



A detailed description of a Brazilian *Holophrya teres* (Ehrenberg, 1834) and nomenclatural revision of the genus *Holophrya* (Ciliophora, Prostomatida)

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Abstract

I studied a Brazilian population of *Holophrya teres* (Ehrenberg, 1834) Foissner, Berger and Kohmann, 1994, using live observation, morphometry, silver impregnation, and scanning electron microscopy. This showed a fair similarity with European populations, especially in having a large (about $13 \times 5 \mu\text{m}$ in vivo) micronucleus pyriform in broad-side view and cuneate in narrow-side view. Several new structures were discovered, viz., an internal oral basket, teeth on anterior end of the oral basket rods, and a buccal seal closing the oral basket when not feeding. Based on this knowledge, I provide an improved diagnosis for *H. teres*, which can be used as template in further species descriptions. Depending on brosse implantation in the somatic ciliature, the genus was split in *Holophrya*, *Hillerophrya* nov. gen., *Vdacnyophrya* nov. gen., and *Bardeleophrya* nov. gen. Twenty-one *Prorodon* species were combined with the holophryid genera, using brosse and thick oral basket rods as main markers. This revealed two new species, viz., *Holophrya longiarmata* nov. spec. and *H. agamalievi* nov. spec.

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Introduction

“To study the genus *Prorodon* (now *Holophrya*, see below) belongs to the most frustrating job in infusorian taxonomy” as stated by Kahl (1928). He made the first and also the last review on holophryids (Kahl 1930). Since then, some progress was made by Dragesco (1960, 1963, 1965, 1966a,b,c, 1970), Foissner (1983, 1997), Dragesco and Dragesco-Kernéis (1986), Leipe (1989), Augustin and Foissner (1992), Alekperov (2005), and by the excellent studies of Hiller and Bardele (1988) and Hiller (1993a,b); Foissner et al. (1994, 1999) and Foissner and Pfister (1997) added reviews on selected holophryids and related genera.

Some *Holophrya* or *Prorodon* species were referred to new genera, e.g., *Pleurofragma* Jankowski, 1976 (type species *Prorodon mimeticus* Kahl, 1930) and *Paraprorodon* Foissner, 1983 (type species *Prorodon morgani* Kahl, 1930).

A main reason for the slow progress might be the often large size ($\geq 150 \mu\text{m}$), which makes live observation and various preparations difficult. Further, holophryids usually have low abundance in environmental samples and thus need cultivation.

Not only morphological descriptions are poor in most old (e.g., Tannreuther 1926) and even more recent publications (e.g., Benčat'ová et al. 2019; Kim and Jung 2017) but also nomenclature. It was shocking when Foissner et al. (1994) recognized that Fromentel (1875) fixed type species for *Holophrya* Ehrenberg, 1831 and *Prorodon* Ehrenberg,

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1834 different from those used by Kahl (1930) and other researchers. Thus, many new combinations were required. Foissner et al. (1994) did this only for some indicator species and mentioned that the big remainder would be done later – and later is now because I know now the main diagnostic characteristics of holophryids, viz., brosse; thick, inflexible oral basket rods made of nematodesmata bundles; and a complex, unique silverline pattern quite different from that of sometimes highly similar haptorids, e.g., *Enchelyodon Claparède and Lachmann, 1859* and *Enchelys Müller, 1773* (Foissner 1984, 2016).

The present study brings order into the *Holophrya/Prorodon* problem and should serve as an example for solid morphological descriptions of holophryids hopefully producing more reliable identifications. Certainly, molecular investigations should be intensified because family assignation of rather many prostomate genera is questionable; some might belong to new families, others to the haptorids, especially to *Enchelys* or *Enchelyodon*.

Material and methods

Sampling and cultivation, voucher material

Holophrya teres was collected on 1.12.1996 in Brazil, i.e., near the village of Praja do Forte about 85 km south of the town of Salvador, 12°34'31"S, 38°00'30"W. The sample was taken from a dammed, swamp-like part of a small brown water river, viz., the Lagao Timeantube. Here, the river contained many macrophytes, such as water lilies, water ferns, *Utricularia* and a variety of filamentous green algae (e.g., *Spirogyra*) as well as many microscopic organisms, such as nematodes, diatoms, desmids. There was also a great number (~70) of ciliate species, including several remarkable taxa, such as *Coleps bicuspis* Noland, 1925, *Paramecium multimicronucleatum* Powers and Mitchell, 1910, *Glaucoma reniformis* Schewiakoff, 1892, and *Holophrya seyrlii* Foissner, 1997. About eight species were very likely undescribed leaving a lot of work for the future.

Holophrya teres developed well near the bottom of the sample jar and fed mainly on starch grains, very likely from a decaying piece of a water lily. After a week, I collected many specimens and some mud and transferred them to a Petri dish with 50 ml tap water and cultivated *Paramecium aurelia* Müller, 1773 as food because the large *P. multimicronucleatum* was rarely fed by *H. teres*. This culture grew so well that I had sufficient specimens for applying a variety of methods.

All methods mentioned in the paper are described in Foissner (1991) and in Foissner et al. (2002). I did no sequence analysis because this was not standard in 1998 and a sequence for *H. teres* became available (Stechmann et al. 1998).

Eight voucher slides with silver nitrate-impregnated Brazilian specimens (Chatton-Lwoff method) have been

deposited in the Oberösterreichische Landesmuseum in Linz (LI). Relevant specimens have been marked with black ink circles.

Terminology

For the aim of this study, an ordinary terminology has been used (Corliss 1979; Lynn 2008; Vd'áčný and Foissner 2013). Since this is a taxonomic paper, nomenclatural references are listed in the reference section.

ZooBank registration

ZooBank registration number of present work (see Recommendation 8A of ICZN 2012): urn:lsid:zoobank.org:pub:04AB456D-9510-4C16-8D40-9CEEED8606C.

Results and discussion

Description of a Brazilian *Holophrya teres* (Ehrenberg, 1834) and comparison with main literature data (MLD)

In cultures, it is impossible to separate theronts and trophonts. Thus, all measurements and counts contain both.

Body size: Measured under four different conditions (Table 1), viz., in vivo 150–200 × 100–130 µm, average 180 × 108 µm (only five cells and thus not very valuable); Chatton-Lwoff silver nitrate impregnation, dark cells with many food vacuoles: average 212 × 169 µm; Chatton-Lwoff silver nitrate impregnation, transparent cells with few food vacuoles: average 195 × 150 µm; Chatton-Lwoff silver nitrate impregnation, transparent cells with few starch grains, average: 181 × 124 µm. With 5% preparation shrinkage (Foissner 2016, p. 24), one obtains a “usual” in vivo size of about 200 × 130 µm. Interpopulation variability considerable while intravariability is less than 15% except for body width in cultures with few starch grains (CV 19.8%, Table 1).

MLD. My data match well those from Kahl (1927, 1930), i.e., length 130–250 µm, usually around 200 µm; Foissner (1983): length 160–250 µm; Hiller (1993a), cultures fixed in 5% glutaraldehyde: theronts on average 163 × 69 µm, trophonts about 200 × 100 µm; and Foissner et al. (1994, review): 80–300 × 40–200 µm, usually 150–250 µm long. The measurements from Kahl (1927) are too low by about 25% (Foissner and Wenzel 2004). Specimens smaller than 150 µm are post-dividers or, when common, very likely misidentifications.

Body shape: Inconspicuous, anterior body end slightly convex and oblique, posterior broadly rounded. Depending on life cycle slenderly to broadly ovate, obovate or cylindroid, slightly flattened laterally. Theronts smaller and narrower than trophonts, the former more or less broadly cylindroid, the latter broadly ellipsoid or almost globular when studded

Table 1. Morphometric data on *Holophrya teres* from Brazil.

Characteristic ^a	Method ^b	Note ^b	Mean	M	SD	SE	CV	Min	Max	n
Body, length	IV	RV	180.0	180.0	21.2	9.5	11.8	150.0	200.0	5
Body, width	IV	RV	108.0	100.0	13.0	5.8	12.1	100.0	130.0	5
Body length: width, ratio	IV	RV	1.7	1.5	0.3	0.1	17.4	1.4	2.0	5
Body, length ^c	CHL	DC	212.1	210.0	15.3	4.4	7.2	190.0	250.0	12
Body, width ^c	CHL	DC	168.8	172.5	13.5	3.9	8.0	140.0	180.0	12
Body length: width, ratio ^c	CHL	DC	1.3	1.3	0.1	0.1	10.9	1.1	1.6	12
Body, length ^c	CHL	TC	194.9	195.0	19.5	3.6	10.0	150.0	230.0	30
Body, width ^c	CHL	TC	150.3	150.0	18.6	3.4	12.4	120.0	190.0	30
Body length: width, ratio ^c	CHL	TC	1.3	1.3	0.1	0.1	8.6	1.1	1.6	30
Body, length	CHL	WSG	181.4	180.0	23.5	5.1	12.9	140.0	230.0	21
Body, width	CHL	WSG	123.8	130.0	24.5	5.3	19.8	75.0	160.0	21
Body length: width, ratio	CHL	WSG	1.5	1.4	0.3	0.1	17.7	1.1	2.0	21
Anterior body end to macronucleus, distance	CHL	TC	79.5	77.5	23.6	4.3	29.6	40.0	130.0	30
Anterior body end to macronucleus, distance	CHL	WSG	64.8	62.0	17.0	3.7	26.2	25.0	95.0	21
Macronucleus, length	CHL	TC	26.0	27.0	3.0	0.5	11.4	22.0	32.0	30
Macronucleus, width	CHL	TC	21.2	20.0	3.2	0.6	15.0	17.0	29.0	30
Macronucleus, length	CHL	WSG	30.0	29.0	4.3	0.9	14.2	22.0	39.0	21
Macronucleus, width	CHL	WSG	20.8	20.0	3.8	0.8	18.0	15.0	30.0	21
Macronucleus, length of central mass	CHL	TC	9.1	10.0	1.5	0.5	16.6	7.0	11.0	11
Macronucleus, width of central mass	CHL	TC	7.4	8.0	1.4	0.4	18.4	5.0	10.0	11
Macronucleus, length of central mass	CHL	WSG	10.2	10.0	2.3	0.6	22.9	5.0	15.0	17
Macronucleus, width of central mass	CHL	WSG	7.4	7.0	2.1	0.5	27.9	5.0	12.0	17
Micronucleus, length	CHL	TC	9.5	9.5	2.4	0.3	25.7	5.0	14.0	20
Micronucleus, width	CHL	TC	4.3	4.0	0.6	0.2	15.9	3.0	5.0	16
Micronucleus, length	CHL	WSG	13.5	13.0	1.6	0.4	11.9	10.0	16.0	13
Micronucleus, width	CHL	WSG	4.8	5.0	0.4	0.2	9.2	4.0	5.0	5
Ciliary rows, number	CHL	WSG	96.6	96.0	6.6	1.7	6.9	80.0	106.0	16
Ciliary rows, number	SC	WSG	97.8	98.0	4.3	1.1	4.4	90.0	105.0	17
Basal bodies in mid-body in 20 µm	CHL	WSG	12.2	12.0	1.5	0.3	12.1	10.0	15.0	21
Brosse, length	CHL	WSG	50.4	50.0	9.4	1.3	18.7	40.0	70.7	12
Ciliary rows abutting to right side of brosse	CHL	WSG	19.4	20.0	2.6	0.6	13.9	15.0	23.0	17
Oral basket, length	CHL	WSG	42.4	44.0	6.1	1.1	14.4	30.0	53.0	30
Oral basket, width at anterior end	CHL	WSG	21.2	20.0	3.2	0.6	15.0	17.0	29.0	30
Oral basket rods, number	SC	WSG	39.9	40.0	0.9	0.3	2.3	39.0	41.0	7
Toxicysts, length	IV	WSG	15.6	15.5	1.4	0.3	8.8	13.0	18.0	12
Starch grains, length	CHL	WSG	23.7	24.0	5.2	1.1	22.0	11.0	35.0	21
Starch grains, width	CHL	WSG	16.3	15.0	5.3	1.2	32.6	9.0	30.0	21

^aData based on well-impregnated specimens from a raw culture supplemented with cultivated *Paramecium aurelia* as food. Measurements in µm.

^bAbbreviations: CHL – Chatton-Lwoff silver nitrate impregnation, CV – coefficient of variation in %, DC – dark cells, IV – in vivo, M – median, Max – maximum, Mean – arithmetic mean, Min – minimum, n – number of cells investigated, RV – rough values, SC – silver carbonate impregnation, SD – standard deviation, SE – standard error of arithmetic mean, TC – transparent cells, i.e., with few or without starch grains, WSG – without or with few starch grains (a second preparation two weeks later).

^cFirst preparation with food vacuoles containing mainly starch grains making cells dark (DC). All other measurements and counts were made from cells without or with few starch grains.

with food vacuoles and lipid droplets; often slightly narrowed in or slightly anterior of mid-body; narrowing usually not preserved in preparations (Figs. 1a–d, 2a–d).

MLD: Shapes match those of Ehrenberg (1838), Kahl (1927, 1930), Foissner (1983), Foissner et al. (1994) and Hiller (1993a).

Nuclear apparatus: On average in anterior third of cell (Table 1), in well-fed specimens frequently dislocated posteriad, rarely anteriad, variation coefficients thus high (CV 30% and 26%, Table 1). Macronucleus small compared to size of cell (Figs. 1a, d, f, 2p–r, u, w–y, 3l, 4a): about 30 × 20 µm in

vivo, in Chatton-Lwoff silver nitrate preparations on average 26 × 21 µm (transparent cells) and 30 × 21 µm (cells without starch grains); slightly to moderately flattened (Fig. 2y); contains a central mass bulging surface (“central nucleolus”) and sometimes deeply impregnated with silver nitrate; usually studded with pale nucleoli(?) 1–2 µm across, rarely full of globular and rather large, irregular inclusions (Fig. 2r).

Micronucleus in flat concavity of macronucleus, very conspicuous because pyriform, refractive and comparatively large: 5–14 × 3–5 µm, on average 9.5 × 4.0 µm and 10–16 × 4–5 µm, on average 13.5 × 5.0 µm in Chatton-

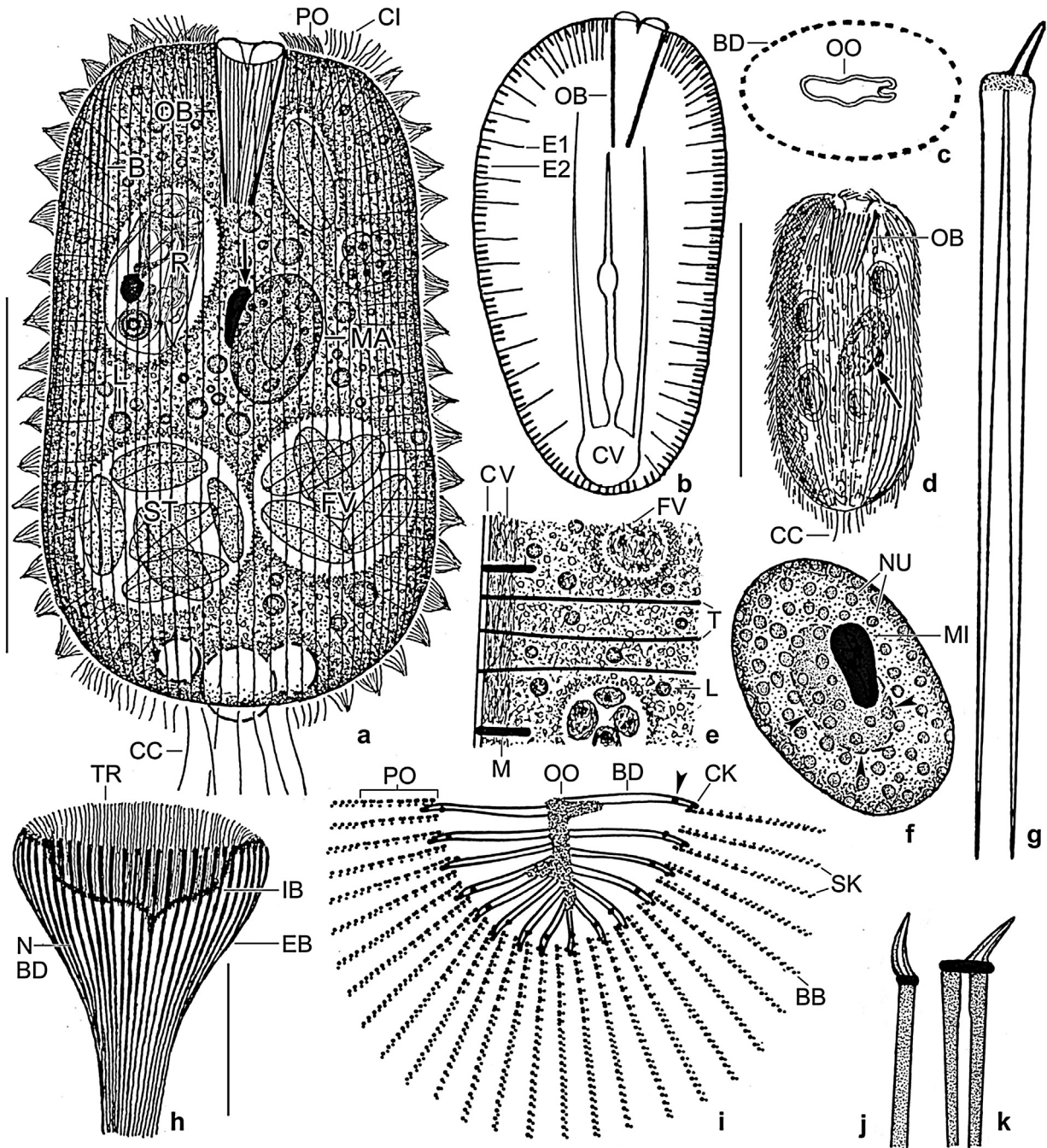


Fig. 1. a–k. *Holophrya teres* from life (a–g, j, k) and after silver nitrate impregnation (h, i). **a, b:** A massive specimen and an obovate shape variant, showing main organelles, length 200 μm . The arrow marks the conspicuous micronucleus. **c:** Polar view of oral basket, width $\sim 40 \mu\text{m}$. **d:** *H. teres*, length 200 μm (from Kahl 1930). **e:** *H. teres* has $\sim 15 \mu\text{m}$ long toxicysts and $\sim 4 \mu\text{m}$ long mucocysts. **f:** Nuclear apparatus, showing the pyriform, about $15 \times 6 \mu\text{m}$ -sized micronucleus and the about $45 \times 30 \mu\text{m}$ -sized macronucleus which has a central mass (arrowheads). **g, j, k:** The about 45 μm long oral basket rods have a tooth shown from the narrow and the broad side (j, k). **h:** The conical external oral basket is made of nematodesmata while the bowl-shaped internal basket is made by transverse microtubule ribbons of the perial cilia. **i:** Semischematic view of oral structures (from Foissner 1983). The arrowhead marks the transverse microtubule ribbons which are so sharply bent that they make dots. B – brosse, BB – basal body, BD – oral basket rods, C – cortex, CC – caudal cilia, CI – ordinary somatic cilia, CK – circumoral kinety, CV – contractile vacuole, EB – external oral basket, FV – food vacuoles, IB – internal oral basket, L – lipid droplets, M – mucocysts, MA – macronucleus, MI – micronucleus, N – nematodesmata, NU – nucleoli, OB – oral basket, OO – oral opening, PC – parasomal sac, PO – perial ciliature, R – rotifer, S – starch grains, SK – somatic kineties, T – toxicysts, TR – transverse microtubule ribbons, V – viscous plasm. Scale bars 15 μm (h) and 100 μm (a, b).

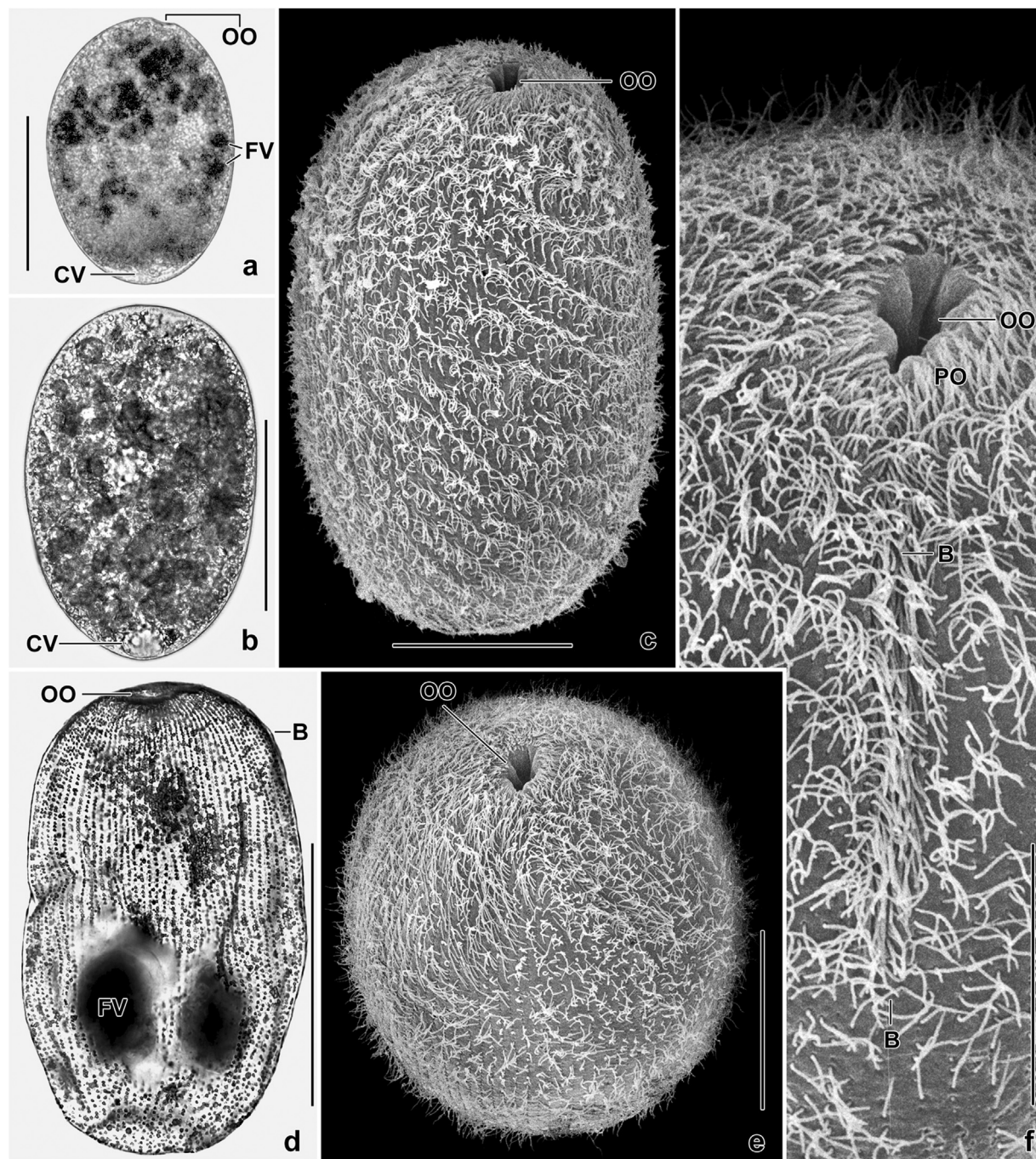


Fig. 2. a–f. *Holophrya teres* from life (a, b), after Chatton-Lwoff silver nitrate impregnation (d), and in the scanning electron microscope (c, e, f). **a, b:** Freely motile, well-nourished specimens are broad and rather opaque due to many food vacuoles. **c:** Overview, showing an ellipsoid specimen with nice metachronal ciliary waves. **d:** Overview, showing the ciliary rows of an ellipsoid specimen. **e:** Oblique polar view. **f:** Anterior region, showing the nearly closed oral opening and the brosse composed of three rows of soft cilia highly similar to the ordinary somatic cilia. B – brosse, CV – contractile vacuole, FV – food vacuoles, OO – oral opening, PO – perioral ciliature. Scale bars 25 μm (c, e) and 100 μm (a, b, d).

Fig. 2. g–k. (on p. 7). *Holophrya teres* from life (g), in Chatton-Lwoff silver nitrate preparations (h–j), and after silver carbonate impregnation (k). **g:** The canals of the contractile vacuole extend near to the ciliary rows. Arrowheads mark diastolic regions. **h, j:** Oblique polar views, showing the oral opening and the three-rowed dextrotrop brosse whose posterior region is curved leftwards (arrow); about 19 ciliary rows abut to right side of brosse. **i:** Polar view of a closed oral opening surrounded by perioral dikinetids. **k:** Posterior body region, showing minute excretory pores (arrowheads) surrounding larger pores in pole area (arrows). B – brosse, CK – circumoral kinety, CL – canals of contractile vacuole, L – lipid droplets, OO – oral opening, PO – perioral ciliature, SK – somatic kineties. Scale bars 15 μm (g), 40 μm (k) and 50 μm (h, j).

Lwoff silver nitrate preparations (Table 1); broad part thickened, thus more or less cuneate in lateral view (Figs. 1a, d, f, 2p–r, u, w–y).

MLD: The macronucleus matches previous descriptions, e.g., Kahl (1927) and the measurements of Hiller (1993a): $32 \times 24 \mu\text{m}$ in Feulgen stains which is close to my data (see above) when 5% preparation shrinkage is added. Kahl (1927) mentioned and figured the large central “nucleolus” (Fig. 1d) but wrote in (1930) “without Binnenkörper”, i.e., without central nucleolus.

When I saw the large, pyriform micronucleus, I supposed to have discovered a new species; this was emphasized by the small, globular micronucleus described by Foissner (1983) and the “spherical to lenticular”, $8.5 \times 4.7 \mu\text{m}$ -sized micronucleus described by Hiller (1993a). Thus, I was disappointed when I saw Kahl (1927, 1930) and micrographs from a Salzburg population studied years ago, both showing a micronucleus highly similar to that of the Brazilian specimens (cp. Figs. 1a, f, 2p–r, 4a with Fig. 1d). I suppose that my observations from 1983 are incorrect and that from Hiller (1993a) only partially correct. As a large, pyriform micronucleus has been observed in Germany (Kahl 1930, Fig. 1d), Austria (Fig. 4a), and Brazil (Figs. 1a, f, 2p–r), I am convinced that this is typical for *H. teres*.

Contractile vacuole and cytoproct: In posterior end of body, with as many collecting canals as ciliary rows, extend at left margin of rather deep ciliary furrows (Hiller 1993a) and show many diastolic extensions (Fig. 2g). Two types of excretory pores: some large in pole center and rather many small ones in posterior quarter (Fig. 2k).

Foissner (1972) reported on the defecation in *H. teres*, using serial micrographs: (1) The frequency of defecation and the number of faecal balls are in direct relation to food supply. As a rule, only one faecal ball is discharged. (2) Defecation occurs almost regularly shortly before encystment and immediately after excystment. (3) The faecal ball consists of numerous individual egestion vacuoles and it is usually approximately spherical with a diameter of $20\text{--}50 \mu\text{m}$. (4) The faecal ball is covered by a distinct membrane usually

splitting several minutes after release from body; it is composed of a granular mass including various larger materials. (5) The excretion lasts $10\text{--}60$ s on the average. (6) During defecation the cortex closing the cytoproct is resorbed and, at the same time, a new cortex is formed around the faecal ball which then leaves the cell body.

MLD: The collecting canals were discovered by Puytorac (1964) and later studied in great detail by Hiller (1993a) to whom the reader is referred to. Canals present also in some other large Prostomata, such as *Prorodon akliolophon* Hiller and Bardele, 1988 (now type species of *Vdacnyophrya* nov. gen., see below) and *Pelagothrix* Foissner et al., 1999. Very likely, canals are absent in small holophryids.

Extrusomes: *Holophrya teres* has two types of extrusomes, both difficult to recognize in vivo because either very thin (toxicysts) or rather short (mucocysts), attached to cortex between ciliary rows. Toxicysts in vivo $13\text{--}18 \mu\text{m}$ long, less than $0.5 \mu\text{m}$ thick, slightly curved, densely spaced around oral opening, leave distinct “holes” in cortex when exploded, occasionally deeply impregnated with silver carbonate (Figs. 1a, b, e, 2s, t, v, z, 3r, s).

Mucocysts very numerous, rod-shaped, in vivo about $4.0 \times 0.5 \mu\text{m}$ in size and thus twice as thick as toxicysts, become up to $10 \mu\text{m}$ long blueish rods with deeper stained anterior end when methyl green-pyronin is applied; occasionally deeply impregnated with silver carbonate (Figs. 1a, b, e, 2v, 3o, p).

MLD: Although extrusomes are an important feature, most taxonomists overlooked the studies by Kahl (1927), Krüger (1934) and Wohlfarth-Bottermann and Pfefferkorn (1953), who described both, toxicysts and mucocysts. More recently, Foissner (1983) described the mucocysts and Puytorac (1964) provided electron micrographs of the toxicysts. Hiller (1993a) documented both, toxicysts and mucocysts. The Brazilian *H. teres* matches these studies.

The mucocysts of the Brazilian specimens are possibly a special type because they swell only slightly in methyl green-pyronin where the Austrian specimens produced a voluminous, slimy envelope (Foissner 1983).

Fig. 2. 1–o. (on p. 8). *Holophrya teres* in Chatton-Lwoff silver nitrate preparations (l, m, o) and in the scanning electron microscope (n). **1:** Anterior polar view, showing 100 ciliary rows of which 17 abut in sharp angles to the right side of the dextrotrop brosse and two are posterior of the brosse (not recognizable but see Figs. 2h, o, 3e). The basal bodies of the cilia are very narrowly spaced and the perioral ciliature is indistinctly separated from the somatic ciliature. **m:** Posterior polar view of a specimen with 103 ciliary rows (for details, see Fig. 2k). **n, o:** Division cysts are covered with a very thin membrane. The arrow in (o) marks three very narrowly spaced post-brosse kineties. B – brosse, CK – circumoral kinety, OO – oral opening. Scale bars $100 \mu\text{m}$.

Fig. 2. p–z. (on p. 9). *Holophrya teres* from life (p–r, t), after Chatton-Lwoff silver nitrate impregnation (u, w–z), and in silver carbonate preparations (s, v). **p, q:** Slightly pressed nuclear apparatuses, showing the conspicuous, pyriform micronucleus, a main feature of this species. **r:** A globular macronucleus (but possibly oriented “frontally”) to which the pyriform micronucleus is attached in a flat concavity. Note the big inclusions in the macronucleus. **s:** An exploded toxicyst. **t:** Resting toxicysts of which one is seen completely (arrow). **u:** A specimen with a very large micronucleus in a flat concavity of the macronucleus which has a prominent central mass “nucleolus”. **v:** Exploded mucocysts. **w:** Nuclear apparatus and large starch grains which were the main food during the first week in the raw culture. **x, y:** Further micrographs of nuclear apparatus, that shown in (y) is “frontally” oriented, i.e., showing the flattened macronucleus and the large micronucleus. **z:** Shows the very narrowly spaced dikinetids in the three-rowed brosse and “holes” produced by released extrusomes. B – brosse, E – extrusomes, MA – macronucleus, MI – micronucleus, N – central nucleolus, NU – nucleoli? Scale bars $5 \mu\text{m}$ (r), $10 \mu\text{m}$ (x), $15 \mu\text{m}$ (p, q, t–v), $25 \mu\text{m}$ (w, z) and $50 \mu\text{m}$ (s).

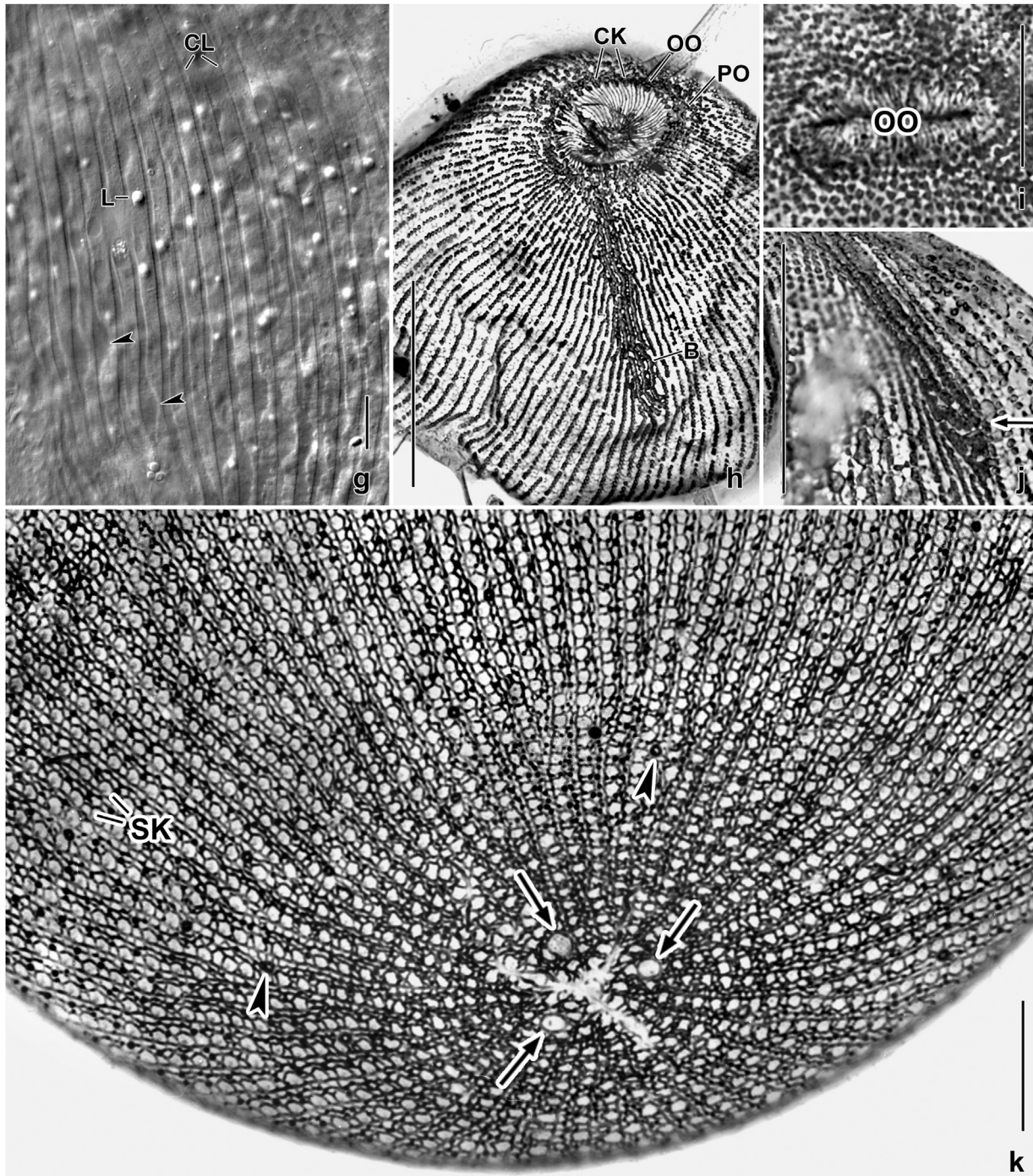


Fig. 2. (Continued)

Cortex and silverline pattern: Cortex flexible, about $0.6\ \mu\text{m}$ thick; underlain by a $2\text{--}3\ \mu\text{m}$ thick, highly viscous zone followed by ordinary cytoplasm (Fig. 1e); contains four silverline patterns dependent on impregnation method and intensity (Fig. 3r, t, u, v) as well as on structures investigated (Fig. 3a, d, e, g, j).

Silver carbonate produces only one pattern (but see MLD) slightly dependent on body site (Fig. 3a–g, j) and cortex extension (Fig. 3r, t): “large” circular to roughly rectangular

meshes contain the greyish impregnated ciliary basal bodies and, to the left, two rows of minute polygonal meshes (Fig. 3r–t) disappearing periorally and at right anterior end of brosse kineties (Fig. 3a–g, j).

Silver nitrate produces two patterns, the second highly different to that obtained with silver carbonate: basal bodies greyish impregnated and surrounded by circular, comparatively large meshes followed by three rows of very minute polygonal meshes resembling the silver carbonate pattern (cp.

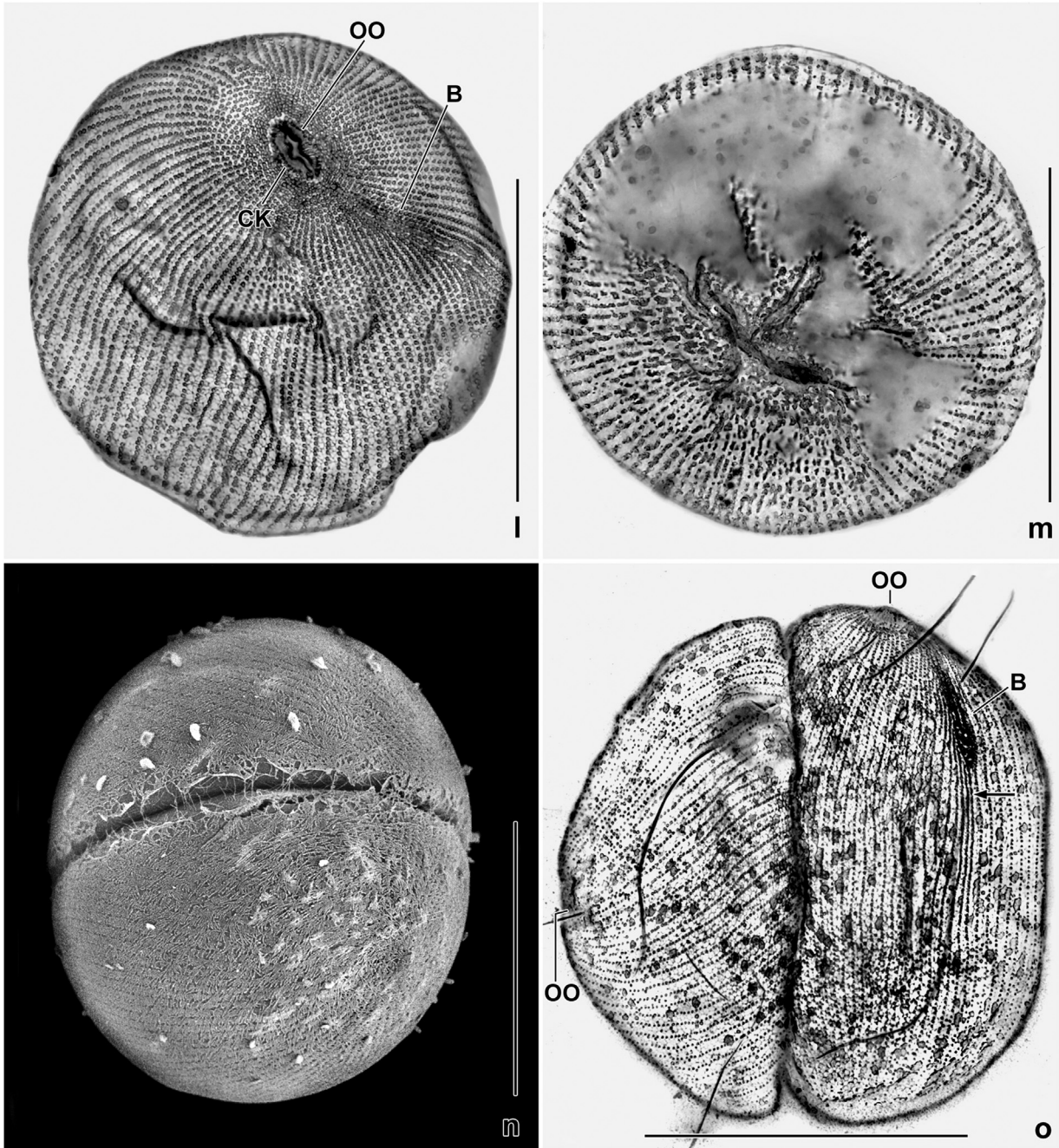


Fig. 2. (Continued)

Fig. 3e and u); when deeply impregnated, basal body rows become very prominent (Fig. 3v). The second pattern highly resembles the platyophryid pattern occurring in colpodids (Foissner 1993), i.e., a zigzagging median silverline extends between each two ciliary rows and contacts basal bodies with minute transverse silverlines (Fig. 3w, x).

MLD: This is the first time that three main silverline patterns have been studied in detail. A fourth pattern, the infraciliary lattice, was observed by Hiller (1993a) in silver carbonate preparations. It is “simple” and near proximal end of the ciliary basal bodies where transverse silverlines con-

nect basal bodies of two kineties each. Thus, four patterns can be distinguished: the silver carbonate pattern, a fine-meshed and a platyophryid pattern in Chatton-Lwoff silver nitrate preparations close underneath the cortex membranes, the very narrow-meshed pattern overlaid by the platyophryid pattern (Fig. 4e), and the infraciliary lattice (see above). The shape of the platyophryid pattern is rather different in various preparations possibly depending on fixation (Figs. 3w, x, 4d–f, and *H. discolor* in Foissner et al. 1994); alternatively, there might be a further pattern.

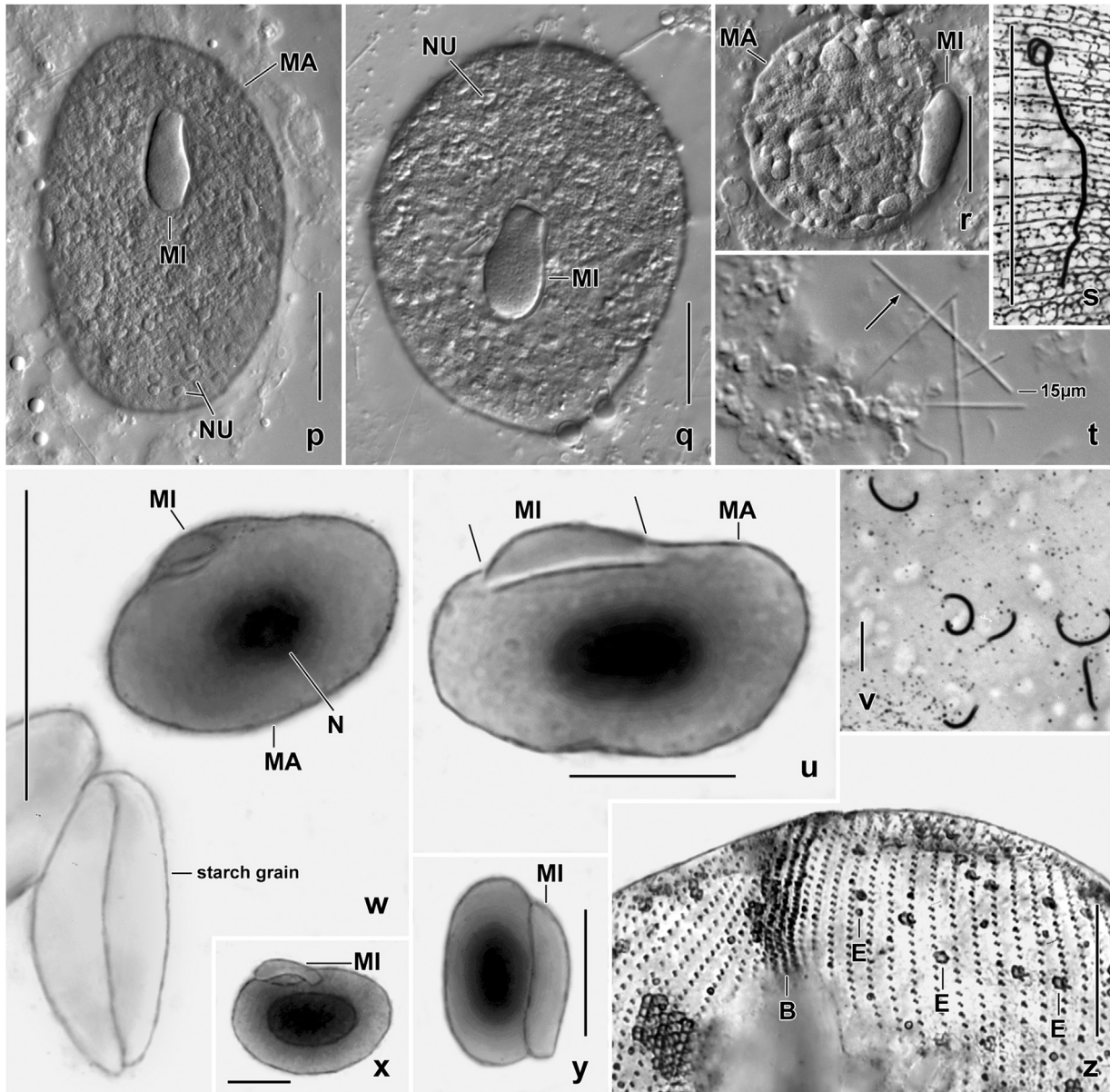


Fig. 2. (Continued)

Cytoplasm, movement, life cycle: Cytoplasm colourless; usually turbid from food vacuoles, lipid droplets, and granules; spotted when feeding mainly on various algae or dark at a magnification of $\leq \times 100$ when studded with food vacuoles containing mainly heterotrophic organisms (Figs. 1a, d, 2a, b, 3o, q); Brazilian specimens fed on starch grains (Figs. 1a, 2a, b), heterotrophic flagellates (*Chilomonas* sp.), several ciliates, and rotifers; food remnants defecated in posterior pole area (Foissner 1972).

Movement inconspicuous, i.e., moderately rapid rotating about main body axis; rather flexible and thus also wallowing in mud; when prey is large, several individuals may form a blow out. For a more detailed review on food, see Foissner et al. (1994).

Holophryids have a special life cycle, i.e., reproduce in division cysts containing two or four offspring (Figs. 2n, o, 5a); just excysted specimens are theronts which slowly become trophonts when feeding. As yet, detailed data are not available for *H. teres* because the recent description by Benčat'ová et al. (2019) is based on a misidentified species with a size of only $90\text{--}120 \times 50\text{--}60 \mu\text{m}$, as typical for, e.g., *H. discolor*.

Somatic ciliature (without brosse belonging to oral apparatus): Ordinary cilia in vivo $8\text{--}10 \mu\text{m}$ long, forming metachronal waves (Figs. 1a, 2c); $6\text{--}10$ perioral cilia circles, composed of very narrowly spaced dikinetids with about $5 \mu\text{m}$ long cilia, forming a tuft directed to oral opening (Figs. 1a, i, 2c, f, 3h, i, k); caudal cilia about $25 \mu\text{m}$ long,

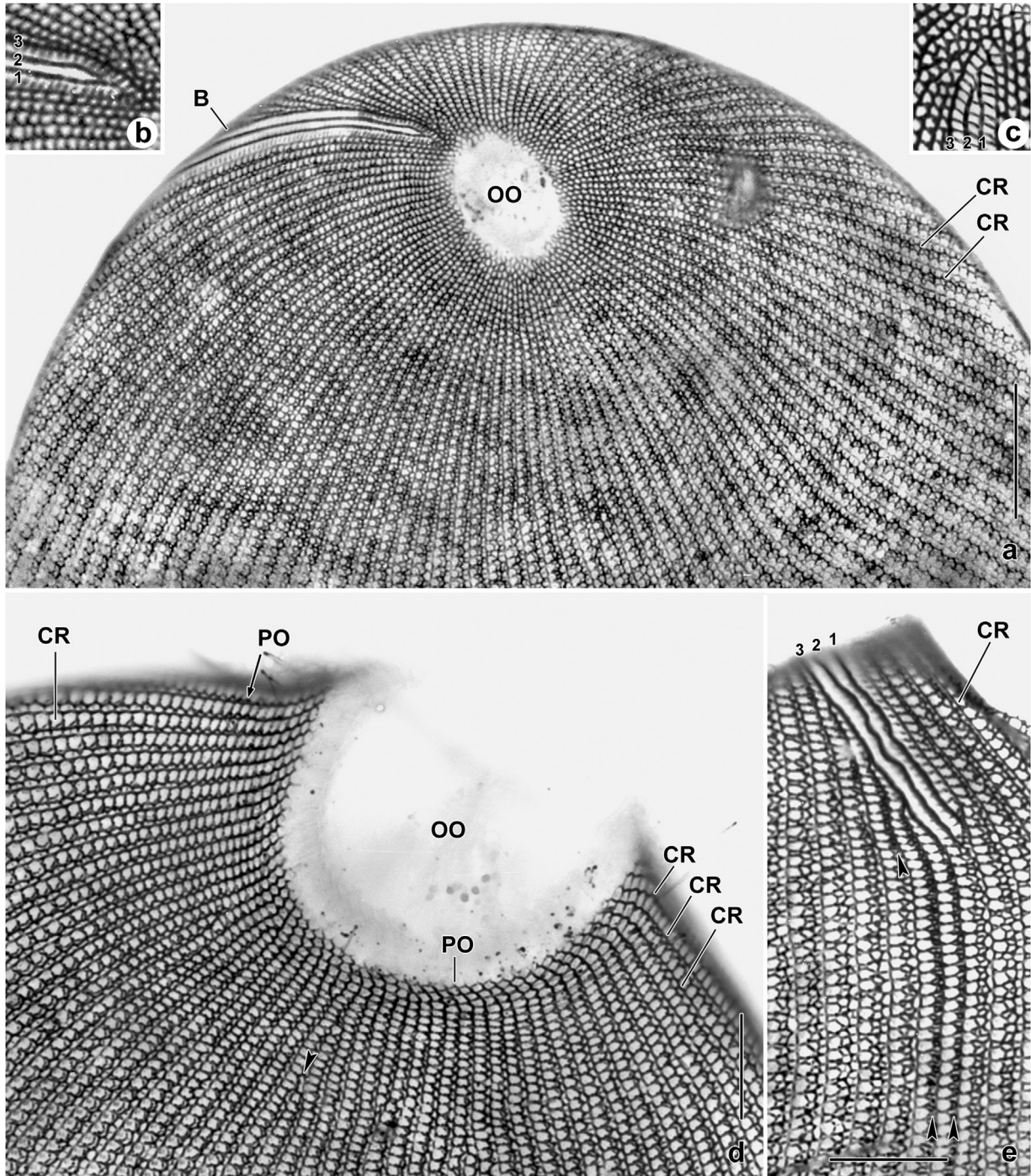


Fig. 3. a–e. *Holophrya teres*, cortex in silver carbonate preparations. **a–c:** Anterior body region, showing oral opening and anterior region of brosse which consists of three ciliated rows connected by transverse silverlines to the first somatic kinety right and left to the brosse producing minute rectangular meshes. Brosse row 2 is slightly shortened anteriorly and thus forms a pointed arch with rows 1 and 3. **d:** There are six to ten perioral, rectangular meshes without very small meshes left of the ordinary somatic ciliary rows (cp. Fig. 3e, j). **e:** Posterior half of brosse. At the right side, the ciliary (mesh) rows abut at sharp angles on brosse row 3 while the left side rows are parallel to brosse row 1. The three arrowheads mark three darkly impregnated post-brosse ciliary rows of which the short row right of the long rows is usually absent. B – brosse, CR – ciliary (mesh) rows, OO – oral opening, PO – perioral ciliature, 1, 2, 3 – brosse rows. Scale bars 25 μm (d, e) and 30 μm . **Fig. 3. f–j.** (on p. 12). *Holophrya teres*, brosse and circumoral kinety (h, i, arrowheads) in silver carbonate preparations (f, g, j) and in the scanning electron microscope (h, i). The circular oral opening is covered by a membrane, the so-called buccal seal (f, h, i). The oral opening is surrounded by the circumoral kinety which has minute, paired cilia (Figs. 2h, 3h, i). The brosse extends in anterior third of cell and consists of three ciliary rows slightly curved leftwards posteriorly (f, g, j). The kinetids are very narrowly spaced, their cilia are as thick as the ordinary somatic cilia and 1–3 μm long anteriorly while 6–8 μm posteriorly (h–j and Fig. 2f). At the right side of the brosse, 16–19 somatic kineties abut in sharp

difficult to recognize in vivo and in preparations due to the thick body (Fig. 1a, d).

On average 97 ordinarily spaced ($\sim 4.5 \mu\text{m}$ interkinetal distance) ciliary rows each with an average of about 122 cilia resulting in a total of about 12,000 cilia (Table 1); rows extend meridionally in flat, narrow furrows; ciliary distances increase slightly from anterior to posterior; each basal body has a parasomal sac left of posterior half (Figs. 1a, i, 2c, d, h, l, m, 3a, f).

MDL: The somatic ciliature of the Brazilian specimens matches Kahl (1927, 1930), Foissner (1983) and Hiller (1993a,b).

Oral apparatus: Consists of oral basket, circumoral kinety, perioral ciliature, and brosse.

Oral basket and oral opening: Slightly out of body centre, i.e., distance to brosse larger than to dorsal side (Figs. 1a, b, d, 2c, d); conical, on average $42 \mu\text{m}$ long and $21 \mu\text{m}$ wide at anterior end in Chatton-Lwoff silver nitrate preparations (Figs. 1a–c, 2h, l, 3a, f, l–n, 4a; Table 1); consists of an external basket s. str. and an internal basket hardly recognizable in vivo (Figs. 1h, 2h, 3l–o). External basket made of an average of 40 thick, paired nematodesmata attached to circumoral dikinetids; conspicuous because in vivo about $45 \times 3 \mu\text{m}$ in size, gradually spread posteriorly (Figs. 1a–d, g–i, 2h, 3l, p, q; Table 1); anterior end with a distinct, $3 \mu\text{m}$ long tooth associated with a dense base (Figs. 1g, j, k, 3p, q). Internal basket bowl-shaped, likely produced by transverse microtubule ribbons of perioral dikinetids, about $16 \mu\text{m}$ wide and $10 \mu\text{m}$ deep (Figs. 1h, 3n). Extended basket opening in vivo elliptic to circular, in well preserved cells closed by the buccal seal (Foissner and Al-Rasheid 2006), a very fragile membrane recognizable only in the scanning electron microscope

(Figs. 1c, 2h, l, 3h, i); in preparations usually almost closed, i.e., elliptic or slit-like, inner surface strongly folded (Figs. 1e, f, 2c, e, f, h, i, l, 3a, f).

Circumoral kinety, perioral ciliature, and brosse: Circumoral kinety associated with oral basket rods, difficult to recognize, composed of dikinetids with ciliary stumps (Figs. 1i, 2h, l, 3h, i).

Perioral ciliature made of 6–10 dikinetids at beginning of ciliary rows, form a dense girdle with about $5 \mu\text{m}$ long cilia directed to oral opening (Figs. 1a, d, i, 2e, f, h, i, l, 3k); in silver carbonate preparations marked by “simple”, quadrangular meshes, i.e., minute mesh rows absent (Fig. 3a, d).

Brosse on average $50 \mu\text{m}$ long in Chatton-Lwoff silver nitrate preparations, begins at or very close to circumoral kinety, composed of three rows of very narrowly spaced dikinetids having ciliated only anterior basal body; brosse cilia about $5 \mu\text{m}$ long, very flexible, as thick as ordinary somatic cilia; rows bordered by minute ridges, rows 1 and 3 anteriorly slightly longer than row 2 thus forming a pointed arch, posteriorly usually curved left, occasionally wavy possibly due to slight body contractions (Figs. 1a, 2f, h, j, l, z, 3a–c, f, g, i, j, 4b; Table 1). Brosse dextrotrop, i.e., an average of 19 ciliary rows about to row 3 in sharp angles; three, rarely two or four post-brosse ciliary rows anteriorly usually more narrowly spaced than ordinary somatic ciliary rows (Figs. 2h, j, l, o, 3f, g, j; Table 1). Silverline pattern modified to narrowly spaced transverse meshes between rows and first somatic kinety left of brosse, very narrowly spaced polygonal mesh rows absent (Fig. 3a, c, e–g, j).

MLD: Only Foissner (1983) and Hiller (1993a,b) provided detailed data on the oral apparatus of *H. teres*. Thus, I

angels to brosse row 3 (g, j). B – brosse, BS – buccal seal, CR – ciliary rows, OO – oral opening, PO – perioral ciliature, 1, 2, 3 – brosse rows. Scale bars $10 \mu\text{m}$ (i), $25 \mu\text{m}$ (h), $50 \mu\text{m}$ (g, j) and $100 \mu\text{m}$ (f).

Fig. 3. k–q. (on p. 13). *Holophrya teres* in the scanning electron microscope (k), in Chatton-Lwoff silver nitrate preparations (l–n), and in vivo (o–q). **k:** Polar view, showing the oral opening and the about $10 \mu\text{m}$ long somatic cilia as well as the only $5 \mu\text{m}$ long perioral cilia directed to the oral opening. **l, m:** The cone-shaped oral basket is about $45 \mu\text{m}$ long and composed of an average of 40 rods. **n:** The external oral basket is made of microtubular nematodesmata while the internal basket is very likely made of the transverse microtubule ribbons of the perioral kinetids (cp. Fig. 2h). **o:** A pressed specimen, showing a $16 \mu\text{m}$ long toxicyst and a $4 \mu\text{m}$ long mucocyst (arrowhead). **p, q:** Pressed specimens, showing details of the oral basket rods which are composed of an about $3 \mu\text{m}$ long tooth associated with the left branch of the rod; a rather dense tooth base (arrowheads); and the rod s. str. divided into two cuneate branches separated by a gap (arrows, cp. Fig. 1g). BD – oral basket rods, EB – external oral basket, FV – food vacuoles, IB – internal oral basket, L – lipid droplets, M – mucocyst, MA – macronucleus, OB – oral basket, OO – oral opening, PO – perioral ciliature, SK – somatic kineties, T – toxicysts, TH – teeth. Scale bars $3 \mu\text{m}$ (p), $10 \mu\text{m}$ (q), $20 \mu\text{m}$ (k, o), $30 \mu\text{m}$ (m, n) and $40 \mu\text{m}$ (l).

Fig. 3. r–x. (on p. 14). *Holophrya teres*, silverline patterns in silver carbonate (r–t) and in Chatton-Lwoff silver nitrate (u–x) impregnated specimens. **r–t:** Silver carbonate produces only one pattern looking slightly different, depending on cortex stretching (cp. r, t). The larger more or less quadrangular meshes contain the greyish impregnated basal bodies of the cilia (s, arrows in t). Left of the basal body meshes are usually two rows of minute, polygonal meshes. **u–x:** Silver nitrate produces two patterns (cp. u, v with w, x) highly different from the silver carbonate pattern (r–t). The first pattern consists of very small meshes: the rightmost mesh row consists of more or less circular meshes containing the greyish impregnated basal bodies of the cilia (u, arrows). Left of the basal body meshes are three, rarely four rows with very minute, polygonal meshes. The second pattern is very different from the first (w, x) and from the silver carbonate pattern (cp. r–t with w, x). The basal bodies of the cilia are deeply impregnated and thus produce distinct kineties (w, x): between each two kineties, there are two mesh rows separated from each other by a zigzagging midline (arrows). The dry silver nitrate method produces a seemingly different pattern, which, however, is caused by strong cortex distortions due to the air-drying of the cell (Fig. 4d). BB – basal bodies, E – hole left by an exploded extrusome, SK – somatic kineties (ciliary rows). Scale bars $5 \mu\text{m}$ (u) and $10 \mu\text{m}$ (r–t, v–x).

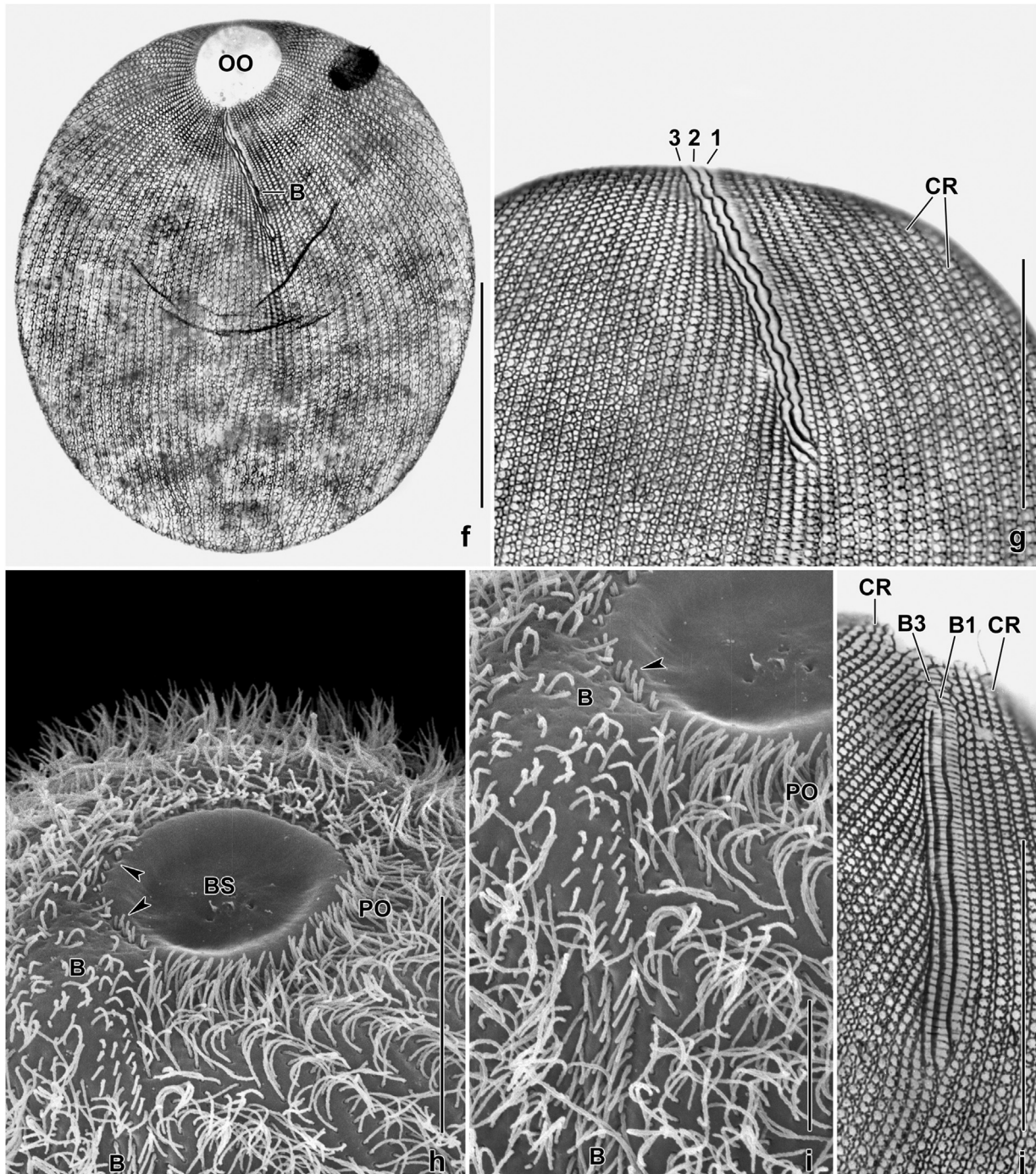


Fig. 3. (Continued)

expected to discover rather many new or misinterpreted structures: (1) the cytostomial funnel of *Holophrya* is not slit-like in cross-section, as stated by Hiller and Bardele (1988) in *H. aklitophon* and Hiller (1993b) in *H. teres* but broadly elliptic or circular, as recognizable in Fig. 4B, 5B and 7A of Hiller and Bardele (1988) and in my Figs. 1c, 2l, 3a, f, h; (2) there are an external and an internal oral basket, the latter possibly described by Puytorac and Savoie (1968) as “cytoplasme buccal”; (3) the same applies to the buccal

seal first clearly shown in several hypotrichs by Foissner and Al-Rasheid (2006); (4) I agree with Hiller (1993b) that the circumoral dikinetids are ciliated but the cilia are minute stumps (Fig. 3h, i); (5) according to Kahl (1927), the oral basket rods are only 15 μm long, resembling Fig. 4a. This is unlikely, i.e., the posterior portion can be seen only in pressed specimens or in silver preparations (Fig. 3l, m; Table 1); (6) all, even Hiller (1993b) missed the tooth of the oral basket rods but Fig. 12 in Hiller (1993b) shows three teeth each with a

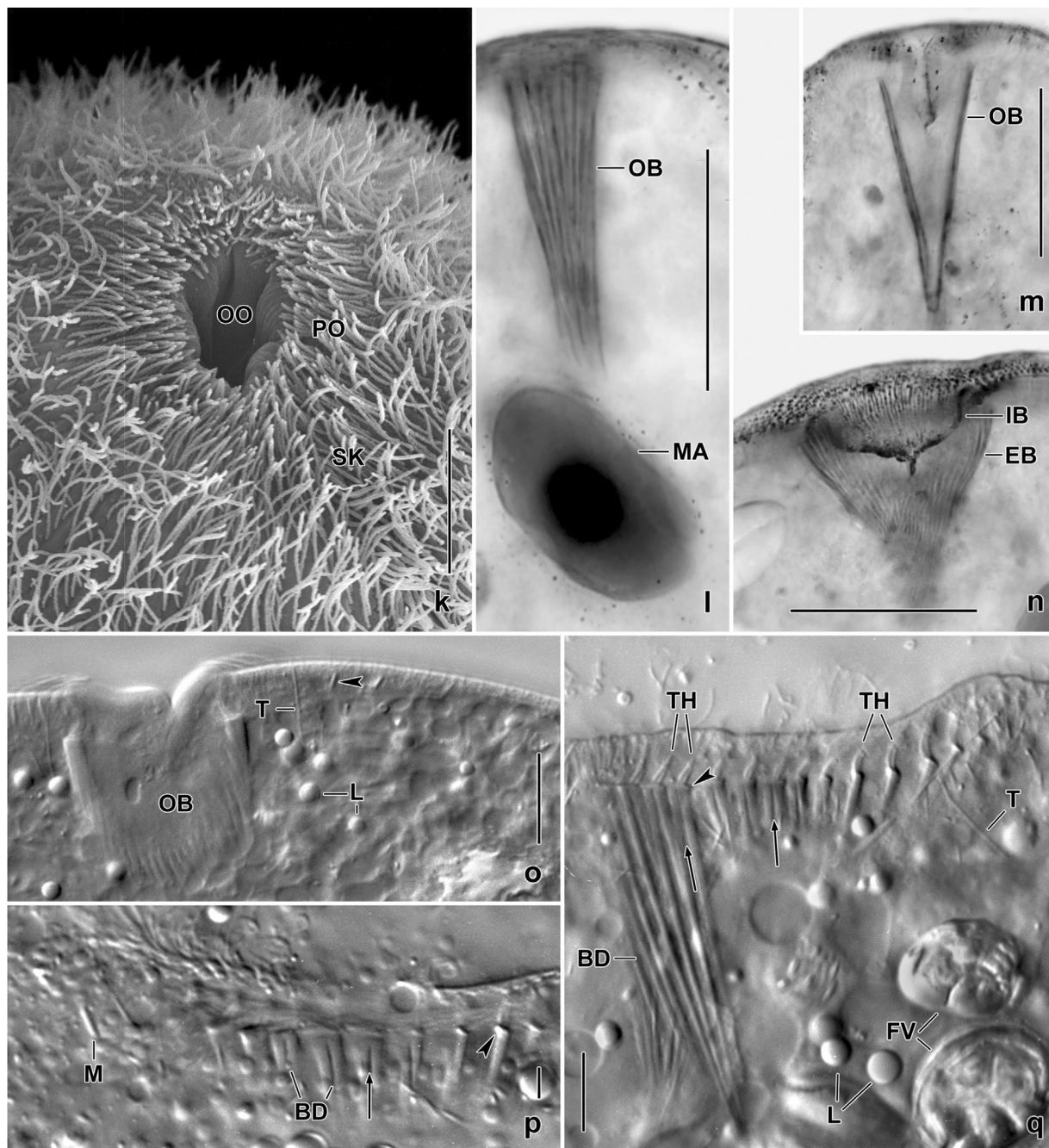


Fig. 3. (Continued)

“dense cap” very likely representing a tooth; (7) the brosse is considered to be ancient adoral ciliature (Hiller 1993b). Its anterior and posterior end is shown clearly for the first time. I agree with Hiller (1993b) that the brosse dikinetids have ciliated only the anterior basal body while the number of somatic kineties abutting to the right side of the brosse is rather variable, viz., about 14 (Hiller 1993a), about 16 in the Austrian population studied by Foissner (1983, reassessed), or about 19 on average (Brazil specimens, Table 1). Further, the rows are usually curved left at posterior end while Foissner (1983) shows a meridional end.

Ecology and distribution: For these, I refer to the review of Foissner et al. (1994), who collected a lot of records but detailed ecological investigations are not available. Briefly, *H. teres* occurs over the year and becomes occasionally numerous in the mud and the pelagial of stagnant and running waters. Benthic cells wallow in bacterial masses and mud feeding on a great variety of heterotrophic and autotrophic protists and small metazoans (Fig. 1a); sometimes become numerous in infusions and in activated sludge; holoeuryhalin, terrestrial records are very likely misidentifications; indicates moderately to strong pollution in running waters; very likely

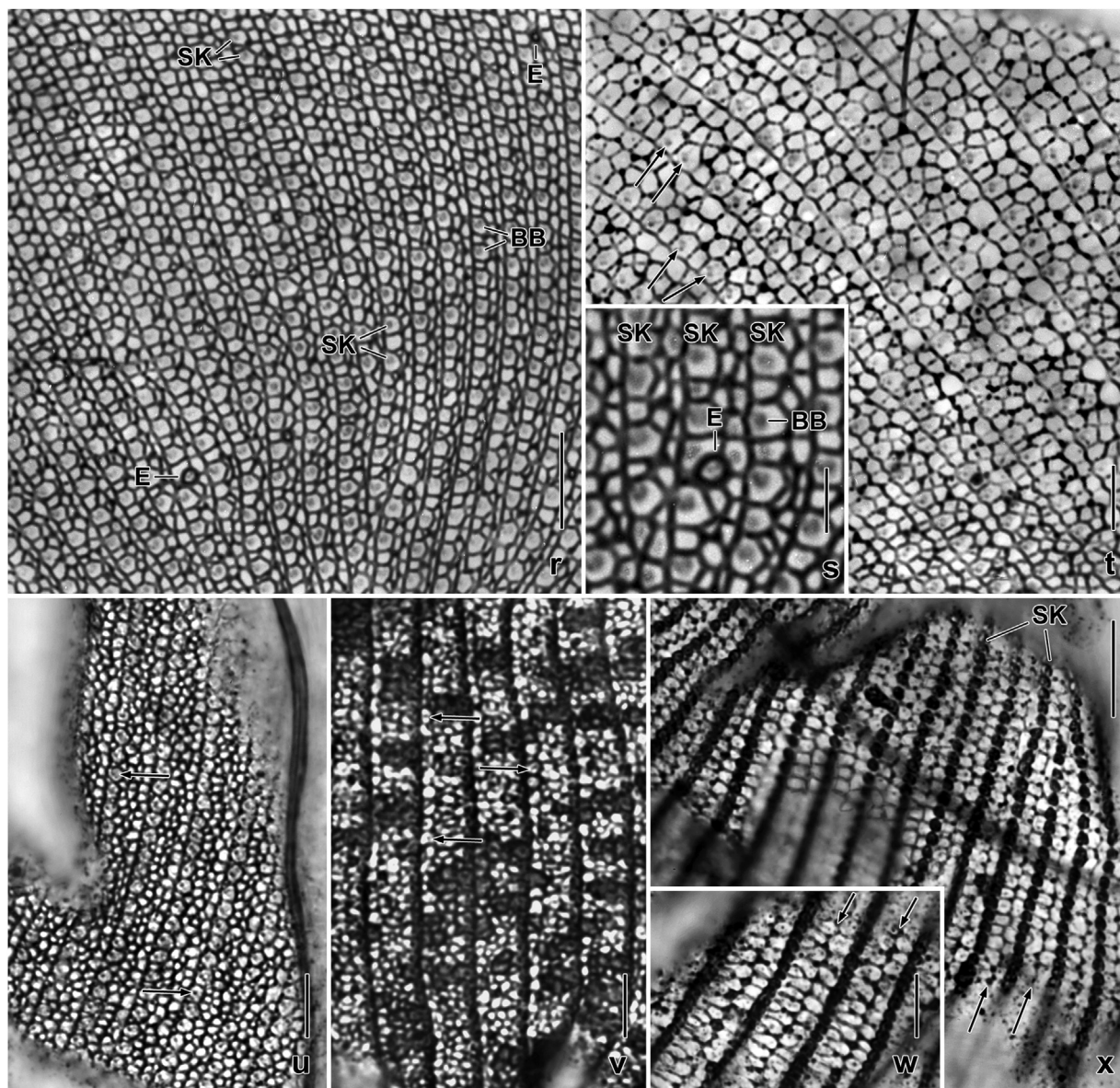


Fig. 3. (Continued)

cosmopolitan though records from Australia, the Arctic and Antarctica are absent.

Identification of Brazilian *Holophrya teres*

The detailed comparison of two German, one Austrian, and one Brazilian population of *Holophrya teres* revealed two distinct differences. The first is massive and concerns the shape and size of the outstanding micronucleus here documented with micrographs for the first time: pyriform and $10\text{--}13 \times 4\text{--}5 \mu\text{m}$ in size (CV's 10% and 16%, Brazil; Table 1); pyriform (Kahl 1927, 1930, Germany); spherical to lenticular, $8.5 \times 4.7 \mu\text{m}$ on average (CV's 18% and 22%, Hiller 1993a, Germany); small and globular (Foissner 1983, Austria, but see Fig. 4a). I am rather sure that the small and globular micronucleus in Foissner (1983) is a misobservation

because I was a beginner in 1978. On the other hand, Hiller's data indicate the possibility of a small, globular micronucleus. If so, such populations should be ranked as subspecies or species.

The second feature is the number of ciliary rows abutting to the right margin of the brosse: 20 on average, CV 14%, Brazil; 14 on average, CV 11%, Hiller (1993a), Germany; 16 on average, CV 14%, Foissner (1983), Austria. These are remarkable differences with a moderate variability, possibly justifying subspecies rank for the Brazilian population.

Other structures, such as the internal oral basket, the teeth on the anterior end of the oral basket rods, and the buccal seal are difficult to recognize and were thus never used in the taxonomy of *Holophrya*. I suppose that these features are of diagnostic value mainly for generic and/or family classification.

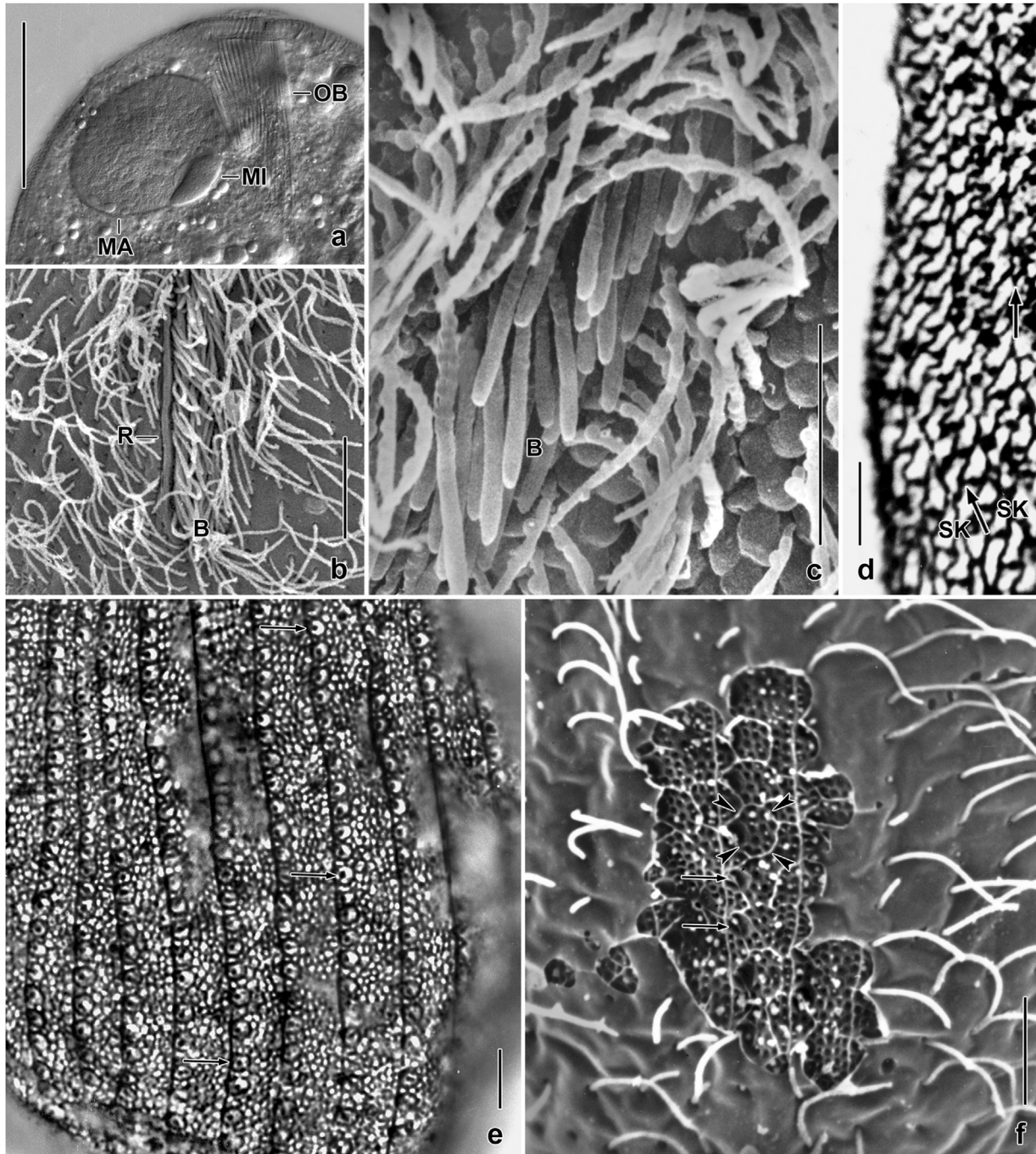


Fig. 4. a–f. *Holophrya teres* from Brazil (b), Austria (a, d) and Germany (c). *Holophrya seyrli* (e) and *H. discolor* (f) from life (a), in a Klein-Foissner (d) and in a Chatton-Lwoff (e) silver nitrate preparation, and in the SEM (b, c, f). **a:** This specimen is from a forest pond in Salzburg. In side view, it has a cuneate micronucleus, as *H. teres* from Germany (Fig. 1d) and Brazil (Fig. 2u). **b, c:** Comparison of brosse cilia which are flexible and as thick as the ordinary cilia in Brazil while they are stiff and distinctly thicker than the ordinary cilia in *Holophrya* sp. from the Simmelried moorland (Kreutz and Foissner 2006). **d:** *H. teres* from the Austrian Alps (Foissner 1983). The cortex is strongly distorted so that the real silverline pattern (Fig. 3w, x) is difficult to recognize. The arrows mark the zigzagging silverlines between two ciliary rows each. **e:** *H. seyrli* from Foissner (1997). This species has much more very small, polygonal meshes left of the basal body meshes (arrows) than *H. teres* (Fig. 3u, v). Arrows mark basal body rows. **f:** Two mesh-types are recognizable in *H. discolor* from the Ager River in Upper Austria. The large upper meshes (arrowheads) resemble the platyophryid pattern in *H. teres* (Fig. 3w, x) while the minute polygonal meshes are highly similar to those found in *H. teres* (cp. 3u, v). The arrows mark circular meshes around the basal bodies of the ciliary rows. B – brosse, MA – macronucleus, MI – micronucleus, OB – oral basket, R – brosse ridge, SK – somatic kineties. Scale bars 5 μm (c, f), 10 μm (b, d, e) and 30 μm (a).

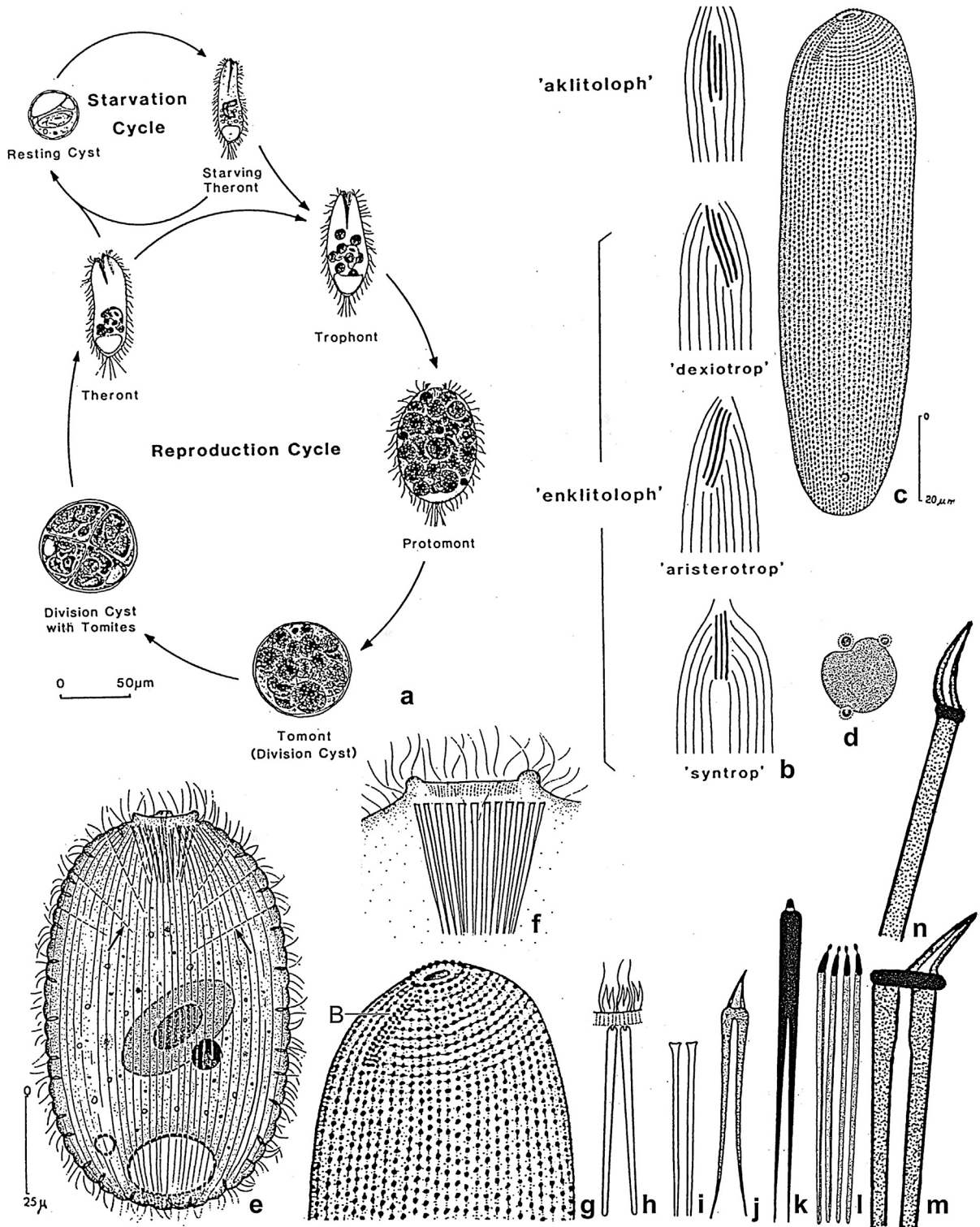


Fig. 5. a–n: Various. a, b: Life cycle and brosse types (from Hiller and Bardele 1988). c, d, g: *Holophrya agamalievi* nov. spec.; B – brosse (from Agamaliiev 1978). e, f: *Holophrya longiarmata* nov. spec.; arrows mark long toxicysts (from Dragesco 1966a). h–n: Anterior region of holophryid oral basket rods. h: *H. penardi* (from Dragesco 1960). i: *H. magna* (from Dragesco 1966a). j: *H. ovum* (from Foissner et al. 1994). k: *H. seyrli* (from Foissner 1997). l: *H. africana* (from Dragesco 1970). m, n: *H. teres*, broad and narrow side view (this study).

Main features for holophryid species recognition and description

Basically, all features described in the Brazilian population are important but some are very important, i.e., without these characters a reliable species recognition is impossible:

- 1) Shape and size of micronucleus; possibly, there are species with a \pm globular and less than 10 μm -sized micronucleus.
- 2) Number of macronuclear nodules; usually one but some have two or more.
- 3) Number of contractile vacuoles; usually one in rear end but some have two or many.
- 4) Shape and size of toxicysts and mucocysts.
- 5) Number of ciliary rows.
- 6) Number and length of external oral basket rods including the highly diverse anterior end (Fig. 5g–n).
- 7) Brosse to distinguish the holophryid genera (Fig. 5b).
- 8) Habitat. Very likely, freshwater and brackish or marine habitats contain different species.
- 9) The silverline pattern needs further investigations before it can be used for generic and species definitions. Unfortunately, no silverline data are available for the three new genera established below.

Improved diagnosis of *Holophrya teres* (averages are given for a mixture of trophonts and theronts)

Size in vivo about $200 \times 130 \mu\text{m}$; cylindroid. Macronucleus about $30 \times 20 \mu\text{m}$ in vivo, contains a large, central mass. Micronucleus conspicuous because about $13 \times 5 \mu\text{m}$ and bright in vivo, pyriform in broad-side view, cuneate in narrow-side view. Single contractile vacuole in posterior body end. Toxicysts very thin, about $15 \mu\text{m}$ long in vivo, less than $0.5 \mu\text{m}$ thick; mucocysts about $4.0 \times 0.5 \mu\text{m}$ in vivo. About 100 meridional ciliary rows each with about 120 cilia. Caudal cilia $25 \mu\text{m}$ long. External oral basket conical, in vivo $45 \times 20 \mu\text{m}$ in size, consists of 40 thick rods each with a triangular, $3 \mu\text{m}$ long tooth. Perioral ciliature made of about eight dikinetids at beginning of ciliary rows, cilia about $5 \mu\text{m}$ long and oriented to oral opening. Brosse dextiotrop, composed of three rows of dikinetids with about $5 \mu\text{m}$ long, flexible cilia as thick as ordinary somatic cilia; about 16 somatic ciliary rows abut to brush row 3. Freshwater; possibly cosmopolitan.

Remarks: The “improved diagnosis” is based on the main characteristics given in the relevant literature and in the previous chapter. Possibly, the silver carbonate silverline pattern should be added because the number of minute mesh rows left of the ciliary rows is distinctly different in, e.g., *H. teres* and *H. seyrli* (2–3 vs. 5–6; cp. Fig. 3r, u with Fig. 4e).

Sizes and counts are given for a mixture of theronts and trophonts as usually occurring in nature and in cultures. This is supported by the morphometric analysis which shows ordinary (<15%) coefficients of variation; the lower boundaries are very likely theronts, the upper are trophonts (Table 1).

I do not provide extremes (minimum, maximum) in any “diagnosis” because more or less distinct crossings may occur with the extremes of other populations, increasing the risk of making unjustified synonymies. The description and the morphometric table are the right place for extremes.

Similar genera

Since the last review by Kahl (1930) many new prostomatid and haptorid genera have been described (for reviews, see Jankowski 2007 and Lynn 2008). For the purpose of the present study, there are two genera which look sometimes rather similar to *Holophrya*, viz., *Enchelys* and *Enchelyodon* (for representative examples, see Foissner 1984, 2016 and Foissner et al. 2002). *Enchelys* differs from *Holophrya* mainly by the oral opening occupying the entire anterior body end and the absence of a circumoral kinety because the oral basket is made by fine nematodesmata originating from oralized somatic monokinetids in the anterior region of the somatic ciliary rows. *Enchelyodon* differs from *Holophrya* by a usually distinct oral bulge frequently button-like projecting from body proper. The oral basket is made by rather thin nematodesmata bundles originating from the dikinetids of the circumoral kinety. Accordingly, a preliminary definition of *Holophrya* might read as follows: oral opening flat and distinctly smaller than anterior body end. Oral basket made by comparatively thick nematodesmata bundles produced by the dikinetids of a distinct circumoral kinety (see final diagnosis in chapter “Family Holophryidae” below).

There is clear molecular evidence that *Holophrya* belongs to the Prostomatea while *Enchelys* and *Enchelyodon* belong to the Haptoria (Lynn 2008; Rajter and Vd’ačný 2018; Zhang et al. 2014).

Taxonomic and nomenclatural revision of *Holophrya*, including three new genera and two new species

Family Holophryidae Perty, 1852

Many holophryids were classified in *Prorodon*, following Kahl (1930) and others, who overlooked the typification of *Holophrya* and *Prorodon* by Fromentel (1875), lately recognized by Foissner et al. (1994); however, they combined only those species contained in the “Ciliate Atlas” (Foissner et al. 1994). Jankowski (2007) added some species, most not belonging to *Holophrya*. Other species have been referred to new genera, e.g., *Prorodon mimeticus* Kahl, 1930 (now in *Pleurofragma* Jankowski, 1976) and *Prorodon raabei* Czapiak, 1965 (now in *Paraprorodon* Foissner, 1983). The family home of these and many other prostomatid genera and species is not known.

Here, I recognize or combine only those species which were originally classified in *Holophrya* and have at least one of the two main characteristics of *Holophrya*, viz., a brosse

and/or thick, inflexible oral basket rods. Accordingly, this is not a total revision of *Holophrya* as made by Kahl (1930).

Diagnosis: Prostomatida Schewiakoff, 1896 with flat oral opening distinctly smaller than anterior body end. Oral basket rods comparatively thick, inflexible, and often paired. Brosse usually three-rowed, in between somatic ciliary rows in anterior half of body. Silverline pattern complex.

Type genus: *Holophrya* (subsequent typification by Fromental 1875). See also Foissner et al. (1994).

Remarks: Only few of many genera possibly belonging to the Holophryidae (see reviews by Corliss 1979, Jankowski 2007, and Lynn 2008) are included in the diagnosis, viz., *Holophrya*, *Hillerophrya*, *Vdacnyophrya*, and *Bardeleophrya*. Hiller and Bardele (1988, p. 234) classified the brosse types in *Holophrya* (formerly *Prorodon*) and supposed that they could be used to establish new genera. I agree and do it because this action is supported by recent morphological and molecular studies, showing that special structures, such as the brosse in prostomatids or the brush in haptorids, are reliable generic features (Foissner 2016; Kwon et al. 2014; Rajter and Vdačný 2016; Rajter and Vd'ačný 2018; Vdačný and Foissner 2012, Vd'ačný and Foissner 2013; Zhang et al. 2014).

Holophrya Ehrenberg, 1831

Diagnosis: Holophryidae with dextrotrop brosse, i.e., with some or many ciliary rows abutting to right side of brosse (Fig. 5b).

Type species: *Holophrya ovum* Ehrenberg, 1831 (subsequent designation by Fromental 1875; authoritative redescription by Foissner et al. 1994).

Etymology: *Holophrya* is a composite of the Greek adjective *holo* (complete) and the Greek noun *ophrys* (eyebrow ~cilia ~ciliate), meaning completely ciliated. Feminine gender.

Species assignable: See the following compilation.

Holophrya abietum (Penard, 1922) nov. comb.

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| 1922 | <i>Prorodon abietum</i> sp. n. – Penard, Études infusoires, p. 40 (oral basket rods holophryid, brosse dextrotrop; see Fig. 41/2). |
| 1927 | <i>Prorodon abietum</i> Penard – Kahl, Arch. Protistenk., 60: 23 (confirms Penard's description). |
| 1930 | <i>Prorodon abietum</i> Penard, 1922 – Kahl, Tierwelt Dtl., 18: 81 (revision). |
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Holophrya africana Dragesco, 1965 (Fig. 5l)

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|------|---|
| 1965 | <i>Holophrya africana</i> n. sp. – Dragesco, Cah. Biol. mar., 6: 358 (oral basket rods holophryid, brosse syntrop-like according to Alekperov 2005, p. 28). |
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Holophrya brachyodon (Kahl, 1927) nov. comb

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- | | |
|------|--|
| 1927 | <i>Prorodon brachyodon</i> spec. n. – Kahl, Arch. Protistenk., 60: 85. |
| 1966 | <i>Prorodon brachyodon</i> Kahl (?) – Dragesco, Protistologica, 2: 64 (oral basket rods clearly holophryid, brosse not shown). |
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Holophrya discolor Ehrenberg, 1834

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| 1834 | <i>Holophrya discolor</i> n. sp. – Ehrenberg, Abh. dt. Akad. Wiss. Berl., Year 1833: 251. |
| 1838 | <i>Holophrya discolor</i> Ehrenberg, 1833 – Ehrenberg, Infusionsthierchen, p. 314 (revision). |
| 1930 | <i>Prorodon (Holophrya) discolor</i> Ehrb.-Blochm.-Schew. and <i>Prorodon (Holophrya) ovum</i> Ehrb.-Kahl – Kahl, Tierwelt Dtl., 18: 76 (revision). |
| 1974 | <i>Prorodon discolor</i> Ehr.-Blochm.-Schew. – Jordan, Acta Protozool., 13: 5 (states 60–70 oral basket rods because she did not recognize that the rods are paired). |
| 1983 | <i>Prorodon ovum</i> (Ehrenberg, 1831) – Foissner, Annln naturh. Mus. Wien, 84/B: 54 (misidentification; redescription from life and after silver impregnation. Brosse dextrotrop). |
| 1986 | <i>Prorodon discolor</i> Ehr., Bloch, Schew – Dragesco and Dragesco-Kernéis, Faune tropicale, 26: 135 (brief taxonomic and ecological review). |
| 1992 | <i>Prorodon ovum</i> (Ehrenberg, 1831) Blochmann, 1895 – Augustin and Foissner, Arch. Protistenk., 141: 244 (misidentification, it is <i>H. discolor</i> ; detailed redescription from life and after silver impregnation). |
| 1994 | <i>Holophrya discolor</i> Ehrenberg, 1833 – Foissner, Berger and Kohmann, “Ciliate Atlas III”: 328 (authoritative redescription, brosse dextrotrop, oral basket rods holophryid. Differs from <i>H. ovum</i> mainly by the absence of zoochlorellae). |
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Holophrya grisea (Claparède and Lachmann, 1859) nov. comb.

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| 1859 | <i>Prorodon griseus</i> – Claparède and Lachmann, Mem. Inst. natn. génev., 6: 319. |
| 1922 | <i>Prorodon griseus</i> Cl. et L. (1859) – Penard, Études infusoires, p. 36 (oral basket rods holophryid). |
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Holophrya laurenti (Dragesco, 1966) nov. comb.

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| 1966 | <i>Prorodon laurenti</i> n. sp. – Dragesco, Protistologica, 2: 62 (oral basket rods clearly holophryid, brosse not shown). |
| 2005 | <i>Prorodon laurenti</i> Dragesco, 1966 – Alekperov, Atlas of free-living infusoria, p. 28 (redescription of silver nitrate-impregnated specimens). |
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***Holophrya lemani* (Dragesco, 1960) nov. comb.**

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- 1960 *Prorodon teres* Ehrenberg var. *lemanii* n. var. – Dragesco, Trav. Stn. biol. Roscoff (N.S.), 12: 77 (of subspecific rank because published before 1961; see [ICZN 1999](#), Article 45.6.4).
- 1965 *Prorodon lemani* n. sp. – Dragesco, Cah. Biol. mar., 6: 360 (1960 variety raised to species rank due to misunderstanding the ICZN).
- 1966 *Holophrya lemani* n. sp. – Dragesco, Protistologica, 2: 60 (oral basket rods holophryid, brosse not shown). A new name is required due to the transfer of *Prorodon lemani* to *Holophrya* (secondary homonymy, see above): *Holophrya lata* nom. nov. (*lata* = the thick *Holophrya*).
- 1966 *Prorodon lemani* n. sp. – Dragesco, Protistologica, 2: 63 (creation as new species again. Indeed, it is very different from those mentioned above). Thus, a new species is necessary: *Holophrya longiarmata* described below.
- 1986 *Prorodon lemani* [Dragesco, 1965](#) – Dragesco and Dragesco-Kernéis, Faune tropicale, 26: 133 (oral basket rods holophryid, brosse not shown).
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***Holophrya longiarmata* nov. spec. (Fig. 5e, f)**

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- 1966 *Prorodon lemani* n. sp. – Dragesco, Protistologica, 2: 63. See above.
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Diagnosis (according to data from [Dragesco 1966a](#)): Size in vivo about 110 × 65 µm; ellipsoid to indistinctly pyriform. Macronucleus ellipsoid, with large central nucleolus (?). Micronucleus attached to macronucleus, conspicuous because 8 µm across. Single contractile vacuole in posterior body end. Fine, 20–30 µm long toxicysts in anterior third of body. Cortex crenate due to small, thick mucocysts. About 100 bipolar ciliary rows; brosse not known. Oral apparatus as typical for genus, i.e., about 30 holophryid oral basket rods.

Type locality: Fine sand at coast of Lake Geneva, France, biological station Thonon-les-Bains.

Type material: Not mentioned by [Dragesco \(1966a\)](#). Thus, I fix the specimen shown here in [Fig. 5e](#) as holotype of *Holophrya longiarmata* nov. spec., which is in accordance with article 73.1.4 of the [ICZN \(1999\)](#).

Etymology: Composite of the Latin adjectives *longus* (long) and *armatus* (armed), referring to the long toxicysts in anterior body third.

***Holophrya magna* (Dragesco, 1960) nov. comb. (Fig. 5i)**

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- 1960 *Prorodon nucleolatus* Penard var. *magnus* n. var. – Dragesco, Trav. Stn. biol. Roscoff (N.S.), 12: 78 (of subspecific rank because published before 1961; see [ICZN 1999](#), Article 45.6.4).
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- 1966 *Prorodon magnus* Dragesco – Dragesco, Protistologica, 2: 61. Variety from 1960 raised to species rank due to re-investigation from type locality (oral basket rods holophryid, brosse not shown).
- 1998 *Prorodon magnus* Dragesco, 1966 – [Franco](#), Esteban and Téllez, Bol. R. Soc. Esp. Hist. Nat. (Sec. Biol.), 94: 16 (redescription, brosse dextiotrop).
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***Holophrya meridionalis* (Dragesco, 1966) nov. comb.**

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- 1966 *Prorodon meridionalis* n. sp. – Dragesco, Arch. Protistenk., 109: 159 (“armature buccale, constituée par de longues némademes réfringentes”; brosse not shown).
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***Holophrya nucleata* (Švec, 1897) nov. comb.**

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- 1897 *Prorodon nucleatus* n. sp. – Švec, Bull. int. Acad. tcheque Sci., 4: 37.
- 1922 *Prorodon nucleatus* Švec 1897 – Penard, Études infusoires, p. 37 (redescription showing holophryid basket rods).
- 1930 *Prorodon nucleolatus* Penard, 1930 (*nucleatus* Pen., 1922 nec Švec) – Kahl, Tierwelt Dtl., 18: 74 (Kahl considered the prorodons of Švec (1897) and [Penard \(1922\)](#) as different species and informed Penard that he named it *nucleolatus*. However, Penard did not follow him; see next entry).
- 1938 *Prorodon nucleatus* – Penard, Les infiniment petits, p. 109.
- 1966 *Prorodon nucleolatus* Penard, 1930 – [Dragesco](#), Biol. Gabon., 2: 92 (authoritative redescription; brosse dextiotrop).
- 1986 *Prorodon nucleolatus* [Penard, 1938](#) – Dragesco and Dragesco-Kernéis, Faune tropicale, 26: 130 (brief repetition of the 1966 description; wrong date, see above).
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***Holophrya ovum* Ehrenberg, 1831 (Fig. 5j)**

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- 1831 *Holophrya ovum* E.! – Ehrenberg, Abh. dt. Akad. Wiss. Berl., year 1831: 102 (without figure).
- 1838 *Holophrya ovum* [Ehrenberg, 1831](#) – Ehrenberg, Infusionsthierchen, p. 314 (type of genus; revision).
- 1840 *Prorodon viridis* – [Ehrenberg](#), Mber. Preuss. Akad. Wiss. Berlin, year 1840: 201 (this is a forgotten name best considered as a nomen oblitum because it has not been used later and the description is meagre not accompanied by a figure. When describing *Prorodon viridis* as a new species, [Kahl \(1927\)](#) did not refer to [Ehrenberg](#)).
- 1927 *Prorodon viridis* spec. n. – Kahl, Arch. Protistenk., 60: 79 (synonym).
- 1930 *Prorodon viridis* Ehrb.-[Kahl, 1927](#) – Kahl, Tierwelt Dtl., 18: 74 (revision).
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- 1994 *Holophrya ovum* Ehrenberg, 1831 – Foissner, Berger and Kohmann, “Ciliate Atlas III”: 322 (very detailed redescription; brosse dextiotrop).

***Holophrya palustris* (Puytorac and Savoie, 1968) nov. comb.**

- 1968 *Prorodon palustris* nov. sp. – Puytorac and Savoie, Protistologica, 4: 53 (oral basket rods holophryid, brosse dextiotrop).

***Holophrya parafricana* (Dragesco and Dragesco-Kernéis, 1986) nov. comb.**

- 1986 *Prorodon parafricanus* n. sp. – Dragesco and Dragesco-Kernéis, Faune tropicale, 26: 136 (brosse dextiotrop).

***Holophrya penardi* (Dragesco, 1954) nov. comb. (Fig. 5h)**

- 1954 *Prorodon penardi* n. sp. – Dragesco, Bull. Soc. zool. Fr., 79: 63.
 1960 *Prorodon penardi* Dragesco – Dragesco, Trav. Stn biol. Roscoff (N.S.), 12: 67 (oral basket rods holophryid; brosse not shown).
 1970 *Prorodon penardi* Dragesco, 1954 – Kattar, Zool. Biol. Mar., 27: 148 (description of a Brazilian population).

***Holophrya platyodon* (Blochmann, 1895) nov. comb.**

- 1895 *Prorodon platyodon* Blochm. – Blochmann, Mikroskopische Thierwelt, p. 90 (without figures).
 1927 *Prorodon platyodon* Blochmann – Kahl, Arch. Protistenk., 60: 83 (with two figures, one showing a dextiotrop brosse).

***Holophrya portaransasii* Alekperov, Buskey and Snegovaya, 2007**

- 2004 *Holophrya portaransasii* sp. n. – Alekperov et al., Protistology, 5 (2/3): 107. A small (~50 µm) marine species with prominent oral basket rods while a brosse was not recognizable in protargol preparations; this and the enormous oral basket are indicative for a new genus.

***Holophrya robusta* (Penard, 1922) nov. comb.**

- 1922 *Prorodon robustus* sp. n. – Penard, Études infusoires, p. 39 (very likely, the long “trichites” are oral basket rods; redescription required).

***Holophrya salinarum* Foissner et al., 2002**

- 2002 *Holophrya salinarum* nov. spec. – Foissner, Agatha and Berger, Denisia, 5: 537 (brosse shown).

***Holophrya seyrli* Foissner, 1997 (Fig. 5k)**

- 1997 *Holophrya seyrli* nov. spec. – Foissner, Limnologica (Berlin), 27: 213 (brosse dextiotrop, holophryid oral basket rods clearly described).

***Holophrya spirogyrophaga* (Leipe, 1989) Foissner et al., 2002**

- 1989 *Prorodon spirogyrophagus* nov. spec. – Leipe, Eur. J. Protistol., 24: 393.
 2002 *Holophrya spirogyrophaga* (Leipe 1989) nov. comb. – Foissner, Agatha and Berger, Denisia, 5: 538 (combination with *Holophrya*).

***Holophrya taeniata* (Blochmann, 1895) nov. comb.**

- 1895 *Prorodon taeniatus* Blochm. – Blochmann, Mikroskopische Thierwelt, p. 89 (oral basket rods very likely holophryid: “basket made of about 50 robust, flattened rods”; brosse not shown).
 1930 *Prorodon taeniatus* Blochmann, 1895 – Kahl, Tierwelt Dtl., 18: 80 (revision).

***Holophrya teres* (Ehrenberg, 1834) Foissner et al., 1994 (Fig. 5m, n)**

- 1834 *Prorodon teres* n. sp. – Ehrenberg, Abh. dt. Akad. Wiss. Berl., year 1833: 308.
 1838 *Prorodon teres* Ehrenberg, 1833 – Ehrenberg, Infusionsthierchen, p. 316 (first reviser).
 1930 *Prorodon teres* Ehrbg., 1838 – Kahl, Tierwelt Dtl., 18: 80 (revision).
 1962 *Prorodon teres* Ehrenberg – Liebmann, Handbuch der Frischwasser- und Abwasser-Biologie I, p. 355 (saprobiological characterization).
 1983 *Prorodon teres* Ehrenberg, 1838 – Foissner, Anln naturh. Mus. Wien, 84/B: 57 (redescription from life and silver preparations; brosse dextiotrop).
 1993 *Prorodon teres* Ehrenberg, 1838 – Hiller, J. Euk. Microbiol., 40: 467, 486 (detailed light- and electron-microscopic study; brosse dextiotrop, oral basket rods holophryid).
 1994 *Holophrya teres* (Ehrenberg, 1833) nov. comb. – Foissner, Berger and Kohmann, “Ciliate Atlas III”: 336 (monographic treatment of taxonomy and ecology).

***Holophrya trichocystus* (Dragesco, 1954) nov. comb.**

1954	<i>Prorodon trichocystus</i> nov. sp. – Dragesco, Vie et Milieu, 4: 633 (very brief description).
1960	<i>Prorodon trichocystus</i> Dragesco – Dragesco, Trav. Stn biol. Roscoff (N.S.), 12: 72 (detailed description).
1986	<i>Prorodon trichocystus</i> Dragesco, 1960 – Dragesco and Dragesco-Kernéis, Faune tropicale, 26: 137 (“brosse” as in <i>H. teres</i> , i.e., dextiotrop).

***Hilleroophrya* nov. gen.**

Diagnosis: Holophryidae with aristerotrop brosse, i.e., with ciliary rows abutting to left side of brosse (Fig. 5b).

Type species: *Prorodon cinereus* Penard, 1922.

Etymology: *Hilleroophrya* is a composite of the surname of Dr. Stephan Hiller, who did excellent research on several prostomatids at Tübingen University, Germany, and the noun *ophrys* (eyebrow ~cilia ~ciliate). Feminine gender.

Species assignable: *Hilleroophrya cinerea* (Penard, 1922) nov. comb. (basionym: *Prorodon cinereus* Penard, 1922 as redescribed by Groliere (1977), and *Hilleroophrya agamalievi* nov. spec. described below.

***Hilleroophrya agamalievi* nov. spec. (Fig. 5c, d, g)**

1978	<i>Prorodon mimeticus</i> Kahl, 1930 – Agamaliev, Acta Protozool., 17: 422 (misidentification, see following description).
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Diagnosis: Size (in vivo?) about 120–150 × 30 μm; cylindroid. Macronucleus about 15 μm across, several micronuclei attached. 65–80 meridional ciliary rows and 3 aristerotrop brosse rows only 11 μm long; about 7 ciliary rows abut to left side of brosse. Oral entrance in centre of anterior pole, surrounded by about 10 ciliary girdles produced by very regularly arranged cilia in anterior region of rows.

Type locality: Fine and medium-sized sand and in the periphyton of brackish water in the Caspian Sea.

Type material: Not mentioned but possibly existing because the description is based on Chatton-Lwoff silver nitrate-impregnated specimens. For the present purpose, I fix the specimen shown in Fig. 5c of the present paper as holotype of *H. agamalievi* nov. spec. This is in accordance with article 73.1.4 of the ICZN (1999).

Etymology: Named in honour of Dr. F. G. Agamaliev from the Azerbaijan Academy of Sciences, Baku.

Description (according to Agamaliev 1978): Body length 120–150 μm, sometimes up to 200 μm (exactly as written by Kahl 1930); cylindroid. Macronucleus about 15 μm across, several micronuclei attached. Ciliature dense, 65–80 meridional rows, begin at mouth rim with highly ordered basal bodies forming about 10 perial ciliary circles. Brosse composed of three, only about 11 μm long rows with very narrowly spaced basal bodies having elongated cilia; about

seven ciliary rows shortened anteriorly and abutting in sharp angles to left margin of brosse; two post-brosse ciliary rows.

Cytostome subapical, very slightly out of pole centre, funnel-shaped, surrounded by a girdle of strong cilia. Cytopharyngeal basket visible.

Remarks: Very likely, Agamaliev (1978) did not study this ciliate in vivo, as indicated by body measurements (see above) and the lack of data on the contractile vacuole(s). Thus, several important features are lacking, such as shape and size of extrusomes, brosse details, and the shape of the oral basket rods. Without any doubt, Agamaliev (1978) misidentified this ciliate as *Prorodon mimeticus* Kahl, 1930 which has, for instance, several contractile vacuoles and a complex brosse clearly different from that shown by Agamaliev (1978, cp. Borror 1963).

I could not find a species in the literature that matches the ciliate described by Agamaliev (1978). Rather similar is a moorland ciliate, viz., *Vdacnyophrya gracilis* (Groliere, 1977) which, however, has caudal cilia, only 36 vs. 65–80 ciliary rows, and an aklitoloph brosse (see below).

***Vdacnyophrya* nov. gen.**

Diagnosis: Holophryidae with aklitoloph brosse, i.e., ciliary rows not shortened along both sides of brosse (Fig. 5b).

Type species: *Prorodon aklitolophon* Hiller and Bardele, 1988.

Etymology: *Vdacnyophrya* is a composite of Dr. Peter Vd’áčny, an outstanding Slovak ciliatologist, and the Greek noun *ophrys* (eyebrow ~cilia ~ciliate). Feminine gender.

Species assignable: *Vdacnyophrya aklitolophon* (Hiller and Bardele, 1988) nov. comb. (basionym: *Prorodon aklitolophon* Hiller and Bardele, 1988); *Vdacnyophrya gracilis* (Groliere, 1977) nov. comb. (basionym: *Prorodon gracilis* Groliere, 1977); *Vdacnyophrya ovalis* (Dragesco, 1970) nov. comb. (basionym: *Prorodon ovalis* Dragesco, 1970); *Vdacnyophrya pyriformis* (Groliere, 1977) nov. comb. (basionym: *Prorodon pyriformis* Groliere, 1977).

***Vdacnyophrya aklitolophon* (Hiller and Bardele, 1988) nov. comb.**

1988	<i>Prorodon aklitolophon</i> n. spec. – Hiller and Bardele, Arch. Protistenk., 136: 214.
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***Vdacnyophrya gracilis* (Groliere, 1977) nov. comb.**

1977	<i>Prorodon gracilis</i> n. sp. – Groliere, Anns Stn. biol. Besse-en-Chandesse, 10: 275 (volume 10 comprises the years 1975 and 1976, which was available in 1977).
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***Vdacnyophrya ovalis* (Dragesco, 1970) nov. comb.**

1970	<i>Prorodon ovalis</i> n. sp. – Dragesco, Anns Fac. Sci. Univ. féd. Cameroun (numero hors-serie), p. 25. Brosse aklitoloph.
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- 1986 *Prorodon ovalis* Dragesco, 1970 – Dragesco and Dragesco-Kernéis, Faune tropicale, 26: 131 (brief repetition of original description).
- 2005 *Prorodon ovalis* Dragesco, 1970 – Alekperov, Atlas of free-living infusoria, p. 26 (confirmation of brosse type).

Vdacnyophrya pyriformis (Groliere, 1977) nov. comb.

- 1977 *Prorodon pyriformis* n. sp. – Groliere, Anns Stn. biol. Besse-en-Chandesse, 10: 272 (volume 10 comprises the years 1975 and 1976, which was available in 1977).

Bardeleophrya nov. gen.

Diagnosis: Holophryidae with syntrop brosse, i.e., with some ciliary rows abutting to both sides of brosse (Fig. 5b).

Type species: *Prorodon africanus* Dragesco, 1970.

Etymology: *Bardeleophrya* is a composite of Prof. Dr. Christian Bardele, University of Tübingen, who was the adviser of Dr. Stephen Hiller (see genus *Hillerophrya*), and the Greek noun *ophrys* (eyebrow ~cilia ~ciliate). Feminine gender.

Species assignable: *Bardeleophrya africana* (Dragesco, 1970) nov. comb. (basonym: *Prorodon africanus* Dragesco, 1970); *Bardeleophrya lucens* (Alekperov, 1985) nov. comb. (basonym: *Prorodon lucens* Alekperov, 1985).

Bardeleophrya africana (Dragesco, 1970) nov. comb

- 1970 *Prorodon africanus* n. sp. – Dragesco, Anns Fac. Sci. Univ. féd. Cameroun (numero-hors-serie), p. 22.
- 1986 *Prorodon africanus* Dragesco, 1970 – Dragesco and Dragesco-Kernéis, Faune tropicale, 26: 131 (brief repetition of original description).
- 2005 *Prorodon africanus* Dragesco, 1970 – Alekperov, Atlas free-living infusoria, p. 28 (confirmation of brosse type).

Bardeleophrya lucens (Alekperov, 1985) nov. comb.

- 1985 *Prorodon lucens* sp. n. – Alekperov, Zool. Zh., 64: 1461 (brosse syntrop).

Author contributions

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References

- Agamaliev, F.G., 1978. Morphology of some free-living ciliates of the Caspian Sea. *Acta Protozool.* 17, 419–444, Plates I–IV.
- Alekperov, I.K., 1985. New free-living ciliates from fresh waters of Azerbaijan. *Zool. Zh.* 64, 1461–1467.
- Alekperov, I.K., 2005. Atlas of Free-Living Infusoria (Classes Kinetofragminophora, Colpodea, Oligohymenophora, Polyhymenophora). Institute of Zoology NAS of Azerbaijan, Baku (in Russian).
- Alekperov, I., Buskey, E., Snegovaya, N., 2007. The free-living ciliates of the Mexican Gulf coast near Port Aransas city and its suburbs (South Texas, USA). *Protistology* 5, 101–130.
- Augustin, H., Foissner, W., 1992. Morphologie und Ökologie einiger Ciliaten (Protozoa: Ciliophora) aus dem Belebtschlamm. *Arch. Protistenk.* 141, 243–283.
- Benčat'ová, S., Křižanová, F., Tirjaková, E., 2019. Current knowledge of the starvation and reproduction stages of the limnic species *Holophrya teres* (Ciliophora: Prostomatea). *Biologia* 75, 413–422.
- Blochmann, F., 1895. Die mikroskopische Thierwelt des Süßwassers. Abteilung I: Protozoa, 2nd ed. Lucas Gräfe and Sillem, Hamburg.
- Borror, A.C., 1963. Morphology and ecology of the benthic ciliated protozoa of Alligator Harbor, Florida. *Arch. Protistenk.* 106, 465–534.
- Claparède, É., Lachmann, J., 1859. Études sur les infusoires et les rhizopodes. *Mém. Inst. Natn. Génév.*, 6 (year 1858), 261–482, Planches 14–24.
- Corliss, J.O., 1979. The Ciliated Protozoa. Characterization, Classification and Guide to the Literature. Pergamon Press, Oxford, New York, Toronto, Sydney, Paris, Frankfurt.
- Czapik, A., 1965. *Prorodon raabei* sp. n. et sa biologie. *Acta Protozool.* 3, 21–26, Planches I–III.
- Dragesco, J., 1954a. Diagnoses préliminaires de quelques ciliés nouveaux des sables. *Bull. Soc. Zool. Fr.* 79, 62–70.
- Dragesco, J., 1954b. Diagnoses préliminaires de quelques ciliés nouveaux des sables de Banyuls-sur-mer (I). *Vie Milieu* 4, 633–637.
- Dragesco, J., 1960. Ciliés mésopsammiques littoraux. Systématique, morphologie, écologie. *Trav. Stn biol. Roscoff* 12, 1–356.
- Dragesco, J., 1963. Compléments à la connaissance des ciliés mésopsammiques de Roscoff. I. Holotriches. *Cah. Biol. Mar.* 4, 91–119.
- Dragesco, J., 1965. Ciliés mésopsammiques d'Afrique Noire. *Cah. Biol. Mar.* 6, 357–399.
- Dragesco, J., 1966a. Ciliés libres de Thonon et ses environs. *Protistologica* 2, 59–95.
- Dragesco, J., 1966b. Observations sur quelques cillies libres. *Arch. Protistenk.* 109, 155–206.
- Dragesco, J., 1966c. Quelques ciliés libres du Gabon. *Biol. Gabon.* 2, 91–117.

- Dragesco, J., 1970. Ciliés libres du Cameroun. *Annls Fac. Sci. Univ. féd. Cameroun (Numéro hors-série)*, 1–141.
- Dragesco, J., Dragesco-Kernéis, A., 1986. Ciliés libres de l’Afrique intertropicale. Introduction à la connaissance et à l’étude des ciliés. *Faune tropicale (Éditions de l’Orstom)* 26, 1–559.
- Ehrenberg, C.G., 1831. Über die Entwicklung und Lebensdauer der Infusionsthier; nebst ferneren Beiträgen zu einer Vergleichung ihrer organischen Systeme. *Abh. preuss. Akad. Wiss., Phys.-math. Kl.* 1–154, Tafeln I–IV.
- Ehrenberg, C.G., 1834. Dritter Beitrag zur Erkenntniß großer Organisation in der Richtung des kleinsten Raumes. *Abh. preuss. Akad. Wiss., Phys.-math. Kl.* year 1833, 145–336, Tafeln I–XI.
- Ehrenberg, C.G., 1838. Die Infusionsthierchen als vollkommene Organismen. Ein Blick in das tiefere organische Leben der Natur. L. Voss, Leipzig.
- Ehrenberg, C.G., 1840. Charakteristik von 274 neuen Infusorien. *Mber. Preuss. Akad. Wiss., Berlin*, year 1840, 197–219.
- Foissner, W., 1972. The cytophyge of ciliata II. Microphotographical documentation of the defecation in *Prorodon teres*. *Acta biol. Acad. Sci. hung.* 23, 353–362.
- Foissner, W., 1983. Taxonomische Studien über die Ciliaten des Großglocknergebietes (Hohe Tauern, Österreich) I. Familien Holophryidae, Prorodontidae, Plagiocampidae, Colepidae, Enchelyidae und Lacrymariidae nov. fam. *Annln naturh. Mus. Wien* 84/B (year 1980, 49–85).
- Foissner, W., 1984. Infraciliatur, Silberliniensystem und Biometrie einiger neuer und wenig bekannter terrestrischer, limnischer und mariner Ciliaten (Protozoa: Ciliophora) aus den Klassen Kinetofragminophora, Colpodea und Polyhymenophora. *Stapfia* 12, 1–165.
- Foissner, W., 1991. Basic light and scanning electron microscopic methods for taxonomic studies of ciliated protozoa. *Eur. J. Protistol.* 27, 313–330.
- Foissner, W., 1993. Colpodea (Ciliophora). *Protozoenfauna* 4/1, 1–798.
- Foissner, W., 1997. Faunistic and taxonomic studies on ciliates (Protozoa, Ciliophora) from clean rivers in Bavaria (Germany), with descriptions of new species and ecological notes. *Limnologica (Berlin)* 27, 179–238.
- Foissner, W., 2016. Terrestrial and semiterrestrial ciliates (Protozoa, Ciliophora) from Venezuela and Galápagos. *Denisia* 35, 1–912.
- Foissner, W., Al-Rasheid, K., 2006. A unified organization of the stichotrichine oral apparatus, including a description of the buccal seal (Ciliophora: Spirotrichea). *Acta Protozool.* 45, 1–16.
- Foissner, W., Pfister, G., 1997. Taxonomic and ecologic revision of urotrichs (Ciliophora, Prostomatida) with three or more caudal cilia, including a user-friendly key. *Limnologica (Berlin)* 27, 311–347.
- Foissner, W., Wenzel, F., 2004. Life and legacy of an outstanding ciliate taxonomist, Alfred Kahl (1877–1946), including a facsimile of his forgotten monograph from 1943. *Acta Protozool.* 43 (Supplement), 3–69.
- Foissner, W., Berger, H., Kohmann, F., 1994. Taxonomische und ökologische Revision der Ciliaten des Saprobiensystems – Band III: Hymenostomata, Prostomatida, Nassulida. *Informationsberichte des Bayer. Landesamtes für Wasserwirtschaft* 1/94, 1–548.
- Foissner, W., Berger, H., Schaumburg, J., 1999. Identification and ecology of limnetic plankton ciliates. *Informationsberichte des Bayer. Landesamtes für Wasserwirtschaft* 3/99, 1–793.
- Foissner, W., Agatha, S., Berger, H., 2002. Soil ciliates (Protozoa, Ciliophora) from Namibia (Southwest Africa), with emphasis on two contrasting environments, the Etosha region and the Namib desert. Part I: text and line drawings. Part II: photographs. *Denisia* 5, 1–1459.
- Franco, C., Esteban, G., Téllez, C., 1998. Morfología, infraciliación y ciclo de vida de *Prorodon magnus* Dragesco, 1966 (Ciliophora, Prostomatida). *Boln R. Soc. Esp. Hist. Nat.* 94, 15–23.
- Fromentel, Ede, 1875. Études sur les microzoaires ou infusoires proprement dits comprenant de nouvelles recherches sur leur organisation, leur classification et la description des espèces nouvelles ou peu connus. G. Masson, Paris.
- Groliere, C.-A., 1977. Contribution à l’étude des cilies des sphaignes et des etendues d’eau acides. I – Description de quelques especes de gymnostomes, hypostomes, hymenostomes et heterotriches. *Annls Stn limnol. Besse* 10, 265–296 (years 1975/1976, available 1977).
- Hiller, S.A., 1993a. Ultrastructure of *Prorodon* (Ciliophora, Prostomatida) I. Somatic cortex and some implications concerning kinetid evolution in prostomatid and colpodid ciliates. *J. Euk. Microbiol.* 40, 467–486.
- Hiller, S.A., 1993b. Ultrastructure of *Prorodon* (Ciliophora, Prostomatida) II. Oral cortex and phylogenetic conclusions. *J. Euk. Microbiol.* 40, 486–501.
- Hiller, S., Bardele, C.F., 1988. *Prorodon aklitolophomn.* spec. and the “dorsal brush” as a character to identify certain subgroups in the genus *Prorodon*. *Arch. Protistenk* 136, 213–236.
- ICZN (International Commission on Zoological Nomenclature), 1999. *International Code of Zoological Nomenclature*. International Trust for Zoological Nomenclature, London.
- ICZN (International Commission on Zoological Nomenclature), 2012. Amendment of articles 8, 9, 10, 21 and 78 of the international code of zoological nomenclature to expand and refine methods of publication. *Bull. Zool. Nom.* 69, 161–169.
- Jankowski, A.V., 1976. Revision of a system of cyrtophorines. In: Dumka, Naukova (Ed.), *Materials of the II All-Union Conference of Protozoologists*. Part I. General Protozoology, Naukova Dumka, Kiev, pp. 167–168 (in Russian).
- Jankowski, A.V., 2007. Phylum Ciliophora Doflein, 1901. Review of taxa. In: Alimov, A.F. (Ed.), *Protista: Handbook on Zoology*, Part 2. Nauka, St. Petersburg, pp. 415–993 (in Russian with English summary).
- Jordan, A., 1974. Morphologie et biologie de *Prorodon discolor* Ehr.-Blochm.-Schew. *Acta Protozool.* 13, 5–8, Planches I–III.
- Kahl, A., 1927. Neue und ergänzende Beobachtungen holotricher Ciliaten. I. *Arch. Protistenk.* 60, 34–129.
- Kahl, A., 1928. Die Infusorien (Ciliata) der Oldesloer Salzwasserstellen. *Arch. Hydrobiol.* 19, 50–123.
- Kahl, A., 1930. Urtiere oder Protozoa I: Wimpertiere oder Ciliata (Infusoria) I. Allgemeiner Teil and Prostomata. *Tierwelt Dtl.* 18, 1–180.
- Kattar, M.R., 1970. Estudo dos protozoários ciliados psamófilos do litoral brasileiro. *Zool. Biol. Mar.* 27, 123–206.
- Kim, J.H., Jung, J.-H., 2017. Brief descriptions of 12 ciliate species previously unrecorded (Protozoa: Ciliophora) in Korea. *J. Species Res.* 6 (Spec. Ed), 15–25.
- Kreutz, M., Foissner, W., 2006. The *Sphagnum* ponds of Simmelried in Germany: a biodiversity hot-spot for microscopic organisms. *Protozool. Monogr.* 3, 1–267.
- Krüger, F., 1934. Untersuchungen über die Trichocysten einiger *Prorodon*-Arten. *Arch. Protistenk.* 83, 275–320.

- Kwon, C.B., Vd'áčný, P., Shazib, S.U.A., Shin, M.K., 2014. Morphology and molecular phylogeny of a new haptorian ciliate, *Chaenea mirabilis* sp. n., with implications for the evolution of the dorsal brush in haptorians (Ciliophora, Litostomatea). *J. Euk. Microbiol.* 61, 278–292.
- Leipe, D., 1989. *Prorodon spirogyrophagus* nov. spec. (Ciliophora, Prostomatea): morphology, infraciliature and food-uptake. *Eur. J. Protistol.* 24, 392–401.
- Liebmann, H., 1962. Handbuch der Frischwasser- und Abwasser-Biologie. Band I. Biologie des Trinkwassers, Badewassers, Fischwassers, Vorfluters und Abwassers. R. Oldenbourg, München.
- Lynn, D.H., 2008. The Ciliated Protozoa: Characterization, Classification, and Guide to the Literature, 3rd ed. Springer, Dordrecht.
- Müller, O.F., 1773. Vermium Terrestrium et Fluviatilia, seu Animalium Infusorium, Helminthicorum et Testaceorum, non Marinarum, Succinata Historia. Heineck and Faber, Havniae and Lipsae.
- Noland, L.E., 1925. A review of the genus *Coleps* with descriptions of two new species. *Trans. Am. Microsc. Soc.* 44, 3–13.
- Penard, E., 1922. Études sur les infusoires d'eau douce. Georg and Cie, Genève.
- Penard, E., 1938. Les infiniment petits dans leurs manifestations vitales. Georg and Cie, Genève.
- Perty, M., 1852. Zur Kenntniss kleinster Lebensformen nach Bau, Funktionen, Systematik, mit Specialverzeichniss der in der Schweiz beobachteten. Jent and Reinert, Bern.
- Powers, J.H., Mitchell, C., 1910. A new species of *Paramecium* (*P. multimicronucleata*) experimentally determined. *Biol. Bull. Mar. Biol. Lab., Woods Hole* 19, 324–332.
- Puytorac, Pde, 1964. Quelques aspects de l'ultrastructure du cilié: *Prorodon viridis* Ehrbg. *Kahl. Acta Protozool.* 2, 147–152, Plates I–VIII.
- Puytorac, Pde, Savoie, A., 1968. Observations cytologiques et biologiques sur *Prorodon palustris* nov. sp. *Protistologica* 4, 53–60, Planches I–VI.
- Rajter, L., Vd'áčný, P., 2016. Rapid radiation, gradual extinction and parallel evolution challenge generic classification of spathidiid ciliates (Protista, Ciliophora). *Zool. Scr.* 45, 200–223.
- Rajter, L., Vd'áčný, P., 2018. Selection and paucity of phylogenetic signal challenge the utility of alpha-tubulin in reconstruction of evolutionary history of free-living litostomateans (Protista, Ciliophora). *Mol. Phylogenet. Evol.* 127, 543–544.
- Schewiakoff, W., 1892. Ueber die geographische Verbreitung der Süßwasser-Protozoen. *Verh. naturh.-med. Ver. Heidelb. (N. S.)* 4, 544–567.
- Schewiakoff, W., 1896. The organization and systematics of the infusoria *Aspirotricha* (*Holotricha auctorum*). *Zap. Imp. Akad. Nauk 8e Série* 4, 1–395 (in Russian).
- Stechmann, A., Schlegel, M., Lynn, D.H., 1998. Phylogenetic relationships between prostome and colpodean ciliates tested by small subunit rRNA sequences. *Mol. Phylogenet. Evol.* 9, 48–54.
- Švec, F., 1897. Beiträge zur Kenntnis der Infusorien Böhmens. I. Die ciliaten Infusorien des Unterpocernitzer Teiches. *Bull. Int. Acad. Tchèque Sci.* 4, 29–47, Tafeln I, II.
- Tannreuther, G.W., 1926. Life history of *Prorodon griseus*. *Biol. Bull.* 51, 303–320.
- Vd'áčný, P., Foissner, W., 2012. Monograph of the dileptids (Protista, Ciliophora, Rhynchostomatia). *Denisia* 31, 1–529.
- Vd'áčný, P., Foissner, W., 2013. Synergistic effects of combining morphological and molecular data in resolving the phylogenetic position of *Semispathidium* (Ciliophora, Haptoria) with description of *Semispathidium breviararmatum* sp. n. from tropical Africa. *Zool. Scr.* 42, 529–549.
- Wohlfarth-Bottermann, K.E., Pfefferkorn, G., 1953. Protistenstudien. I. Pro- und Nesselkapseltrichocysten der Ciliaten-Gattung *Prorodon*. *Z. Wiss. Mikrosk. Mikr. Tech.* 61, 239–248.
- Zhang, Q., Yi, Z., Fan, X., Warren, A., Gong, J., Song, W., 2014. Further insights into the phylogeny of two ciliate classes Nassophorea and Prostomatea (Protista, Ciliophora). *Mol. Phylogenet. Evol.* 70, 162–170.