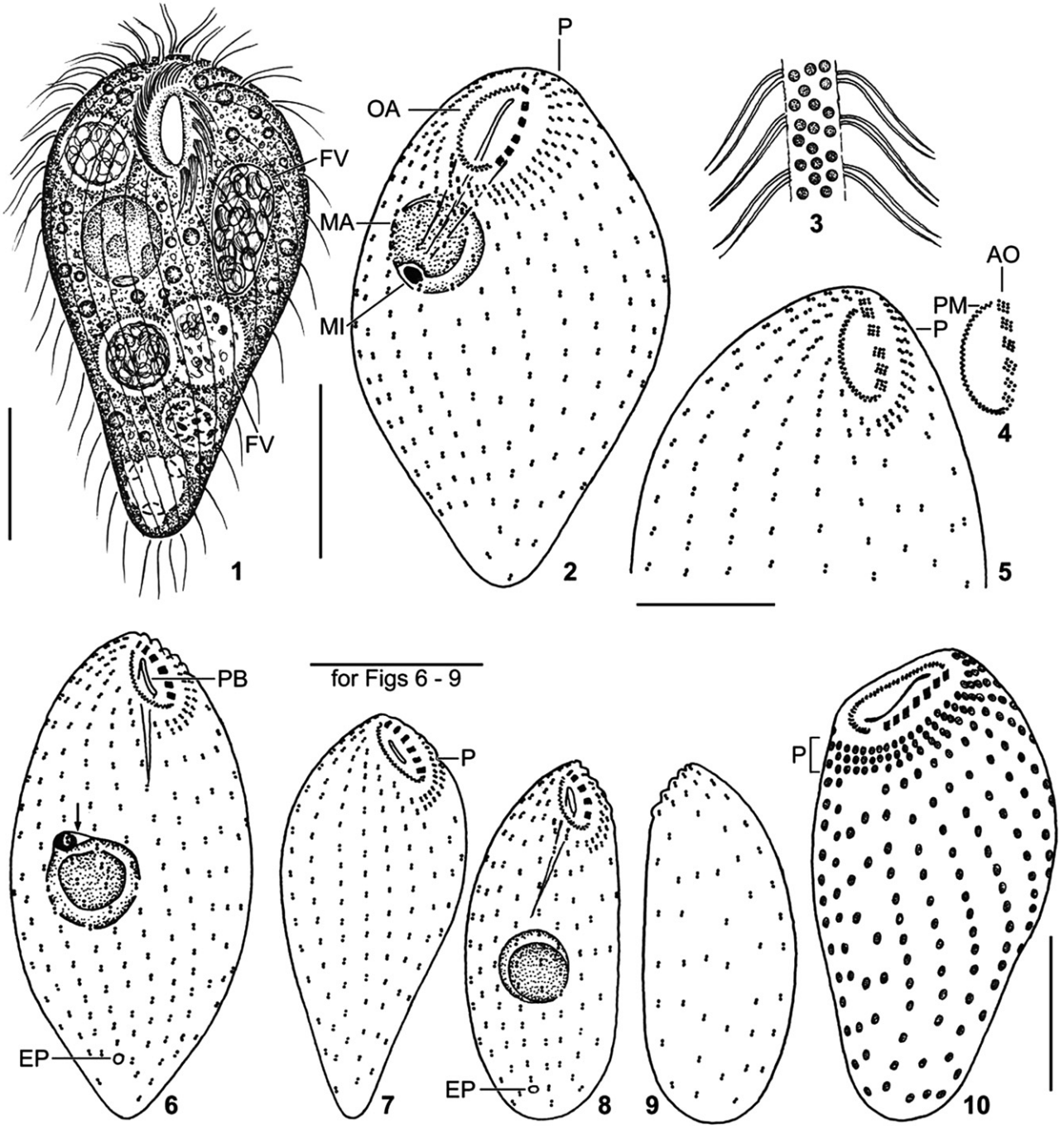
[b]Specimens with 7 adoral organelles occur occasionally in macrostomes (Fig. 10).

[c]Macrostome dividers.

are described together. Briefly, they differ in three main features, all useable for identification in vivo and silver preparations: MI feed on bacteria, MA mainly on large flagellates; MA are larger than MI in most morphometric features by 13% (number of ciliary rows and adoral organelles) to 64% (body width); and the postoral pseudomembrane is composed of two (MI) or three to four (MA) narrowly spaced dikinetids per kinety. These and other differences are shown in Table 1, both as real values and as percentages.

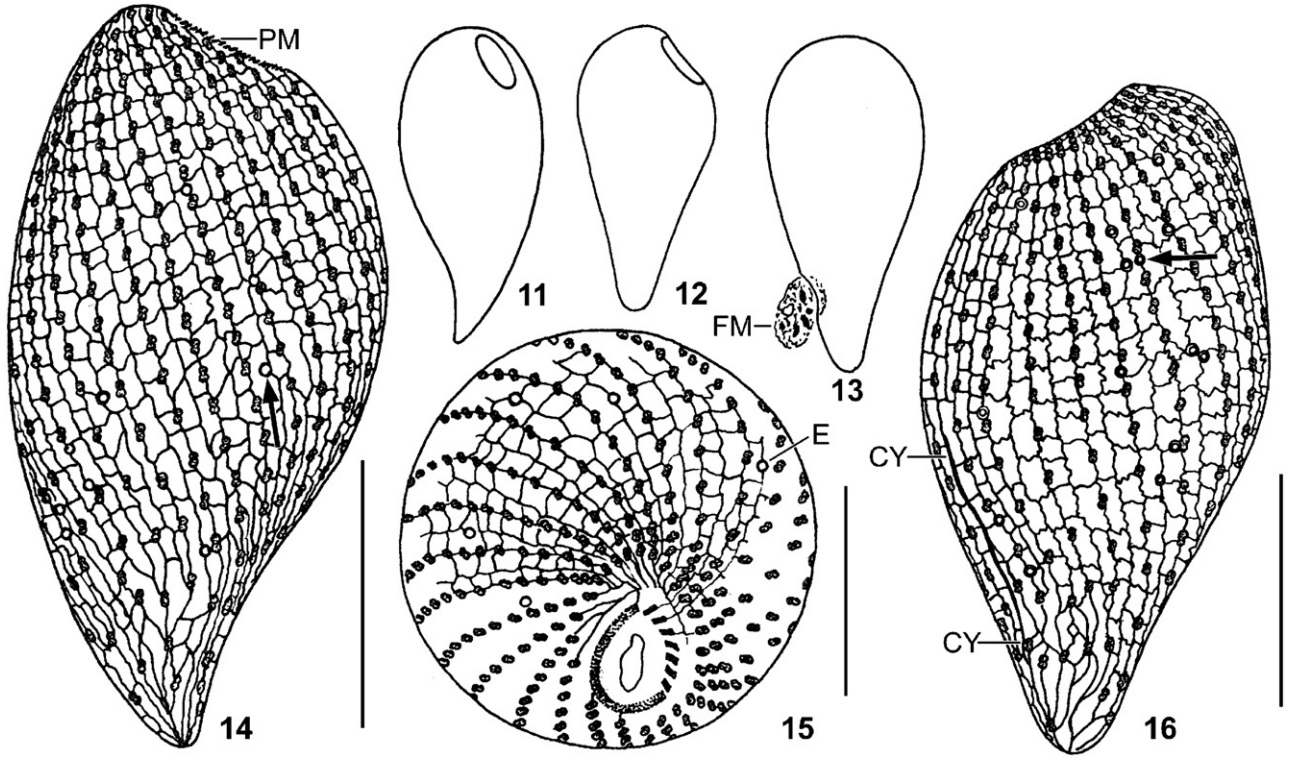
Table 2. Percentage of main shape types in microstome and macrostome specimens of *Platyophrya bromelicola*.

Shape types	Specimens (%)	
	Microstome ($n = 140$)	Macrostome ($n = 36$)
1 (Figs 37, 38)	31.4	33.3
2 (Figs 12, 39)	52.2	55.6
3 (Figs 11, 40)	16.4	11.1

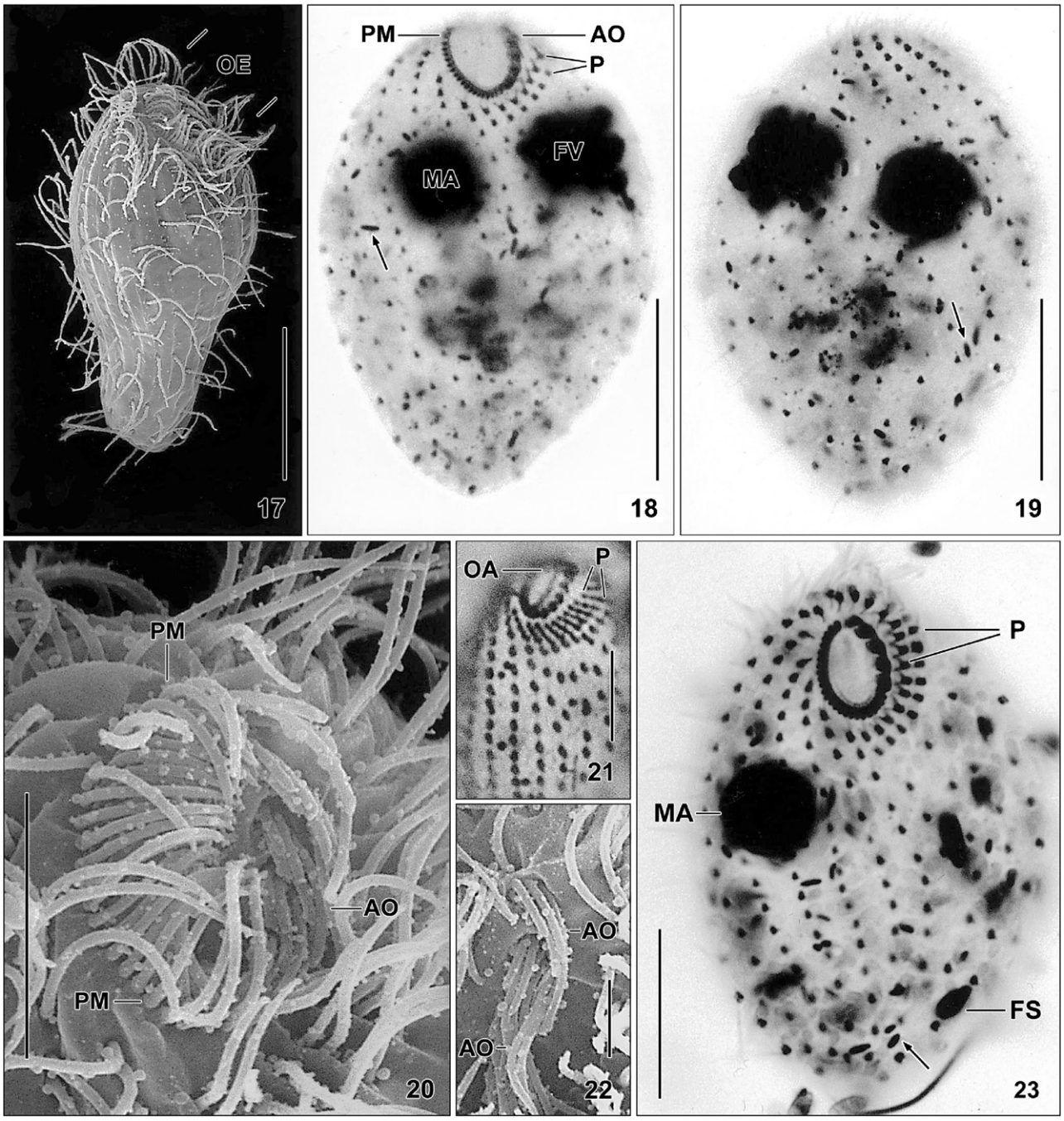


Figs 1–10. *Platyophrya bromelicola*, microstome (5–9) and macrostome (1–4, 10) specimens from life (1, 3) and after protargol (2, 4–9) and Chatton–Lwoff silver nitrate (10) impregnation. **1.** Ventral view of a representative macrostome with many large food vacuoles containing mainly heterotrophic, euglenid flagellates. Microstomes may have a similar shape (7) but their food vacuoles are smaller and contain only bacteria. **2, 10.** Ventral and left side view of somatic and oral ciliary pattern. As usual in colpodids, the ciliature is composed of dikinetids of which, however, the anterior basal body is barren, especially in posterior half of cell and on left side (cp. Figs 1, 17, 24, 25). In macrostomes, each left side kinety commences with three to four narrowly spaced dikinetids forming, together with some short extra kineties, the postoral pseudomembrane (P). **3.** Surface view showing pale cortical granules, possibly extrusomes of the mucocyst type, about 0.7 µm across. **4, 5.** Ventrolateral views showing the somatic and oral ciliary pattern. The adoral organelles are composed of two or three ciliary rows, and the first organelle may be above (5) or in line (4) with the anterior end of the paroral membrane. **6–9.** Size and shape variability of microstomes, where the postoral pseudomembrane (P) is formed by two narrowly spaced rows of dikinetids. The left side is more sparsely ciliated than the right one (8, 9). The micronucleus is probably in the perinuclear space of the macronucleus (6, arrow). AO – adoral organelles, EP – excretory pore of contractile vacuole, FV – food vacuoles, MA – macronucleus, MI – micronucleus, OA – oral apparatus, P – postoral pseudomembrane, PB – pharyngeal basket, PM – paroral membrane. Scale bars 10 µm (Fig. 5) and 15 µm (Figs 1, 2, 6–10).

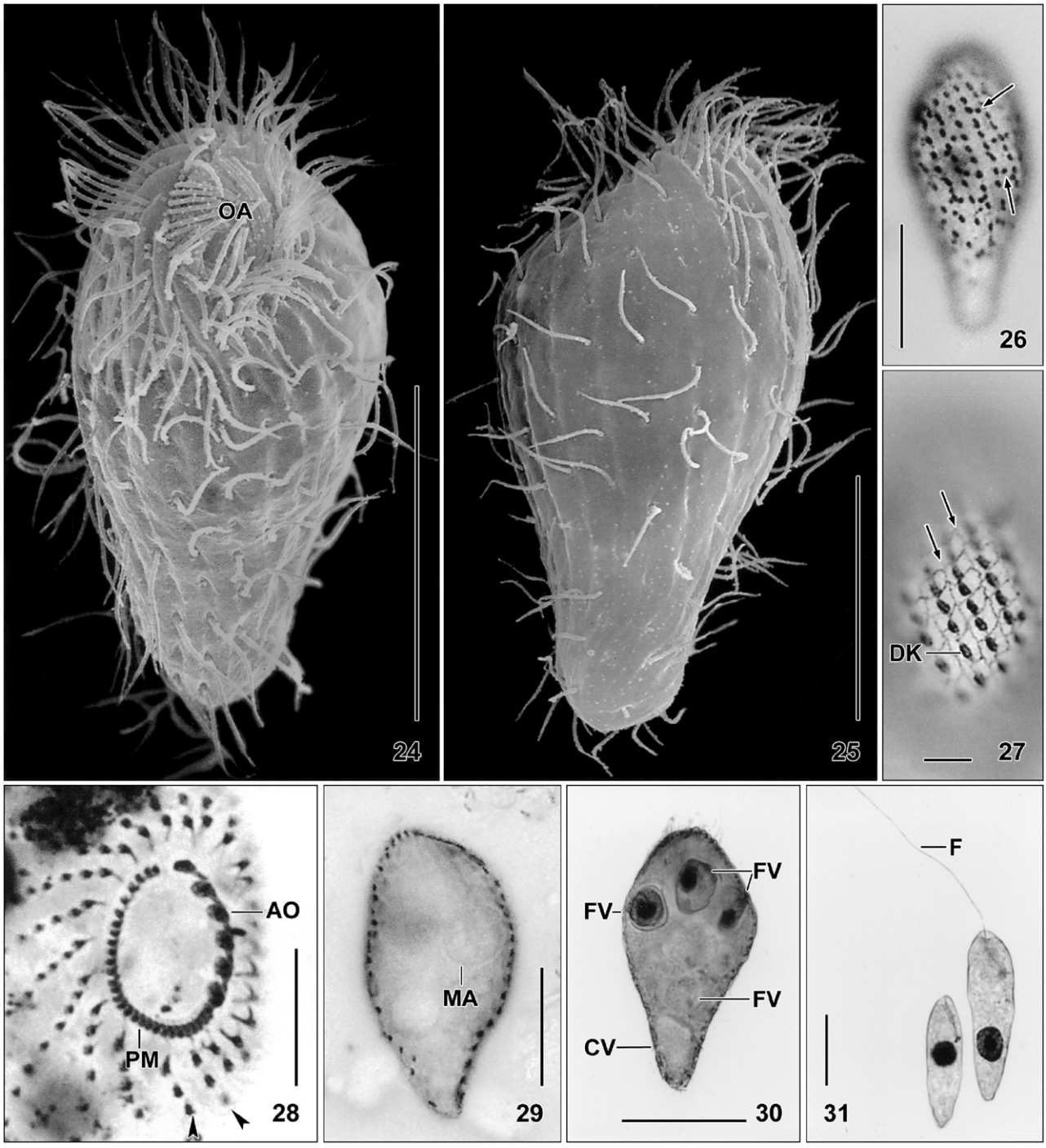
Size 30–50 × 15–25 µm in vivo, usually near 40 × 20 µm in MI, while 45–70 × 25–45 µm, usually about 55 × 35 µm in MA (Tables 1, 2). Shape highly variable but quite similar in MI and MA, as shown by the data compiled in Table 2: pyriform to bluntly pyriform (50–60% of specimens, Figs 1, 2, 7, 10, 12, 13, 16, 17, 24–26, 30, 39); ellipsoidal (~30%, Figs 6, 8, 37, 38); or pyriform to ellipsoidal with acute posterior end (10–20%, Figs 11, 14, 29, 40). Not flattened laterally and not contractile. Nuclear apparatus slightly above mid-body on average, hyaline and thus difficult to recognize in vivo. Macronucleus about 8 µm across (10 µm in MA), nuclear membrane more or less widely separated from nucleoplasm in protargol preparations; nucleoli globular, pale. Micronucleus very likely in perinuclear space of macronucleus (Fig. 6), about 3 × 2 µm in size, in vivo appears as a hyaline blister tightly attached to macronucleus (Figs 1, 2, 6, 8, 18, 23). Contractile vacuole in posterior body end, excretory pore subterminal at end of shortened fourth ciliary row right of postoral pseudomembrane. Cytopyge at border of right and left side kineties, marked by a thick silverline extending in posterior body half (Fig. 16); fecal mass large, leaves cell subterminally above level of excretory pore of contractile vacuole (Fig. 13). Cortex soft and highly flexible, cortical ridges distinct only in anterior third, contains many pale granules, possibly mucocysts about 0.7 µm across and thus difficult to recognize in vivo (Fig. 3), but more or less deeply impregnated with protargol, often disturbing analysis of ciliary pattern. Cytoplasm of MI packed with lipid droplets 2–5 µm across and 3–5 µm-sized food vacuoles each containing often only a single bacillus or its spore; rarely, fungal conidia (Fig. 23) or small (< 10 µm) flagellates are ingested. Macrostomes feed exclusively phagotrophically on comparatively large food items, such as starch grains from the squashed wheat kernels added to the culture and large flagellates, e.g., *Chilomonas* sp. and, especially, a 30–50 µm long heterotrophic, highly metabolic euglenid (Figs 1, 30, 31). Movement striking for this kind of ciliate, i.e., swims and rotates around main body axis like a *Tetrahymena*, occasionally performing curious, pushing movements back and forth.



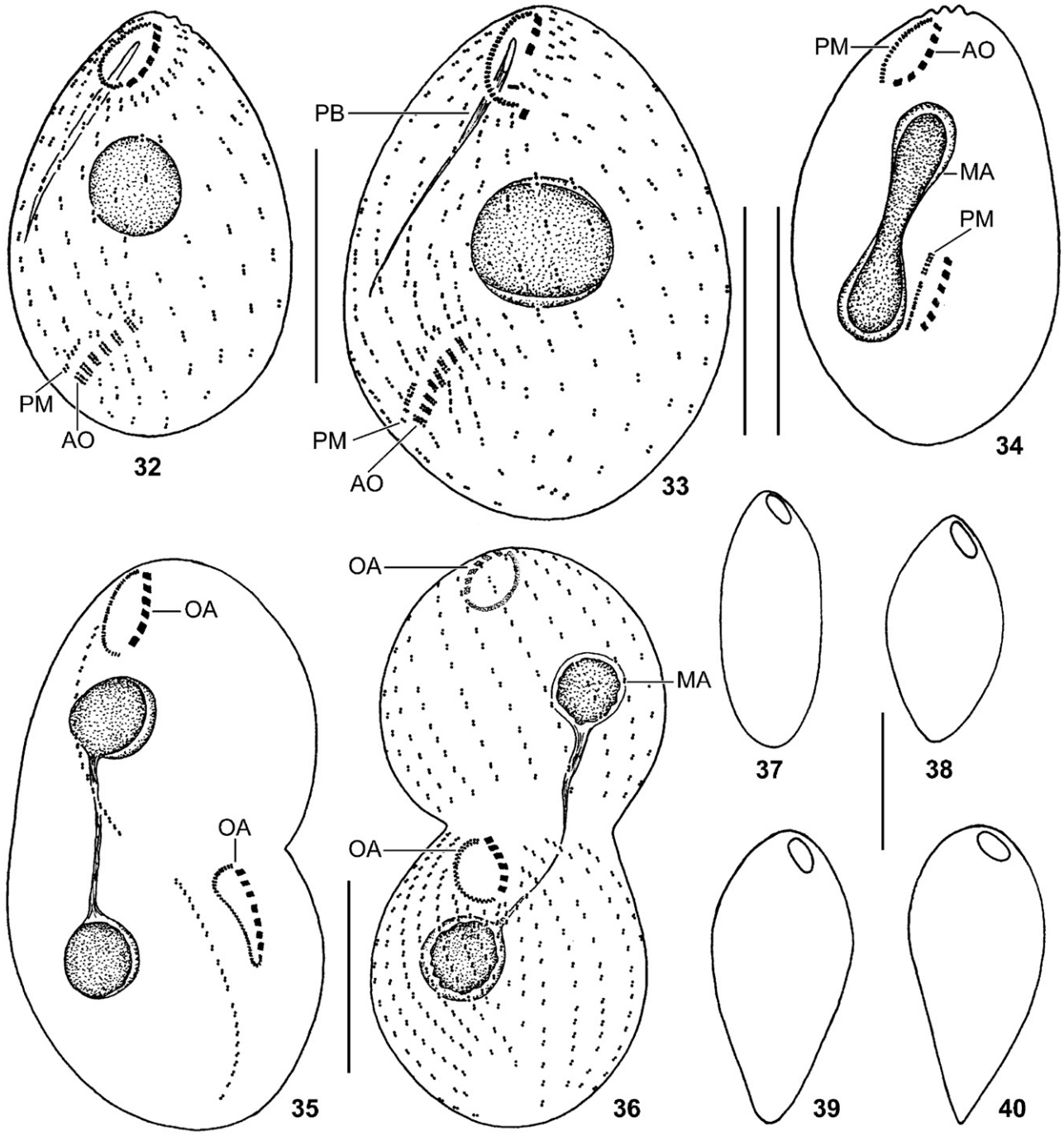
Figs 11–16. *Platyophrya bromelicola*, macrostome specimens from life (11–13) and after Chatton–Lwoff silver nitrate impregnation (14–16). **11, 12.** Right side views showing shape variability. **13.** Ventral view of a defecating specimen. **14, 16.** Right and left side view showing the platyophryid silverline pattern. This highly characteristic structure is produced by a meridional silverline that extends between each two kineties and contacts the silverlines connecting the kinetids of the ciliary rows via many short branches. Attached extrusomes are surrounded by a thickened silverline or two narrowly spaced silverline rings (arrows). The cytopyge (16) is marked by a thick silverline extending in ventral posterior half of body. **15.** Anterior polar view showing the unflattened body, the radially spreading ciliary rows, and the subapically located oral apparatus. CY – cytopyge, E – docked extrusome, FM – fecal mass, PM – paroral membrane. Scale bars 15 µm (Fig. 15) and 20 µm (Figs 14, 16).



Figs 17–23. *Platyophrya bromelicola*, microstome (17–20, 22, 23) and macrostome specimens (21) in the scanning electron microscope (17, 20, 22), and after silver carbonate (18, 19, 23) and Chatton–Lwoff silver nitrate (21) impregnation. **17.** Right side overview of a microstome showing the pyriform body shape and the densely ciliated oral area (OE), where the cilia are paired. **18, 19.** Ciliary pattern of ventral and dorsal side of a microstome specimen. Kineties extend slightly sigmoidally and are more loosely ciliated on the left side, except for two narrowly spaced dikinetids at anterior end, forming the postoral pseudomembrane. Arrows mark short rods, possibly cytoplasmic bacteria. **20, 22.** The microstome oral apparatus consists, inter alia, of a semicircular paroral membrane (PM) and a slightly convex array of adoral organelles (AO). The paroral is composed of obliquely arranged dikinetids. In the adoral organelles, cilia length increases from right to left (22); probably, only two of the three rows composing an organelle are ciliated. **21.** Ventrolateral view of a macrostome showing the oral apparatus and the postoral pseudomembrane (P) which is formed by short extra kineties and three to four narrowly spaced dikinetids in the anterior region of the left side ciliary rows. **23.** Ventral view showing the oral and somatic ciliary pattern, including the postoral pseudomembrane, which, in microstomes, is formed by two narrowly spaced kinetids. Arrow marks a short rod, possibly a cytoplasmic bacterium. AO – adoral organelles, FS – fungal spore, FV – food vacuole, MA – macronucleus, OA – oral apparatus, OE – oral area, P – postoral pseudomembrane, PM – paroral membrane. Scale bars 2 μm (Fig. 22), 5 μm (Fig. 20), 10 μm (Fig. 21), and 15 μm (Figs 17–19, 23).



Figs 24–31. Macrostomes of *Platyophrya bromelicola* (24–30) and its main food, an euglenid flagellate (31), in the scanning electron microscope (24, 25) and after silver carbonate (28), protargol (30, 31), and Chatton–Lwoff silver nitrate (26, 27, 29) impregnation. **24, 25.** Ventral and left side view showing pyriform body shape and sparse ciliation on left side. Paired cilia occur only in the anterior (oral) third of the body, which is thus densely ciliated. **26.** A specimen with rather dense left side ciliation. Arrows mark attached extrusomes. **27**. Part of right side showing the highly characteristic, platyophryid silverline pattern. The reticulate structure is produced by a silverline (arrows) extending between each two kineties and having many lateral branches, which abut to the silverlines connecting the kinetids of the ciliary rows. **28.** Frontal view of oral area. The paroral membrane and the six adoral organelles form the elliptical pattern so characteristic for platyophryid ciliates. The arrowheads mark the three dikinetids forming the postoral pseudomembrane. **29.** Optical section of a specimen with acute posterior end and globular macronucleus. **30, 31.** Macrostomes of *P. bromelicola* feed mainly on a heterotrophic, euglenid flagellate (31) recognizable in the food vacuoles (30); microstomes feed on bacteria. AO – adoral organelles, CV – contractile vacuole, DK – somatic dikinetid, F – flagellum, FV – food vacuoles, MA – macronucleus, OA – oral apparatus, PM – paroral membrane. Scale bars 5 μm (Fig. 27), 10 μm (Figs 28, 31), 15 μm (Figs 24, 25), and 25 μm (Figs 26, 29, 30).



Figs 32–40. *Platyophrya bromelicola*, ontogenesis after protargol impregnation (32–36) and body shape types after Chatton–Lwoff silver nitrate impregnation (37–40). The parental oral apparatus is not reorganized, except for the oral basket which is resorbed in mid-dividers (34). The micronucleus did not impregnate. There are no differences in the ontogenetic processes between microstomes and macrostomes. **32, 33.** Early division stages in a microstome and a macrostome specimen. Note that the specimen shown in Fig. 33 has a malformed adoral ciliature. The new oral apparatus develops subequatorially and right of the ventral surface. Both the adoral organelles and the paroral membrane develop from dikinetids produced within about five kineties. The somatic ciliature develops intrakinetally with basal bodies forming distinct triplets and quadruplets. Rarely, the number of adoral organelles is higher in the opisthe than in the proter (35). The macronucleus increases slightly in size. **34.** An early microstome mid-divider showing the dividing macronucleus and the almost completed new oral apparatus. Note resorption of the parental oral basket. **35, 36.** Late macrostome dividers, showing the torsion of the opisthe relative to the proter and completion of macronucleus division. Likewise, division of the somatic basal bodies has been completed. The oral basket and the postoral pseudomembrane form in postdividers. **37–40.** Main types of body shape, as used for classifying data shown in Table 2. Drawn to scale. AO – adoral organelles, MA – macronucleus, OA – oral apparatus, PB – pharyngeal basket, PM – paroral membrane. Scale bars 20 μm.

Somatic ciliary and silverline pattern as in congeners (Foissner 1993). Thus, we provide only a brief description and refer to the abundant illustration and detailed figure explanations; differ in microstomes (Figs 5–9, 17–19, 23) and macrostomes (Figs 1, 2, 10, 14–16, 21, 24–27) by only one significant feature, viz., the postoral pseudomembrane composed of kineties with two vs. three to four narrowly spaced dikinetids (cp. Figs 5–8, 18, 23 with Figs 2, 10, 21, 28). Cilia about 7 µm long in vivo, paired only around oral apparatus, arranged in an average of 17 (MI) or 20 (MA) almost straight to slightly sigmoidal, bipolar rows more closely spaced and densely ciliated on right than left side of cell; no caudal cilia. Postoral pseudomembrane composed of about 12 (MI) to 14 (MA) narrowly spaced pairs (MI) or triads (MA) of dikinetids about half of which belong to the left side ciliary rows, while the others are short extra kineties. Silverlines in *Platyophrya* pattern throughout, meshes about as widely spaced as dikinetids on right side, slightly narrower on left. Individual silverlines rather distinctly undulating in some specimens, surround docked extrusomes and dikinetids (Figs 14–16, 27).

Oral apparatus in a shallow subapical concavity, on average 6 × 5 µm in MI and 8 × 6 µm in MA, where it is rather conspicuous; outline elliptical with central opening surrounded by a comparatively wide, soft, membranous zone limited by the paroral membrane and the adoral organelles (Figs 1, 2, 4–8, 10, 15, 17, 18, 20, 24, 28, Table 1). Paroral membrane at right mouth margin, slightly curved to almost C-shaped, composed of an average of 27 (MI) or 33 (MA) dikinetids with both basal bodies possibly having an about 3 µm long cilium, as *Ottowphrya* and *Reticulowoodruffia* (Foissner et al. 2002). On average 5 (MI) or 6 (MA) adoral organelles forming a slightly convex array along left mouth margin, uppermost organelle in line with or, rarely, above anterior end of paroral membrane (Figs 2, 4, 5, 28, Table 1); individual organelles composed of six to nine basal bodies in two or three oblique rows with cilia, forming a cirrus-like bundle, about 5 µm long, usually directed posteriorly and only occasionally beating up and down; possibly only two of the three rows ciliated with cilia increasing in length from right to left (Figs 1, 2, 4–6, 20, 22, 28). Pharyngeal basket inconspicuous, extends to mid-body, recognizable only in some protargol-impregnated specimens (Figs 2, 6).

Ontogenesis of *Platyophrya bromelicola*

The basic ontogenetic features could be followed in protargol preparations. However, details are often obscured by the cortical granules, which impregnate more or less deeply and have, unfortunately, a similar size to the basal bodies. Thus, some details could not be clarified. Likewise, the micronucleus did not impregnate.

Division is homothetogenic, pleurotelokinetal, and proceeds in freely motile (non-encysted) condition. It commences with an intense replication of basal bodies in the posterior half of five to six ventro-lateral kineties; soon, the basal bodies form two-rowed adoral organelles and assemble the remaining dikinetids to a paroral membrane; concomitantly, kinetid duplication occurs in all kineties, producing basal body triplets (Figs 32, 33). In mid-dividers, the new (opisthe) oral apparatus is almost complete, the parental pharyngeal basket is resorbed, and the macronucleus becomes dumbbell shaped. The parental and the newly formed oral apparatus are still in line (Fig. 34). When cell division is recognizable, the new oral structures have been completed and a curious rotation commences, moving the opisthe relative to the proter (Fig. 35). When the rotation is completed in late dividers, the oral structures of the proter and opisthe are on different sides of the cell and thus cannot be seen in the same focal plane (Fig. 36). Cell shaping, completion of the pharyngeal basket in proter and opisthe, and formation of the postoral pseudomembrane occur in post-dividers, which are globular and smaller than morphostatic cells.

Discussion

Generic assignment and comparison with congeners

Using the features established by Foissner (1993), the ciliate described belongs to the class Colpodea (somatic dikinetids; Figs 1–3, 17–19), the subclass Colpodia (platyophryid silverline pattern, pleurotelokinetal stomatogenesis; Figs 14–16, 27, 32–36), the order Cyrtolophosidida (micronucleus in perinuclear space of macronucleus; Fig. 6, but must be verified by electron microscopy), the family Platyophryidae (oral aperture slanted rightwards, with postoral pseudomembrane; Figs 6, 7, 17, 18, 21, 23), and the genus *Platyophrya* (adoral organelles obliquely oriented, postoral pseudomembrane distinct, small to medium sized, usually cucumber shaped and with narrow, obliquely truncate or rounded anterior end bearing a comparatively small oral aperture, posterior end without adhesive organelles; Figs 4–7, 14, 21, 28). Except in body shape, the bromeliad tank ciliate matches the diagnosis of *Platyophrya*. This affiliation is corroborated by a comparison of the SSU rDNA sequences, which shows *Platyophrya vorax* as the nearest relative (Dunthorn et al. 2008). Another unique feature of *P. bromelicola* is the ability to switch from a small, bacteriophagous to a large predaceous morph. However, such difference is usually not considered as a generic character, neither in

colpodids (Foissner 1993; Foissner et al. 2002) nor, for instance, in the well-known genus *Tetrahymena* (Corliss 1973; Strüder-Kypke et al. 2001).

We do not know whether or not *P. bromelicola* is confined to the bromeliad habitat. Thus, a conventional species comparison is necessary. Foissner (1993) recognized 10 reliable *Platyophrya* species; of these, the following resemble microstomes of *P. bromelicola*: *P. vorax*, *P. macrostoma*, *P. citrina*, and *P. hyalina*. *Platyophrya bromelicola* differs from these species by body shape (usually pyriform vs. reniform, bursiform or obovate), the lack of lateral flattening, the habit (swimming vs. periphyton creepers), and the ability to form macrostomes. The last mentioned feature can be applied only to *P. vorax*, which neither forms macrostomes in environmental samples nor laboratory cultures (Foissner 1993 and unpubl.). None of the other species mentioned above has ever been cultivated. Additionally, *P. bromelicola* differs from *P. vorax* and *P. macrostoma* by the higher number of ciliary rows (17–20 vs. $\leqslant$13) and adoral organelles (5–6 vs. usually 4). *Platyophrya citrina* has an orange-coloured cytoplasm and mucocysts, producing a conspicuous envelope. The most similar species is *P. hyalina* because it is, like *P. bromelicola*, wider in the anterior than posterior half and has a similar number of ciliary rows ($\sim$15) and adoral organelles (4–5). However, *P. hyalina* is obovate (vs. pyriform, ellipsoidal, and pyriform or ellipsoidal with acute end) and distinctly flattened (vs. unflattened), indicating that it lives in the biofilm (vs. swimming). Nonetheless, if *P. bromelicola* is not restricted to the bromeliad habitat, certain microstomes (Figs 8, 9) might be difficult to separate from *P. hyalina* and *P. vorax*.

Microstome–macrostome transformation

Of the about 200 colpodids known (Foissner 1993; Foissner et al. 2002), macrostomes have been described only in *Hausmanniella patella* (Foissner et al. 2002) and *Platyophryides* sp. (Puytorac et al. 1992). Further, there is some evidence that *Colpoda cavicola* and *Bresslaua vorax* can form large-mouthed morphs (Foissner 1993 and more recent unpubl. observ.). Thus, microstome–macrostome transformation in *P. bromelicola* was unexpected, although it occurs in *Platyophryides* sp. (Puytorac et al. 1992), a genus possibly belonging to the same family as *Platyophrya* (Dunthorn et al. 2008; Foissner 1993), and in another not yet described colpodid from tank bromeliads (Foissner et al. 2003).

Foissner et al. (2003) emphasized the unusually high percentage of ciliates with the ability to switch between a bacteriophagous microstome and a predaceous macrostome morph in bromeliad tanks. This notion is sustained by *P. bromelicola*, which belongs to a group of ciliates where microstome–macrostome transformation is rare (see above). Very likely, macrostome formation is an adaptation to the highly competitive habitat found in bromeliad cisterns (Foissner et al. 2003).

Ontogenesis

Division of *P. bromelicola* is highly similar to that of cyrtolophosidid colpodids (Foissner 1993; Foissner et al. 2002), showing the homogeneity of the group. Unfortunately, the genesis of the postoral pseudomembrane could not be followed.

Function of the postoral pseudomembrane

Platyophrya bromelicola belongs to the cyrtolophosidid colpodids (Foissner 1993). Within this group, there are two kinds of organization, viz., genera with ordinary left side ciliature and others with a so-called postoral pseudomembrane along the left mouth margin. The postoral pseudomembrane consists of narrowly spaced somatic dikinetids originating from two sources: (i) a condensation of the anterior-most dikinetids of the ordinary left side ciliary rows and (ii) an intercalation of short extra kineties between the anterior ends of the ordinary ciliary rows. This creates a distinct, membranous stripe of cilia along the left mouth margin (Figs 2, 5, 7, 23, 24). Foissner (1993) and Foissner et al. (2002) used this special configuration to characterize the family Platyophryidae and to distinguish similar genera from various families.

Based on the location and dense arrangement of the cilia, Buitkamp (1977) suggested that the postoral pseudomembrane has some function in food acquisition. This is supported by the present data, which indicate a special importance for the acquisition of large food items because the postoral pseudomembrane is larger in macrostomes than in microstomes (Figs 2, 5, 21,23).

Acknowledgements

This study was supported by the Austrian Science Foundation (FWF), Projects P–15017 and P–20360–B17. The technical assistance of Mag. Gudrun Fuss, Andreas Zankl, and Robert Schörghofer is greatly acknowledged. Special thanks to Dr. M. Dunthorn for calculating the genetic distance between *P. bromelicola* and *P. vorax*.

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