

Morphology and morphogenesis of *Bursostoma bursaria* Vörösváry, 1950 (Ciliophora, Ophryoglenina)*

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RÉSUMÉ

La morphologie, l'infaciliature et l'argyrome du cilié rare *Bursostoma bursaria* Vörösváry, 1950, sont décrites. La division commence par la résorption des structures orales du tomonte et le développement de 2 champs de cinétosomes qui sont à l'origine des nouvelles structures orales du proter et de l'opisthe. Le développement de la membrane parorale pendant la stomatogénèse et sa résorption ultérieure sont observés. La morphogénèse de *B. bursaria* est ainsi très comparable avec celle d'*Ophryoglena mucifera*. D'autres homologues, telles que la présence d'un

profond vestibule, de cinéties vestibulaires et d'un argyrome de type tétrahyménien conduisent à placer *B. bursaria* dans les Ophryoglenina Canella et Rocchi-Canella, 1964. Ce sous-ordre contient donc 3 familles : les Bursostomidae Vörösváry, 1950, les Ichthyophthiriidae, Kent, 1882 et les Ophryoglenidae, Kent, 1882. Ces 2 dernières sont plus proches entre elles qu'avec les Bursostomidae.

Mots clés : *Bursostoma bursaria*. Morphologie. Morphogénèse.

SUMMARY

The morphology, infraciliature, and silverline system of the rare ciliate *Bursostoma bursaria* Vörösváry, 1950 are described. Division commences with the successive resorption of the parental oral structures and the development of two large fields of basal bodies which produce the new oral structures of the proter and the opisthe. The development of a paroral membrane during stomatogenesis and its complete resorption at the end of this process is documented. Thus, the morphogenesis of *B. bursaria* is very similar to that of *Ophryoglena mucifera*. Further homologues, like the possession of a deep vestibulum, ves-

tibular kineties, and a tetrahymenid silverline system, requires the inclusion of *B. bursaria* in the Ophryoglenina Canella and Rocchi-Canella, 1964. Thus, this suborder now contains three families, the Bursostomidae Vörösváry, 1950, the Ichthyophthiriidae Kent, 1882 and the Ophryoglenidae Kent, 1882. A comparison shows that the Ichthyophthiriidae and the Ophryoglenidae are closer related to each other than to the Bursostomidae.

Key words : *Bursostoma bursaria*. Morphology. Morphogenesis.

INTRODUCTION

In 1950, VÖRÖSVÁRY described a new ciliate, *Bursostoma bursaria* and erected the hymenostomatid family Bursostomidae. Since then, this species has never been found. CORLISS (1979) transferred *Bur-*

sostoma to the Colpodidae without giving any reasons. Fortunately, we rediscovered this curious ciliate in rather high numbers, giving us the possibility to study it with modern methods.

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MATERIAL AND METHODS

Bursostoma bursaria was collected in March 1986 from the bank of the heavily polluted river Salzach in Salzburg. It occurred scattered in flocks of *Sphaerotilus natans* (« sewage fungus »). Some attempts to cultivate this ciliate failed. We obtained an adequate number of individuals by putting the raw samples in a refrigerator for 2 days (4-8°C).

Living observation was performed on cells which were not covered by a cover glass. Details were studied on ± squeezed individuals with an oil immersion objective in

bright field and Normanski contrast. The protargol silver staining method (FOISSNER, 1982; bleaching with Eau de Javel) and the pyridinated silver carbonate method (FERNANDEZ-GALIANO, 1976) were used to reveal the infraciliature. The silverline system was studied by the silver methods of FOISSNER (1976) and CORLISS (1953). All measurements were carried out by an ocular micrometer. For methods of statistical analysis see FOISSNER (1982). The drawings, except fig. 1-3 and 6, were made with the help of a camera lucida.

RESULTS

MORPHOLOGY

In vivo 123-185 X 86-123 µm (n = 6), body ovoid, not flattened and not contractile (fig. 1). Moderately fed individuals more slender, about twice as long as broad (fig. 2). Anterior end distinctly truncated and slightly bent to the ventral side, producing a concave area in the anterior ventral quarter. The remaining 3 quarters and the dorsal outline are convex. Posterior end broadly rounded. Vestibulum slightly subapical, cylindrical, *in vivo* ca. 25 µm deep and 20 µm in diameter. Aperture round, with a slit-like elongation to the ventral side. Strongly beating membranelles, the second, larger one, beats half as fast as the others. Pellicle soft and flexible, with underlying 3-4 X 0.5 µm sized, boomerang-formed trichocysts (fig. 1, 3a, b). Endoplasm colourless, very hyaline, containing colourless, refractile granules, 1-2 µm in diameter. Feeds on *Glaucoma scintillans* and *Trithigmotoma cucullulus*, food vacuoles 15-30 µm in diameter (fig. 14). Macronucleus near the center of the body, *in vivo* about 70 X 30 µm, oval to kidney-formed, with numerous tiny (< 1 µm), irregularly distributed chromatin bodies. Contractile vacuole *in vivo* 25 µm in diameter, located right-laterally, slightly below the middle of the body, during diastole surrounded by smaller vacuoles (~ 5 µm). Somatic cilia *in vivo* 8-10 µm,

caudal cilia rather stiff, 15 µm long. Movement moderately fast, with permanent rotation around the longer axis of the body.

INFRACILIATURE

On the average 114 closely spaced and densely ciliated kineties. 2 sutures, that of the dorsal side commences below the edge of the vestibulum and extends over the anterior third of the body (fig. 9, 12, 15), that of the right side commences in the region underneath the contractile vacuole, reaching the posterior pole (fig. 1, 4). Kineties converge along the lateral suture, leaving a small area where the caudal cilia are inserted. A second field of caudal cilia is located at the posterior pole. Basal bodies arranged in a zigzag pattern, in protargol slides their cilia show darker impregnation than the normal somatic cilia (fig. 16). About 10 anteriorly shortened postoral kineties, the right-most one is defined as kinary number 1. To the right of kinary number 1, the anterior parts of 8 to 10 kineties form a semicircle on the right wall of the vestibulum (table I). Commonly, the first and the last two of these vestibular kineties anteriorly shortened. Distances between the basal bodies slightly enlarged in the anterior parts of the vestibular kineties. Anterior ends of somatic kineties reach inside the upper part of

FIG. 1-8. — *Bursostoma bursaria* from life (1-3), after protargol impregnation (4), Chatton-Lwoff impregnation (5, 7, 8) and dry silver impregnation (6). 1, right-lateral view of a well fed cell. Scale mark, 56 µm. 2, slender form of a moderately fed individual. Scale mark, 53 µm. 3a, layer of trichocysts underneath the pellicle. b, trichocysts higher magnified. 4, infraciliature in right-lateral view. Arrow, contractile vacuole pori. Scale mark, 38 µm. 5, infraciliature of the anterior pole in right-lateral view. Scale mark, 19 µm. 6, silverline system. 7, infraciliature of the anterior pole in ventral view. Scale mark, 14 µm. 8, silverline system in the region of the contractile vacuole pori. Abbreviations: CC, caudal cilia; K1, kinary number 1; KF, kinary fragments; M 1-3, membranelles 1, 2, 3; S, argyrophilic structure (remains of the paroral membrane ?); V, vestibulum; VK, vestibular kineties.

FIG. 1-8. — Schéma de *Bursostoma bursaria* sur le vivant (1-3), d'après imprégnations au Protargol (4), selon Chatton et Lwoff (5, 7, 8) ou à sec (6). 1, vue latérale droite d'une cellule bien nourrie (échelle : 56 µm); 2, forme élancée d'individu modérément nourri (échelle : 53 µm); 3a, couche de trichocystes sous la pellicule; 3b, trichocystes grossis; 4, vue latérale droite de l'infraciliature, avec pore de la vacuole contractile (flèche) (échelle : 38 µm); 5, infraciliature du pôle antérieur, en vue latérale droite (échelle : 19 µm); 6, argyrome; 7, infraciliature du pôle antérieur, en vue ventrale (échelle : 14 µm); 8, argyrome dans la région de la vacuole contractile. CC, cils caudaux; K1, cinétie 1; KF, segments de cinéties; M 1-3, membranelles 1, 2, 3; S, structure argyrophile (restes de la parorale ?); V, vestibule; VK, cinéties vestibulaires.

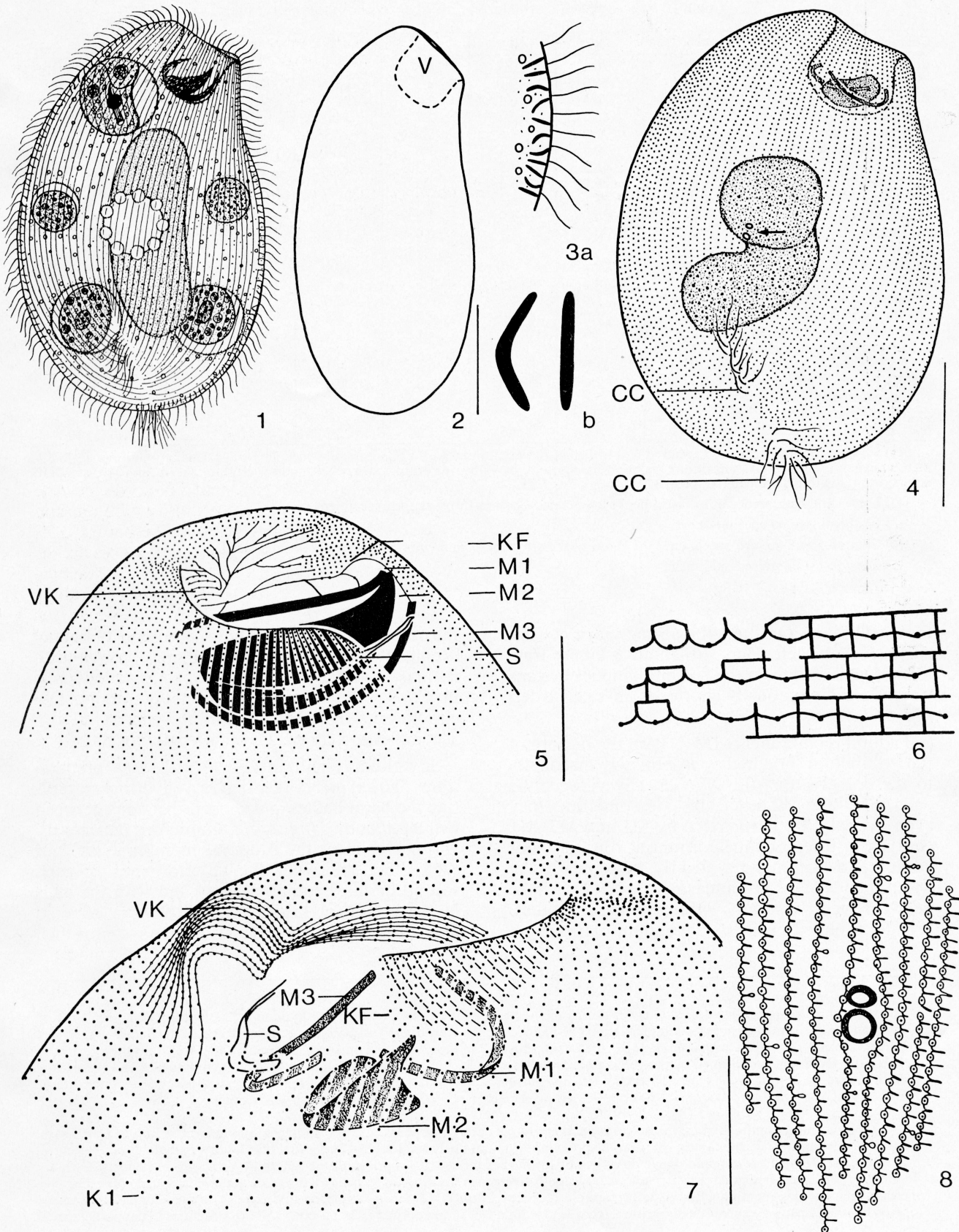


TABLE I. – Biometrical characterization of *Bursostoma bursaria* (1)

Character	$\bar{X}$	$\tilde{X}$	SD	$S_{\bar{x}}$	CV	Min.	Max.	n
Body, length (2)	118.6	120.5	20.5	4.6	17.3	83.0	162.0	20
	121.7	118.5	19.1	4.3	15.7	98.0	173.0	20
Body, width (2)	77.4	76.5	16.3	3.6	21.1	52.0	117.0	20
	86.8	85.5	12.2	2.7	14.0	69.0	117.0	20
Vestibulum, depth (3)	25.4	26.0	3.1	0.7	12.3	18.2	32.0	20
Vestibulum, diameter (3)	20.6	20.8	4.4	1.0	21.4	13.0	28.6	19
Macronucleus, length (3)	66.6	63.5	14.9	3.3	22.4	49.5	95.0	20
Macronucleus, width (3)	28.4	26.0	8.6	1.9	30.2	18.0	52.0	20
M1, length (4)	28.1	28.6	3.2	0.8	11.5	22.1	32.5	16
M2, length (4)	25.6	26.0	3.0	0.8	11.7	18.2	30.0	16
M3, length (4)	29.5	30.5	3.5	0.9	11.7	20.3	33.8	16
Distance, anterior end of body to the CVP (5)	68.7	68.0	9.7	2.6	14.1	55.0	91.0	14
No. kineties	113.5	114.5	7.6	1.9	6.7	96.0	126.0	16
No. postoral kineties	9.8	9.0	2.5	0.5	25.0	3.0	17.0	24
No. kinety fragments	5.3	5.0	0.9	0.2	16.2	4.0	7.0	20
No. kineties between K1 and the first kinety to the right of the CVP	31.2	31.0	1.9	0.5	6.1	27.0	34.0	15
No. CVP	2.0	2.0	0.0	0.0	0.0	2.0	2.0	20
No. kinetosomes in a distance of 20 μ m in the middle of the body (3)	24.2	24.5	5.5	1.2	22.7	17.0	37.0	20

(1) All measurements in μ m. Legend: CV, coefficient of variation in %; CVP, contractile vacuole pori; K1, kinety number 1; M1-3, membranelles 1, 2, 3; Max., maximum value; Min., minimum value; n, sample size; $S_{\bar{x}}$, standard error of the mean; SD, standard deviation; $\bar{x}$, arithmetic mean; $\tilde{x}$, median.

(2) Upper line: protargol stained specimens; lower line: Chatton-Lwoff stained specimens.

(3) Protargol stained specimens.

(4) Chatton-Lwoff stained specimens; the chord of the arc, which the membranelles form, was measured.

(5) Chatton-Lwoff stained specimens.

the vestibulum. On the left wall they turn conspicuously to the left. Here are about 5 kinety fragments, separated from the postoral kineties by gaps which become gradually shorter from right to left (fig. 5, 7, 9).

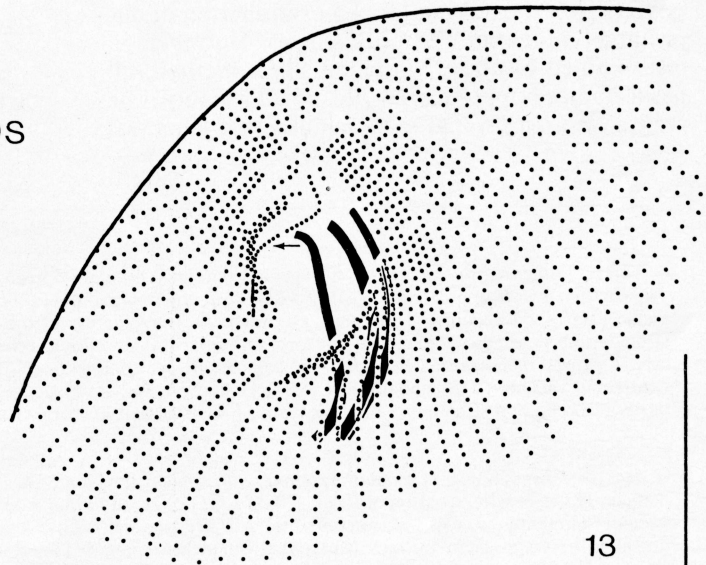
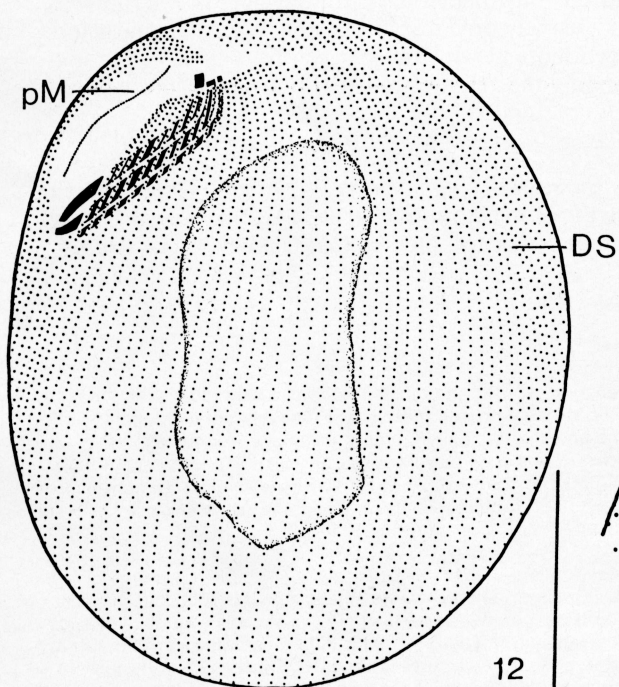
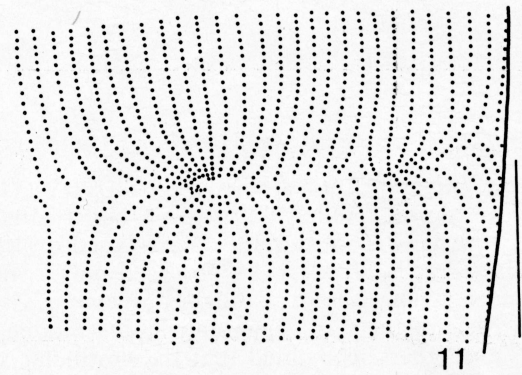
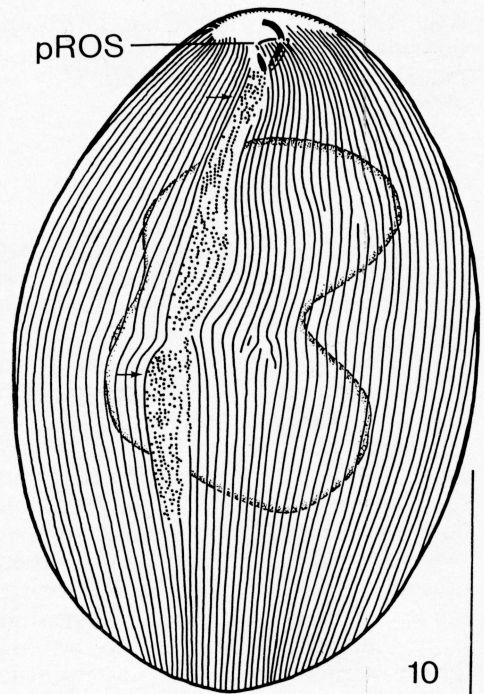
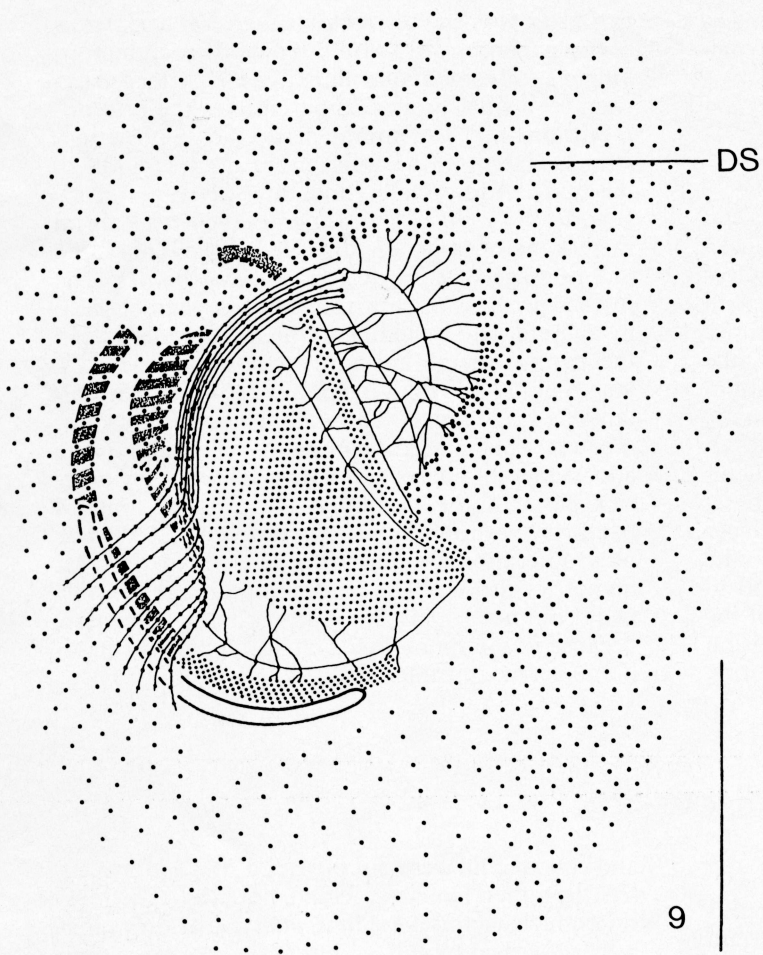
3 adoral membranelles (M 1-3) on the bottom of the vestibulum, oriented approximately diagonally to the dorsal suture (fig. 9). Ventrally viewed, the ends of M1 and M2 lie side by side, sometimes they even overlap. M2 is encircled by M1 and M3. M1 consists of three obliquely arranged rows of basal bodies and commences slightly underneath the anterior ends of the vestibular kineties. M2 is a huge field of very regularly arranged basal bodies, broadly rounded on its dorsal end and tapered on

the other. M3 consists of about six rows of obliquely arranged basal bodies. Immediately above M3, there is an argyrophilic structure, only recognizable in CHATTON-LWOFF preparations. Ventrally, this structure begins slightly before the end of M3 and accompanies it for ca. 2/3 of its length (fig. 5, 7, 9).

Silverline system in CHATTON-LWOFF preparations *Tetrahymena*-like, that is a silverline connecting the basal bodies and short projections between two basal bodies (fig. 8, 20). Numerous delicate silverlines connect the 3 adoral membranelles with each other and with the anterior ends of each second or third somatic kinety and with the ends of the vestibular kineties (fig. 5, 9). Dry silvered individuals show mostly a lattice-like system which

FIG. 9-13. – Infraciliature of *Bursostoma bursaria* during the interphase after Chatton-Lwoff and pyridinated silver carbonate impregnation (9) and during division after protargol impregnation (10-13). 9, top plan view of the vestibulum and the oral structures. Scale mark, 16 μ m. 10, early division stage. The arrows point at the oral primordia for the proter and the opisthe. Scale mark, 46 μ m. 11, division furrow in detail. Note the « centers » formed by converging kineties. Scale mark, 8 μ m. 12, late division stage. The membranelles and the paroral membrane are shortening. Scale mark, 27 μ m. 13, late division stage. Arrow, last basal bodies of the disappearing paroral membrane. Scale mark, 10 μ m. Abbreviations: DS, dorsal suture; pM, paroral membrane; pROS, partly resorbed oral structures.

FIG. 9-13. – Schéma de l'infraciliature de *Bursostoma bursaria* pendant l'interphase, d'après imprégnations selon Chatton et Lwoff et au Carbonate d'argent (9), et pendant la division, d'après imprégnation au Protargol (10-13). 9, vue apicale du vestibule et des structures orales (échelle: 16 μ m); 10, premier stade de division; les flèches indiquent les primordiums oraux du proter et de l'opisthe (échelle: 46 μ m); 11, détail du fuseau de division, avec centres de convergence des cinéties (échelle: 8 μ m); 12, stade ultérieur de division, avec raccourcissement des membranelles et de la parorale (échelle: 27 μ m); 13, stade ultime de division; la flèche indique les derniers cinétosomes de la parorale en vue de disparition, (échelle: 10 μ m); DS, suture dorsale; pM, parorale; pROS, structures orales partiellement résorbées.



resembles that of *Paramecium*. There are, however, transition stages to the above described tetrahymenid silverline system (fig. 6, 21).

MORPHOGENESIS

The morphogenetic process could not be followed in all details, because the number of dividing stages was not very high. Morphogenesis commences with a successive resorption of the oral structures. During this process, the vestibular kineties, the kinety fragments, and the depression of the vestibulum disappear. The anterior parts of the somatic kineties do not bend any more (fig. 17). One individual showed that the resorption of the oral structures commences in M3. A proliferation of basal bodies in the area of the postoral kineties produces two elongated oral primordia for the proter and the opisthe, respectively (fig. 10). To the right and to the left of the oral primordia, in the middle of the body, the kineties commence to form the division furrow. A prominent and constant feature during

this process is the formation of several « centers » at the level of the division furrow, where numerous kineties converge at one point (fig. 11). After separation, each filial product differentiates the oral primordium into 3 membranelles which extend in a straight line from the anterior part to the middle of the body. Additionally, and this was very surprising, to the right of the 3 membranelles a paroral membrane of same length is developed, consisting in this stage of a single row of basal bodies. The further progress of stomatogenesis is characterized by an anteriad shortening of the membranelles and the paroral membrane until they have reached a length of 1/3 or 1/4 of the body (fig. 12, 18). Simultaneously, the invagination of the vestibulum commences. This is accompanied by a bending of the adoral membranelles and a drawing in of the anterior parts of the vestibular and ventral kineties inside the vestibulum (fig. 13). Probably, a last wave of proliferation produces the large field of basal bodies for the M2. The paroral membrane is resorbed completely at the end of stomatogenesis because in interphase individuals no paroral membrane is recognizable.

DISCUSSION

Comparison with the original description

The population studied by VÖRÖSVÁRY (1950) is a little bit smaller (80-120 µm), but it is uncertain whether his measurements are based on living or fixed cells. VÖRÖSVÁRY observed only 2 membranelles. This is understandable, because in vivo large parts of the third membranelle are hidden by the two others. He stated that the vestibular kineties possess paired basal bodies. An examination of our protargol slides showed only singles. However, in cells stained by the pyridinated silver method, all basal bodies appear paired (fig. 15). Probably, one granule is a parasomal sac. Details like trichocysts

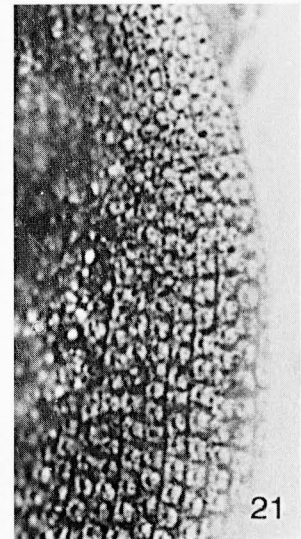
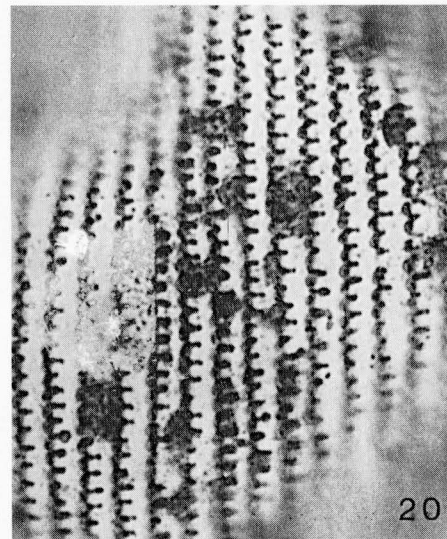
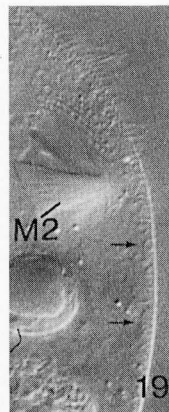
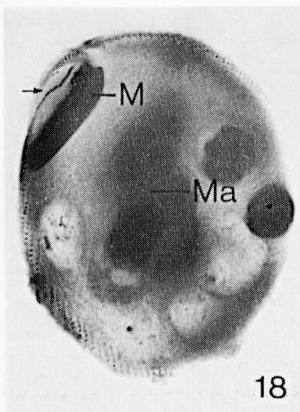
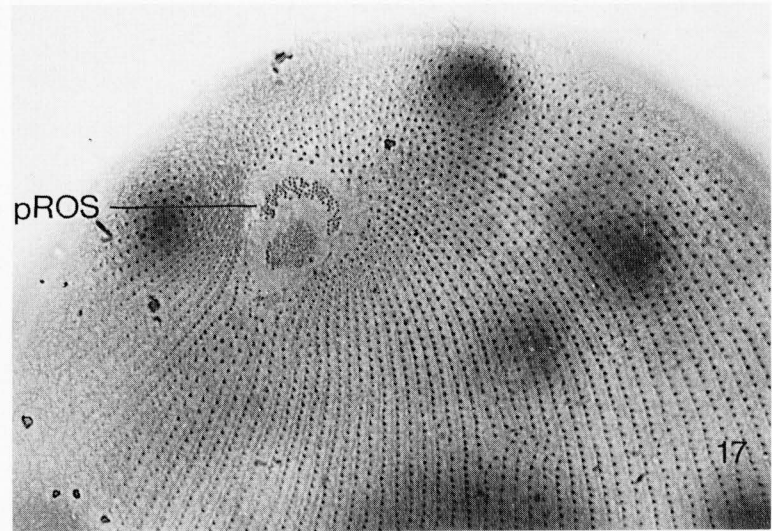
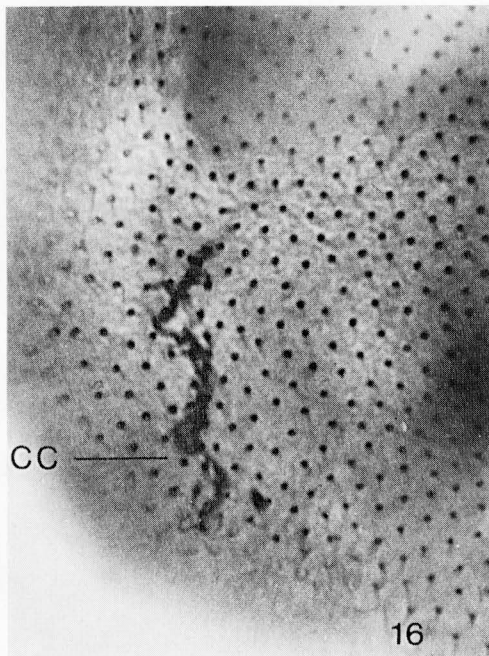
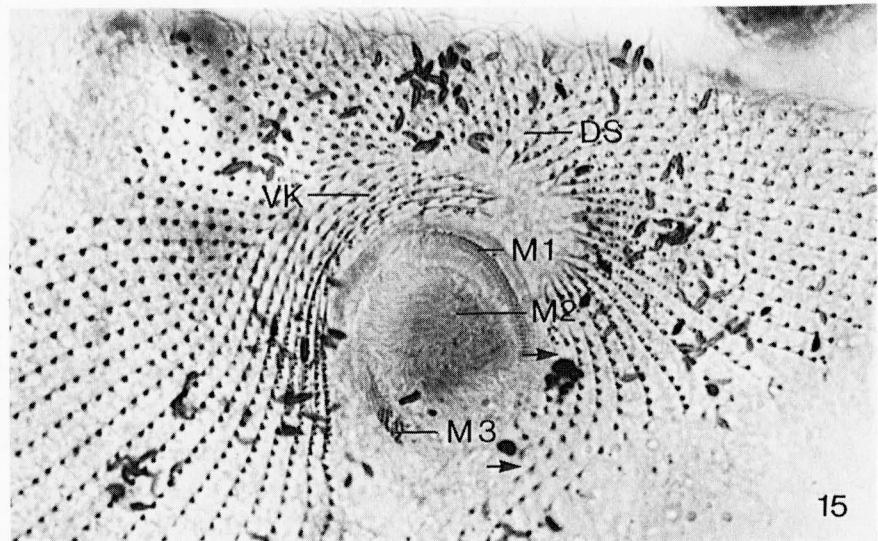
and caudal cilia were not observed by VÖRÖSVÁRY. On the other hand, we could not find the single micronucleus and the 2 long pharyngeal fibers that were described by this author. VÖRÖSVÁRY's population was bacteria-feeding, whereas we noticed exclusively predatory nutrition. All other characters are identical with those given by VÖRÖSVÁRY, suggesting that we worked with the same species.

Taxonomic position of Bursostoma bursaria

Bursostoma bursaria is the single representative of the Bursostomidae VÖRÖSVÁRY, 1950, a family which is not accepted by CORLISS (1979). Our inves-

FIG. 14-21. — *Bursostoma bursaria* from life (14, 19), after protargol impregnation (16, 18), pyridinated silver carbonate impregnation (15, 17), Chatton-Lwoff impregnation (20) and dry silver impregnation (21). 14, strongly pressed individual showing vestibulum, contractile vacuole and food vacuoles (Normanski contrast). 15, infraciliature of the buccal area. Arrows, kinety fragments. 16, lateral suture with strongly impregnated caudal cilia. 17, resorption of the oral structures occurs during early morphogenetical stages. 18, late division stage. Arrow, paroral membrane. 19, detail of the pellicle. Arrows, trichocysts (Normanski contrast). 20, 21, silverline system. Abbreviations: C, contractile vacuole; CC, caudal cilia; DS, dorsal suture; FV, food vacuoles; M1-3, membranelles 1, 2, 3; Ma, Macronucleus; pROS, partly resorbed oral structures; V, vestibulum; VK, vestibular kineties.

FIG. 14-21. — Microphotographies de *Bursostoma bursaria* sur le vivant (14, 19) d'après imprégnations au Protargol (16, 18), au Carbonate d'argent (15, 17), selon Chatton et Lwoff (20), à sec (21). 14, individu compressé montrant le vestibule (V), la vacuole contractile (C), les vacuoles alimentaires (FV); 15, infraciliature de l'aire buccale (flèche: segments de cinéties; M1, M2, M3: membranelles; DS: suture dorsale); 16, suture latérale avec cils caudaux fortement imprégnés; 17, résorption des structures orales (pROS) pendant la division; 18, stade ultime de division (flèche: parorale; M, membranelles; Ma, macronoyau); 19, détail de la pellicule (flèches: trichocystes; M2, membranelle 2); 20, 21, argyrome.



tigations show that *Bursostoma* deserves family status and that the Bursostomidae belong to the Ophryoglenina CANELLA and ROCCHI-CANELLA, 1964. This is supported by the following homologies: a) There are conspicuous similarities in the morphogenetical processes, e.g. the successive resorption of the oral structures. This occurs in each member of the 2 families presently included in the Ophryoglenina (PUYTORAC *et al.*, 1983; CANELLA and ROCCHI-CANELLA, 1976; ROQUE *et al.*, 1967; ROQUE and PUYTORAC, 1967). The process of formation and resorption of the paroral membrane during stomatogenesis is exactly the same in *Bursostoma* and *Ophryoglena* (PUYTORAC *et al.*, 1983). If this holds true also for *Ichthyophthirius multifiliis* FOUQUET, 1876, as is suggested by results of CANELLA and ROCCHI-CANELLA (1976), then the tetrahymenid pattern of the oral structures develops only during stomatogenesis in all 3 families. The argyrophilic structure which we found above the M3 in interphase individuals of *B. bursaria* could be the remains of the paroral membrane. b) The vestibular kineties lining parts of the inner wall of the vestibulum exist also in *Ichthyophthirius* and *Ophryoglena* (CANELLA and ROCCHI-CANELLA, 1976). c) The silverline system of *Bursostoma* is very similar to that of *Ophryoglena* (CANELLA and ROCCHI-CANELLA, 1976). A « polymorphism » of the silverline system as we found in *Bursostoma* is also reported in *Ophryoglena bacterocaryon* ROQUE *et al.*, 1965.

The « flamme », an aggregation of basal bodies at the end of M2 is a prominent character of the oral structures in the Ophryoglenidae (CANELLA and ROCCHI-CANELLA, 1976; PUYTORAC *et al.*, 1983). It is tempting to speculate that the large field of basal bodies that makes up the M2 of *B. bursaria* is the apomorphic condition of this aggregation.

The possession of a « Lieberkühn organelle » is regarded as a key character of the Ophryoglenina (CORLISS, 1979). Now, *B. bursaria* is the second species, besides *Ichthyophthirioides browni* ROQUE and PUYTORAC, 1967, without that organelle.

Characterization of the Bursostomidae VÖRÖSVÁRY, 1950

VÖRÖSVÁRY gave no characterization of his family. From our investigations we suggest the following diagnosis: large, ovoid, free-living Ophryoglenina with a nearly polar located cylindrical vestibulum, a dorsal and right-lateral suture and a greatly enlarged second adoral membranelle. Division in free-swimming condition.

Type genus: *Bursostoma* VÖRÖSVÁRY, 1950.

Type species (designated by monotypy): *Bursostoma bursaria* VÖRÖSVÁRY, 1950.

Characterization of the Ophryoglenina CANELLA and ROCCHI-CANELLA, 1964.

The above mentioned homologies show that the Bursostomidae must be included in the Ophryoglenina which, thus, now contain 3 families. The data compiled in Table II suggest that the Ichthyophthiriidae KENT, 1882 and the Ophryoglenidae Kent, 1882 are more closely related than the Bursostomidae to the Ichthyophthiriidae or the Ophryoglenidae. On the grounds of this comparison we suggest the following characterization of the suborder Ophryoglenina: Parasitic or free-living, histophagous or predatory, densely ciliated hymenostomatid ciliates with a deep vestibulum in slightly or distinctly subapical position. Vestibular kineties and « Lieberkühn organelle » commonly present. Somatic kineties form a praeoral or a dorsal and right-

TABLE II. – Comparison of the three families in the suborder Ophryoglenina, based on the present investigations and on data of CANELLA and ROCCHI-CANELLA (1976), PUYTORAC *et al.* (1983), ROQUE *et al.* (1965, 1967) and ROQUE and PUYTORAC (1967).

Character	Bursostomidae	Ichthyophthiriidae	Ophryoglenidae
Life cycle	Free-living; binary fission without cysts; predatory.	Parasites of freshwater and marine fish; theronts, trophonts, tomites, and tomites; only palintomy in cysts; histophagous.	Both, free-living and parasitic species; theronts, trophonts, tomites, and tomites; division in bi-, tetra-, octogenic cysts, also palintomy occurs; histophagous.
Vestibulum	Slightly subapical; rather simple, without « Lieberkühn organelle ».	Distinctly subapical; rather simple, with « Lieberkühn organelle » (except for <i>Ichthyophthirioides</i>).	Distinctly subapical; very complicated in form and construction, with « Lieberkühn organelle ».
Arrangement of the vestibular kineties	Connected with somatic kineties.	Not connected with somatic kineties.	Not connected with somatic kineties.
Position of sutures	Dorsal and right-lateral.	Praeoral; possibly also postoral.	Praeoral; possibly also postoral.
Postoral kineties	Present (about 10).	Present (only 1).	Absent.
Construction of membranelles	Huge number of basal bodies in M2.	All membranelles similarly constructed	Aggregation of basal bodies (« flamme ») at the end of M2.

lateral suture. Silverline system tetrahymenid. Division in bi-, tetra-, octogenic or palintomic cysts or binary fission in free-swimming condition. Paroral membrane present only during stomatogenesis.

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