Europ. J. Protistol. 32, 336–355 (1996)
August 30, 1996

European Journal of
PROTISTOLOGY

Updating the Trachelocercids (Ciliophora, Karyorelictea). II. *Prototrachelocerca* nov.gen. (Prototrachelocercidae nov. fam.), with a Redescription of *P. fasciolata* (Sauerbrey, 1928) nov. comb. and *P. caudata* (Dragesco & Raikov, 1966) nov. comb.

Wilhelm Foissner
Universität Salzburg, Institut für Zoologie, Salzburg, Austria

SUMMARY

The morphology and infraciliature of *Prototrachelocerca fasciolata* (Sauerbrey, 1928) nov. comb. and *P. caudata* (Dragesco & Raikov, 1966) nov. comb. were studied in live and protargol impregnated specimens. The entire somatic and oral infraciliature consists of dikinetids which have both basal bodies ciliated or only the anterior or posterior ones, depending on the region of the cell. The right side is densely and uniformly ciliated. Its ciliary rows extend onto the left side to the glabrous stripe, where an anterior and posterior secant system are formed, reducing the number of kineties in the narrowed neck and tail region. The left side bears a broad glabrous stripe bordered by slightly irregularly arranged dikinetids having rather stiff, elongated cilia (bristles), possibly forming a continuous, prolate-ellipsoidal (bristle) kinety as indicated by their ciliation. The bristle kinety commences subapically at the right margin of the glabrous stripe, extends posteriorly, then anteriorly at the left, to end up at the right margin again. The dikinetids of the right posterior portion of the bristle kinety have the *posterior* basal bodies ciliated, whereas the *anterior* basal bodies are ciliated in its left and right anterior portion. The ends of the bristle kinety meet subapically at the right margin of the glabrous stripe, as indicated by the diametrically (180°) opposed ciliation of the dikinetids. The anterior region (head) of the cell bears a distinct oral apparatus consisting of a circumoral (paroral?) ciliature interrupted on the left side of the head, where 2–4 small, oblique brosse kineties (adoral?) insert in a distinct pocket. The oral dikinetids are associated with conspicuous nematodesmata forming an oral basket, together with the nematodesmal bundles originating from the oralized somatic dikinetids at the anterior end of the somatic kineties. The circumoral ciliature consists of 2–3 rather irregular rows of dikinetids, possibly composed of many short, superimposed or oblique kinety segments. This pattern is basically different from that known from other trachelocercids and thus used to define a new genus, *Prototrachelocerca*, and a new family, Prototrachelocercidae, which is possibly closely related to the Loxodidae. In addition to the species mentioned above, *Tracheloraphis angustivittata* is assigned to the new genus: *Prototrachelocerca angustivittata* (Borror, 1963) nov. comb.

Introduction

In 1986 the first detailed descriptions of the infraciliature of trachelocercid ciliates were published concomitantly by Wilbert [31] and Dragesco & Dragesco-Kernéis [6]. Although the results basically agree, in one respect they differ so significantly that an impartial reviewer could get the impression that

0932-4739-96-0032-0336$3.50-0

one of the authors was mistaken. This difference concerns the circumoral ciliature, described and figured by Wilbert as a compound structure consisting of three rows of dikinetids, contrasting all species investigated by Dragesco & Dragesco-Kernéis, which have a "simple" circumoral kinety composed of a single row of dikinetids.

In 1994 I studied many trachelocercids from the French Atlantic coast at Roscoff and found, at first glance, all to be equipped with the simple circumoral kinety described by Dragesco & Dragesco-Kernéis [6]. I was thus doubtful regarding Wilbert's [31] description of *Tracheloraphis dogieli*, and asked him for permission to reinvestigate the type slides. This proved, however, that Wilbert's description, although incomplete in many respects, is basically correct. Finally, a careful inspection of the protargol slides I prepared at Roscoff showed that they contained a species having the same character.

Thus, it became clear that trachelocercids fall into two groups, greatly differing in the structure of the circumoral ciliature. The detailed description of the "compound group" is the main purpose of the second paper [14] of our series on the infraciliature of trachelocercid ciliates.

Material and Methods

Prototrachelocerca fasciolata occurred sparsely in the mesopsammon of the French Atlantic coast at Roscoff. Samples were collected and treated exactly as described by Fauré-Fremiet [9], i.e. the specimens were detached from the sand grains by adding about 5 ml of a 12% $MgCl_2$ solution to about 20 ml sand and sea water taken from the surface of the sample collected at least 24 h earlier so that specimens could move upward and concentrate in the upper sand layer. The mixture was then gently rotated in a petri dish so that the sand collected in the centre and the ciliates could be picked up individually with a capillary pipette from the clear supernatant.

Cells were studied in vivo using a high-power oil immersion objective [10]. The infraciliature was revealed by protargol impregnation [10; protocol 2, Wilbert's method], using a special fixative invented by Jean Dragesco (pers. comm.): 5 ml glutaraldehyde (25%), 5 ml saturated, aqueous mercuric chloride, 3 ml aqueous osmium tetroxide (2%), and 1 ml glacial acetic acid are mixed just before use. Specimens are fixed for 15–30 min and washed three times in distilled water.

Counts and measurements on living specimens were conducted at a magnification of X40–1000. Although these provide only rough estimates, it is worth giving such data as specimens usually shrink in preparations and contract during fixation. Standard deviation and coefficient of variation were calculated according to textbooks.

Illustrations of live specimens are based on free-hand sketches, those of impregnated cells were made with a camera lucida.

Prototrachelocerca caudata was studied in Wilbert's type slides (see detailed explanation on the page where the species is redescribed).

Orientation and terminology of trachelocercids, both difficult and controversial, have been discussed and explained in Foissner & Dragesco [14].

All figures are orientated with the anterior end of the organism directed to the top of the page.

Results

Prototrachelocercidae nov. fam.

Diagnosis. Trachelocercida Jankowski, 1978 with compound circumoral (paroral?) ciliature comprising more than one row of dikinetids.

Type genus. Prototrachelocerca nov. gen.

Nomenclature. There is some uncertainty about the authorship of the order Trachelocercida. Puytorac [23] ascribes it to Kent [21] who, however, assigned his family Trachelocercidae to the order Holotricha. Thus, Kent cannot be taken as founder of an order Trachelocercida. In 1975, Jankowski [17] mentioned a new suborder Trachelocercina without, however, providing any characterization; thus it is a nomen nudum. Later, Jankowski [18] erected and vaguely diagnosed the new order Trachelocercida, with *Trachelocerca* as type. Thus, Jankowski [18] should be accepted as founder of the order. Alternatively, the suggestion by Small & Lynn [30] to unite the families Kentrophoridae and Trachelocercidae in a separate order, Protostomatida, may be accepted if further studies confirm the close relationship proposed.

Prototrachelocerca nov. gen.

Diagnosis. Prototrachelocercidae with circumoral ciliature interrupted at brosse cleft. Bristle kinety composed of longitudinal row of dikinetids containing some minute, oblique kineties each comprising 2–5 dikinetids. One or more short, oblique brosse kineties.

Type species. Prototrachelocerca fasciolata (Sauerbrey, 1928) nov. comb.

Derivatio nominis. Composite of "proto" (ancestral), "trachelos" (neck) and "cerca" (tail; Greek noun with latinized termination). Feminine gender.

Redescription of Prototrachelocerca fasciolata (Sauerbrey, 1928) nov. comb. (Table 1, Figs. 1–44)

1928 *Trachelocerca fasciolata* Sauerbrey, Arch. Protistenk., *62*, 368.

1935 *Trachelocerca fasciolata* Sauerbrey – Kahl, Tierwelt Dtl., *30*, 814.

1936 *Trachelocerca fasciolata* Sauerbrey 1928 – Kiesselbach, Thalassia, *2*, 8.

1960 *Tracheloraphis (Trachelocerca) fasciolatus* (Sauerbrey) – Dragesco, Trav. Stn biol. Roscoff, *12*, 127 (*Tracheloraphis fasciolata* nom. corr.).

1963 *Tracheloraphis dogieli* (Raikov, 1957) – Dragesco, Cah. Biol. mar., *4*, 95.

1968 *Tracheloraphis flexuosus* Raikov & Kovaleva, Acta Protozool., *6*, 322 (*Tracheloraphis flexuosa* nom. corr.).

Table 1. Morphometric characteristics from *Prototrachelocerca fasciolata* (upper line) and *P. caudata* (lower line)

Character[1]	$\bar{x}$	M	SD	$SD_{\bar{x}}$	CV	Min	Max	n
Body, length[2]	635.7	625.0	116.1	31.0	18.3	480	820	14
	559.3	580.0	153.6	39.7	27.5	360	820	15
Body, width at head	31.1	32.5	6.9	1.8	22.2	21	40	14
	22.0	20.0	6.8	1.7	30.7	14	33	15
Body, (maximum) width at trunk[3]	94.8	80.0	27.5	7.3	29.0	60	150	14
	72.8	63.0	22.4	5.8	30.8	50	115	15
Glabrous stripe, width in mid-body[3]	35.9	35.0	16.0	4.3	44.5	15	60	14
	26.5	23.5	6.9	1.9	26.2	19	42	14
Nuclear strand, length	356.1	360.0	105.4	27.2	29.6	160	550	15
	282.0	260.0	146.2	37.8	51.8	105	560	15
Macronucleus, length	13.4	12.5	3.9	1.0	29.1	9	22	14
	6.0	6.0	1.1	0.3	18.9	4	8	15
Macronucleus, width	8.9	9.0	1.9	0.5	21.8	5	12	14
	4.5	4.0	0.7	0.2	16.5	4	6	15
Micronucleus, length	6.5	6.0	1.2	0.3	17.8	5	8	14
	2.8	3.0	0.8	0.3	28.2	2	4	9
Micronucleus, width	5.4	5.0	1.2	0.3	22.5	3	7	14
	2.7	2.0	0.7	0.3	32.1	2	4	9
Anterior brosse kinety, length	2.7	3.0	1.1	0.4	38.9	1	5	8
	–	–	–	–	–	–	–	–
Middle brosse kinety, length	4.7	5.0	0.8	0.2	17.9	3	6	15
	5.4	5.5	1.1	0.3	9.0	4	7	12
Posterior brosse kinety, length	5.8	6.0	0.7	0.2	12.5	5	7	15
	6.7	7.0	1.1	0.3	16.9	5	8	12
Somatic kineties, number on head	21.8	22.0	1.6	0.4	7.2	18	25	14
	18.6	19.0	2.4	0.6	12.8	14	22	15
Somatic kineties, (maximum) number on trunk	35.2	35.0	3.1	0.8	8.9	29	42	14
	30.5	30.0	3.2	0.8	10.4	25	35	15
Dikinetids, number in 10 µm in neck region	5.6	6.0	1.0	0.3	18.0	4	7	14
	7.6	8.0	0.8	0.2	10.9	6	9	15
Dikinetids, number in 10 µm in trunk region	10.4	10.0	2.4	0.6	22.8	6	14	14
	9.8	10.0	1.7	0.4	17.3	7	12	15
Brosse kineties, number	2.7	3.0	0.7	0.2	26.8	2	4	15
	2.5	2.0	–	–	–	2	3	17
Macronuclei or nuclear rosettes, number	16.5	16.0	3.7	1.1	22.4	10	24	11
	17.5	15.0	10.3	2.7	58.7	5	37	15
Maronuclei, number per rosette	–	–	–	–	–	–	–	–
	3.4	4.0	1.1	0.3	31.0	2	5	15
Micronuclei or micronuclei per nuclear rosette, number	5.0	5.0	1.7	0.5	34.0	3	7	10
	1.6	2.0	–	–	–	0	2	15

[1] Data are based on the investigation of protargol impregnated and mounted morphostatic specimens. Measurements in µm. CV = coefficient of variation in %; M = median; Max = maximum; Min = minimum; n = number of specimens investigated; SD = standard deviation; $SD_{\bar{x}}$ = standard deviation of arithmetic mean; $\bar{x}$ = arithmetic mean.
[2] Values distinctly different from those of live specimens because they contract strongly when fixed for preparation.
[3] Data of very limited value because specimens are highly contractile and trunk often becomes inflated due to preparation procedures.

History and identification. This species poses many problems due to the poor original description (Figs. 1–3). I agree with Dragesco [4] that "La description de Sauerbrey étant pratiquement inutilisable, il faut se référer à Kahl (1935) pour avoir quelques détails morphologiques précis". However, considering the ongoing literature, *T. fasciolata* should not be treated as species indeterminata but carefully redescribed and provided with an improved diagnosis, just as Raikov [26] has done for *T. phoenicopterus*, another highly ambiguous species. My identification is based on the following remark by Sauerbrey: "If some water is removed, the cell slows down, flattens and folds as shown in Fig. 2. In such specimens a dark brown stripe composed of many fine dots becomes visible on the pellicle (Figs. 2, 3)". This matches a note I made at Roscoff, without knowing Sauerbrey's [29] description: "Glabrous stripe darker, i.e. more brownish than

rest of cell due to very narrowly spaced rows of brown-golden cortical granules".

Kahl [19] at first synonymized Sauerbrey's species with *Trachelocerca phoenicopterus*; later, however, he recognized it as a distinct taxon and provided a short description and a rather schematic figure (Fig. 5): "Up to 3 mm long, becomes wrinkled but not knobby when contracting, tail end comparatively broad; dark brown, protrichocysts (= cortical granules) fine and evenly distributed" [20]. The same is true for Kiesselbach [22], who observed only a single specimen with brown protrichocysts and a size of 850 × 40 µm (Fig. 6). A more detailed description with rather schematic figures (Figs. 7–11) was provided by Dragesco [4]: Brown; rather massive, length 1000–2000 µm, can extend considerably and contracts violently becoming banana-shaped due to absence of myonemes in glabrous stripe; head simple, conical, difficult to observe because filled with refractile granules, without trichocysts; 16–20 ellipsoid macronuclei (a dozen according to Kahl) accompanied by rather many spherical micronuclei; protrichocysts brownish to blackish, evenly arranged between ciliary rows and in glabrous stripe, explode when acidified methyl-green is applied; cytoplasm distinctly vacuolated and full of food residues; 44–58 ciliary rows, glabrous stripe not very wide. Later, Dragesco [5] mentioned that he intermixed this species with *Trachelo-raphis margaritata* and rather incompletely redescribed *T. dogieli* with, however, very similar characters to those previously [4] reported for *T. fasciolata*: Light brown, sometimes pink; length 1000–2200 µm, rather distinctly contractile; brosse cleft conspicuous; 23–37 macronuclei; many protrichocysts; 32–46 ciliary rows (Fig. 4). These features match my population well, which was collected at the same locality.

Raikov & Kovaleva [27] described *T. flexuosa* as follows: "Large (~ 1500 µm) vermiform ciliate with flexible body, sinuous during creeping (Fig. 14). Living specimens yellowish; cytoplasm transparent, strongly vacuolized. "Neck" and "head" not prominent; mouth region usually accumulating mineral granules. Posterior end pointed but forming no "tail" (Fig. 14). Ciliature consisting of approximately 36 longitudinal kineties. Dorsal glabrous stripe as wide as approximately 6 kineties (Fig. 15). Nuclear apparatus represented by 20–30 oval macronuclei and 10–15 micronuclei usually forming groups of 2 macronuclei and 1 micronucleus in each (Figs. 12, 13). The nuclear groups are localized in a longitudinal row (Figs. 12–14). The macronuclei, 5–7 µ long, contain many small nucleoli; the micronuclei are comparatively large – about 3 µ in diameter (Fig. 13). Biotope: fine, slightly muddy sand of the Japan Sea".

Obviously, *T. flexuosa* is very similar to the species I identify as *T. fasciolata*. In fact, Raikov & Kovaleva [27] mention only two characters differing from Dragesco's *T. fasciolata*, viz. that *T. flexuosa* is less distinctly brown (a very weak feature considering that they do not describe the cortical granulation) and has fewer ciliary rows (also weak because they do not provide any data on variation).

There are several other species which are rather similar to *P. fasciolata*, viz. *Trachelocerca multinucleata* ([4], more than 100 ciliary rows), *T. margaritata* ([20], I can confirm Kahl's observation on the unique cortical granulation of this species which has, according to my unpublished material, a simple circumoral kinety),*Tracheloraphis dogieli* ([24, 26], much broader than *T. fasciolata* and with 36–60 ciliary rows), and *T. beninensis* ([6], very broad but probably drawn from fixed specimens, glabrous stripe almost as wide as body).

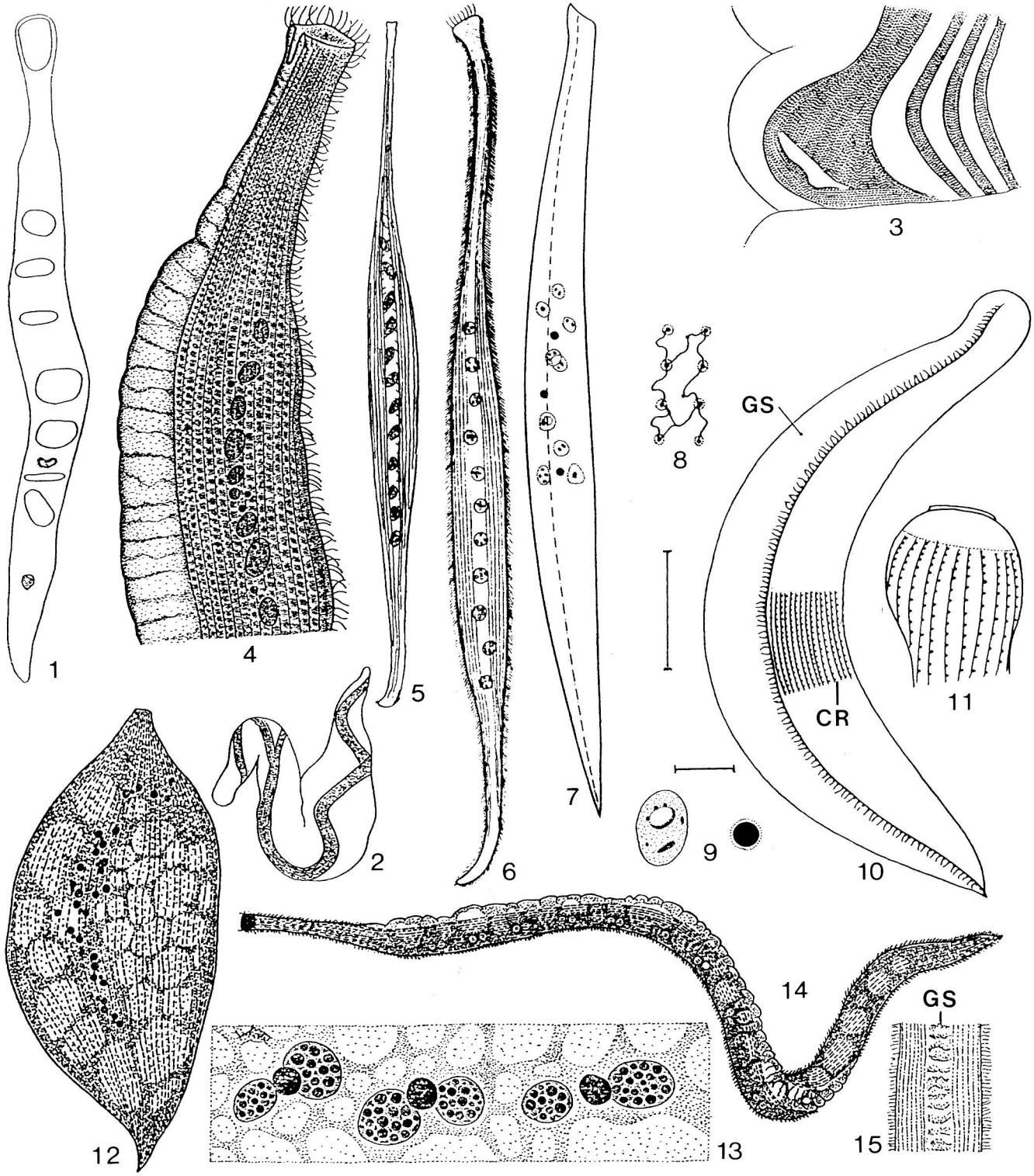
Specimens investigated and type material. The redescription is based on 10 well-impregnated specimens; some others were of usuable quality and served for completing morphometry.

No type material of *P. fasciolata* is mentioned in the literature. Thus, I have deposited two neotype slides with specimens, prepared as described, in the Oberösterreichische Landesmuseum in Linz (LI), Austria. Relevant specimens are marked by a black ink circle on the cover glass.

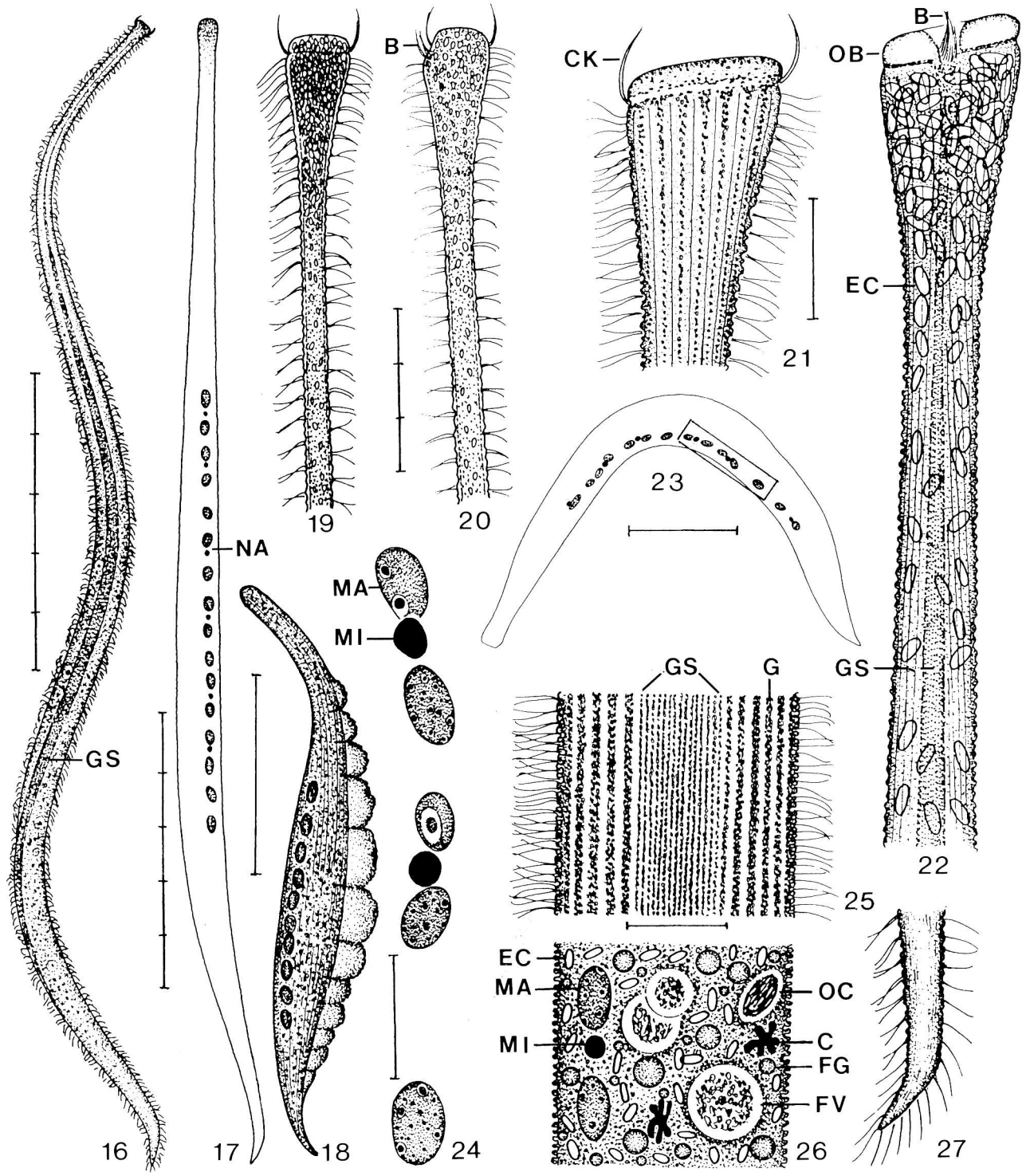
Improved diagnosis (based on present investigations and literature cited in list of synonyms). In vivo about 1000–3000 × 50 µm. Filiform, neck and tail indistinctly separate from trunk, head club-shaped, distal end of tail usually curved. 10–37 macronuclei forming strand in trunk. 29–46 ciliary rows; glabrous stripe distinct, about one third of body width. 2–4, usually 3 brosse kineties. Cortical granules 0.5–1 µm in diameter, yellow-orange to golden yellow, form stripes between ciliary rows and conspicuous band composed of many narrowly spaced rows in glabrous stripe.

Description of Roscoff population (neotype material; Figs. 16–44, Tab. 1). Morphometric data shown in Table 1 are repeated in this section only as needed for clarity. All observations are from field material. Thus, it cannot be excluded that different species were mixed, though this is unlikely due to the highly characteristic circumoral ciliature and the low variation (8.9%) of the somatic kinety number.

Size in vivo about 1700–2300 × 50 µm, highly flexible and contractile, size and shape thus poorly preserved in protargol slides (Tab. 1, Figs. 16, 28); flattened up to 2:1. Yellowish to yellow-brown and opaque in dissecting microscope, yellow-brown to yellow-orange-coloured in bright field microscope at a magnification of X 100, glabrous stripe appears as more intensively coloured band due to narrowly spaced rows of pigment granules (Figs. 16, 25). Shape rather constant, filiform with anterior and posterior third of cell gradually tapering, neck and tail thus indistinctly separate from trunk; head club-shaped in fully extended specimens, cylindroid in slightly and fully contracted cells; distal end of tail pointed and more or less distinctly curved (Figs. 16, 17, 19, 21, 27). Contracted specimens about 300 µm long, banana-shaped, convex side with glabrous stripe distinctly



Figs. 1–15. Synonymy of *Prototrachelocerca fasciolata*. All figures, if not stated otherwise, from life. – Figs. 1–3. *Trachelocerca fasciolata* (from [29]). Fig. 1. General view, length 1240 µm; Fig. 2. Flattened specimen with dark stripe; Fig. 3. Dark stripe at higher magnification. – Fig. 4. *Tracheloraphis dogieli* (from [5]), anterior portion after protargol impregnation. – Fig. 5. *Trachelocerca fasciolata* (from [20]), left lateral view, length 2000 µm. – Fig. 6. *T. fasciolata* (from [22]), left lateral view, 740 × 44 µm. – Figs. 7–11. *Tracheloraphis fasciolata* (from [4]). Fig. 7. General view, composite, size not given; Fig. 8. Silverline system after wet silver nitrate impregnation; Fig. 9. Part of nuclear apparatus, bar 10 µm; Figs. 10, 11. General view (bar 100 µm) and head after wet silver nitrate impregnation. GS = glabrous stripe, CR = ciliary rows. – Figs. 12–15. *Tracheloraphis flexuosa* (from [27]). Figs. 12, 13. General view and detail of nuclear apparatus after hematoxylin staining, length 350 µm and 52 µm; – Figs. 14, 15. General view (length 1500 µm) and glabrous stripe (GS).



Figs. 16–27. *Prototrachelocerca fasciolata* from life (Figs. 16–22, 25–27) and after protargol impregnation (Figs. 23, 24). – Figs. 16, 17. Extended specimens. – Fig. 18. Contracted specimens – Figs. 19, 20. Specimens with dark and hyaline head, depending on the number of ellipsoid inclusions accumulated. – Fig. 21. Right lateral surface view of head showing arrangement of cortical granules. – Fig. 22. Same specimen as shown in Fig. 21, but focused near centre of head and glabrous stripe. – Figs. 23, 24. Nuclear apparatus. Framed area of Fig. 23 is shown at higher magnification in Fig. 24. – Figs. 25, 26. Surface view and optical section of trunk. – Fig. 27. Posterior end. B = brosse, C = crystal, CK = circumoral kineties (ciliature), EC = ellipsoid crystals (inclusions), FG = fat globules, FV = food vacuole, G = cortical granules in stripes between ciliary rows, GS = glabrous stripe, MA = macronucleus, MI = micronucleus, NA = nuclear apparatus, OB = oral bulge, OC = food vacuole with orange-coloured content. Scale bar division = 100 µm (Figs. 16–18, 23) and 20 µm (Figs. 19–22, 24–26).

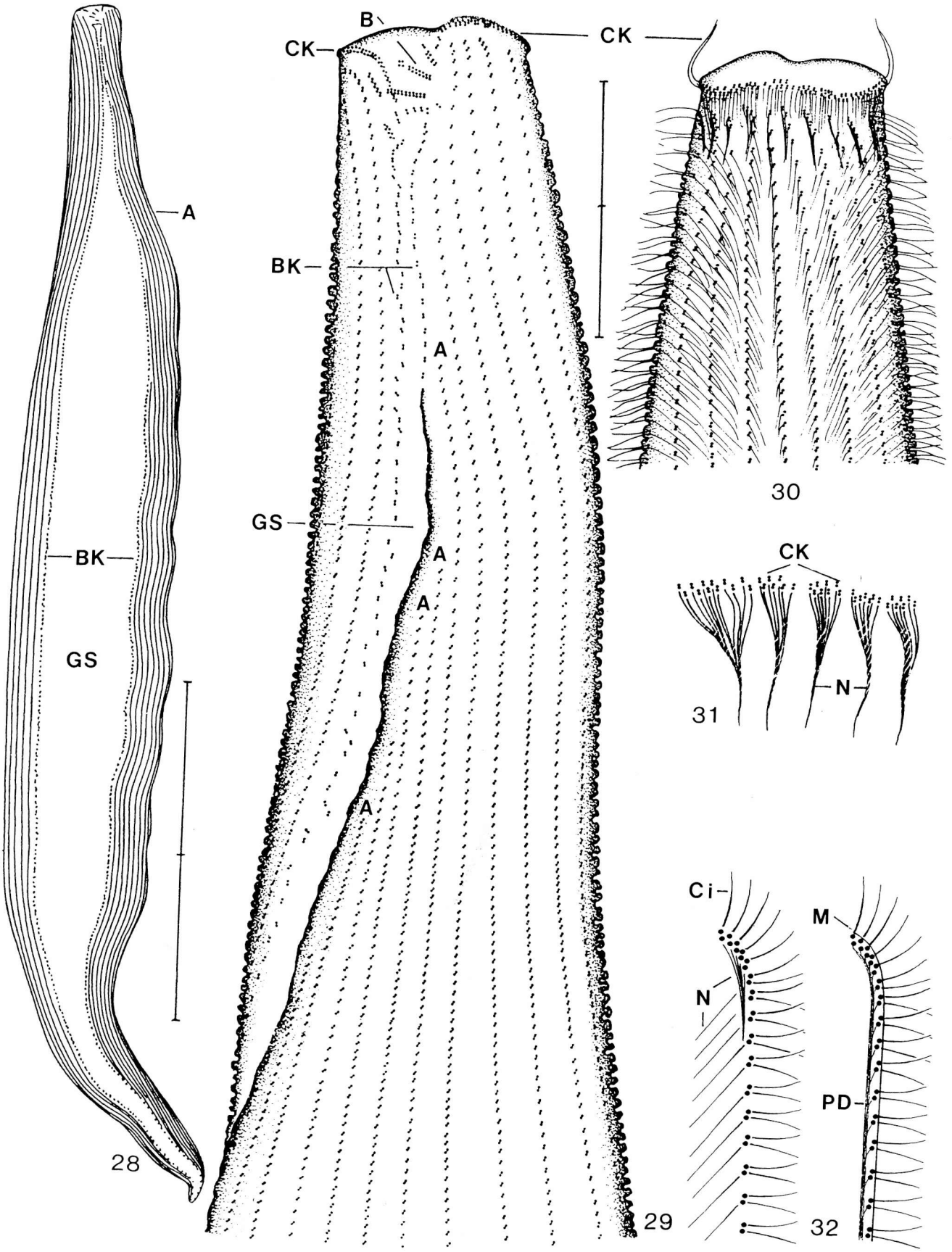
tuberculate (Fig. 18). Macronuclei globular to distinctly (up to 2:1) ellipsoid, most with many small, some with few large nucleoli; not in capsules but individually arranged near right surface of trunk, forming conspicuous strand. Micronuclei globular to ellipsoid, often 1 between each 2 macronuclei (Figs. 17, 23, 24, 26, 38). No contractile vacuole. Cortex highly flexible, forms columnar blisters in contracted specimens. Cortical (pigment) granules globular, minute (0.5–1 µm) but very numerous, yellow-orange to golden yellow, form stripes between ciliary rows and narrowly spaced rows in glabrous zone, which thus appears darker than rest of cell; stain red with methyl green-pyronin (Figs. 16, 21, 25). Cytoplasm colourless, packed with many 1–10 µm sized, brightly shining fat globules; 10–25 µm sized food vacuoles some with orange-coloured content, possibly digesting algae; many about 4 µm sized ellipsoid, flattened (mineral?) inclusions; and some tubercular crystals up to 15 µm in diameter (Figs. 22, 26). Movement like other large trachelocercids, i.e. elegantly gliding and winding between sand grains and organic debris.

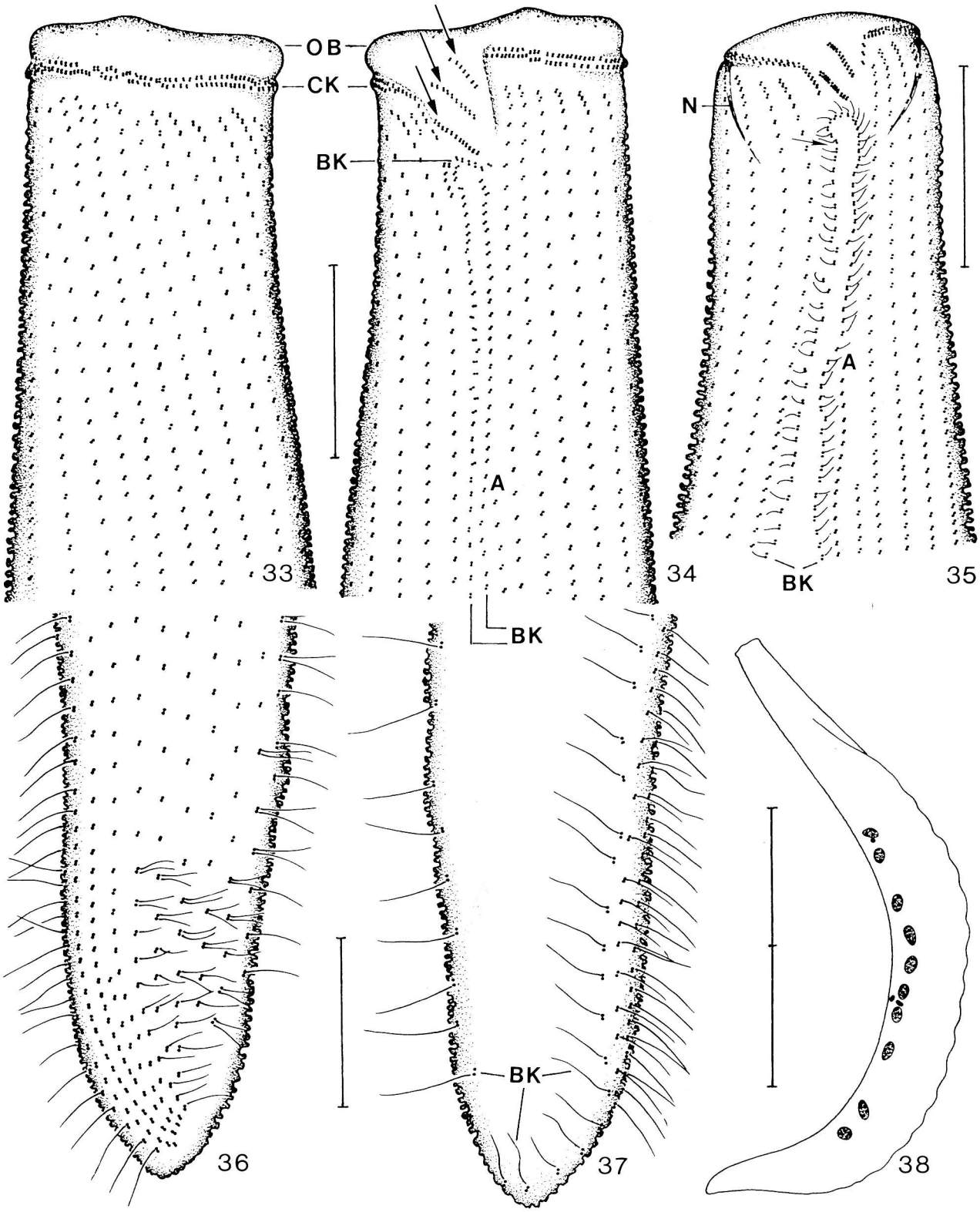
Somatic infraciliature. The surface of *P. fasciolata* is densely ciliated, leaving blank a rather wide zone, the glabrous stripe, extending along the whole body length in the median of the left side (Figs. 16, 25, 28). The cilia, which are rather stiff and can be spread, are about 12 µm long and arranged in longitudinal rows which are distinctly separate from the circumoral ciliature and extend between pronounced cortical crests. The ciliary rows are gradually shortened anteriorly in the neck region left of the glabrous stripe and posteriorly, where the body narrows to the tail, on both sides of the stripe. In other words, an anterior secant system is formed on the left surface of the neck where many kineties abut to the left branch of the bristle kinety. Thus, the head, neck, and tail have about one third less kineties than the trunk (Tab. 1). The ciliary rows neighbouring the right branch of the bristle kinety are unshortened anteriorly, i.e. extend parallel to the glabrous stripe. The distances between the ciliary rows decrease slightly from right to left, i.e. those forming the anterior secant system are more narrowly spaced than those right of the glabrous stripe (Figs. 28, 29, 39, 41, 42).

The entire infraciliature consists of dikinetids which, however, have a highly specialized ciliation and fibrillar system. The dikinetids are rotated 20°–30° counterclockwise to the kinety axis and associated with conspicuous, overlapping postciliary microtubule ribbons, which originate from the posterior basal bodies of the dikinetids and form a thick, faintly impregnated postciliodesma right of each ciliary row. A thin, sharply impregnated fibre, possibly a myoneme or subkinetal microtubule ribbon [28], extends close to left of each ciliary row (Fig. 32). Both basal bodies of the dikinetids are ciliated in the main portion of the cell. The posterior cilium is lacking in 1 to 3 dikinetids at the anterior end of the head kineties (Figs. 30, 32). These kinetids are condensed, i.e. more narrowly spaced than those on the trunk, and associated with distinct nematodesmal fibres originating from the posterior, nonciliated basal bodies. The nematodesmata from the condensed kinetids unite to small bundles extending almost parallel to the cell surface. Similar fibres originate from the neck dikinetids which, however, have both basal bodies ciliated. These fibres do not form bundles but extend obliquely posteriad to the neck midline (Figs. 30, 32, 40, 43). The nematodesmata-bearing kinetids of the head and neck are thus oralized somatic dikinetids as defined by Foissner & Foissner [15]. The posterior cilium is also lacking in 3 to 10 dikinetids at the posterior end of the kineties and in all left lateral kineties abutting to the left branch of the bristle kinety.

The glabrous stripe, which extends along the whole length of the body, is narrow in the head region and widens, respectively narrows, gradually on the neck and tail. Its full width on the trunk corresponds to an area occupied by about 10 kineties, i.e. approximately one third of body width. The glabrous stripe is rather flabby and becomes tuberculate when the cell contracts (Figs. 16, 18, 25, 28, 41). It is bordered by the bristle kinety which consists, like the ordinary ciliary rows, of dikinetids having about 20 µm long, rather stiff cilia. However, the bristle kinety is easily distinguished from ordinary somatic ciliary rows because its dikinetids are more irregularly and loosely arranged and either lack or have very inconspicuous postciliary microtubule ribbons too small to be recognized with the light microscope (Figs. 29, 34, 35, 39, 41). Furthermore, the bristle kinetids have a unique ciliation, most parsimoniously explained with the assumption that they belong to a single kinety extending along the stripe margins, quite similar to the left lateral kinety of the loxodids [13]. Both ends of the bristle kinety are very close together subapically at the right margin of the glabrous stripe (Figs. 29, 34, 35, 39, 41). The left branch curves around the anterior end of the stripe to its left margin, and from there to the posterior end of

Figs. 28–32. *Prototrachelocerca fasciolata,* oral and somatic infraciliature after protargol impregnation. – Fig. 28. Left lateral view of whole specimen. The glabrous stripe is bordered by the bristle kinety. Scale bar division = 100 µm. – Figs. 29, 30. Head and neck region, left and right side of same specimen. Scale bar division = 15 µm. – Fig. 31. Circumoral ciliature at high magnification. – Fig. 32. Anterior portion of two somatic kineties at high magnification. Note that the anterior dikinetids, whose nematodesmata from a distinct bundle, have only the anterior basal bodies ciliated. A = anterior secant system, B = brosse, BK = bristle kinety, Ci = cilia, CK = circumoral kineties (ciliature), GS = glabrous stripe, M = myoneme or subkinetal microtubule ribbon, N = nematodesmata, PD = postciliodesma. ▶


A
BK
GS
28
B
CK
BK
A
GS
A
A
A
29
CK
30
CK
N
31
Ci
N
M
PD
32



Figs. 33–38. *Prototrachelocerca fasciolata*, oral and somatic infraciliature after protargol impregnation. – Figs. 33, 34. Head and neck region, right and left side of specimen having 3 brosse kineties (arrows). Scale bar = 20 µm. – Fig. 35. Left side of head and neck of specimen with 2 brosse kineties. Arrow marks point where ciliation of bristle kinety is diametrically opposed. Scale bar = 20 µm. – Figs. 36, 37. Right and left side of tail. Note highly differentiated ciliature. Scale bar = 20 µm. – Fig. 38. Nuclear apparatus. Scale bar division = 100 µm. A = anterior secant system, BK = bristle kinety, CK = circumoral kineties (ciliature), N = nematodesmal bundle, OB = oral bulge.

the cell. The dikinetids of this portion of the bristle kinety have the *anterior* basal bodies ciliated, whereas the *posterior* basal bodies are ciliated in the other portion, which extends along the right stripe margin from the posterior end of the cell to the anterior end of the bristle kinety. Frequently, the dikinetids of the arched anterior portion are more irregularly and more obliquely arranged than those in the neck region. Furthermore, short, oblique kineties composed of 2–5 dikinetids occur in the trunk portion of the bristle kinety. They are irregularly and sparsely distributed and found more frequently in the right than in the left branch. Very likely, this peculiar pattern (shown only in *P. caudata* where it was better impregnated) does not result simply from the strong contraction of the cell during fixation, although the dikinetids of the bristle kinety are often more irregularly arranged in the heavily contractile trunk, because it is also found in slightly contracted specimens of *P. caudata* (Figs. 65, 66) and in *Tracheloraphis* spp., which have the whole bristle kinety composed of such minute kineties in the trunk region (Foissner & Dragesco, manuscript in preparation).

Oral infraciliature. The head, which bears the oral apparatus, is club-shaped when fully extended (Figs. 19, 21) and cylindroid when contracted (Figs. 29, 41). Usually, it is slightly or distinctly darker than the neck due to some accumulation of the ellipsoid (crystalline?) inclusions scattered in the cytoplasm (Figs. 19, 22). The anterior end of the head bears an inconspicuous, i.e. about 3 µm thick, hyaline oral bulge whose flat to slightly convex surface is pigmented by granules as found in the somatic cortex. The circumoral ciliature, details of which can be recognized only in perfectly impregnated specimens, extends around the base of the oral bulge and is interrupted where the brosse kineties are inserted. Both ends have a short tail composed of dikinetids, the left end commences near the anterior brosse kinety, the right extends subapically to the posterior brosse kinety. The main portion of the circumoral ciliature consists of small dikinetidal segments, as derived from the arrangement of the nematodesmal bundles (Fig. 31), forming two rather irregular, parallel rows of dikinetids; often, the segments are slightly obliquely arranged with ends superimposed (Figs. 29, 30, 33–35, 39–44). Very likely, the dikinetids composing the segments have only one basal body ciliated, possibly the posterior. A nematodesma originates from each dikinetid. The nematodesmata of neighbouring dikinetids unite to conspicuous bundles forming an oral basket together with the nematodesmal bundles originating from the oralized somatic dikinetids at the anterior end of the somatic kineties (Figs. 30–32, 40, 43).

The brosse is located in a distinct depression, the brosse pocket, just above the arch of the bristle kinety, which extends on the slope of the pocket, possibly explaining why Wilbert [31] interpreted the arch as brosse kinety 1. The cilia of the brosse emerge through the brosse cleft, which divides the oral bulge and the circumoral ciliature into a right and a left half. The brosse kineties are obliquely orientated, almost parallel to each other, and consist of closely spaced, sometimes zigzagging dikinetids having only the posterior basal bodies ciliated (Figs. 20, 22, 29, 34, 35, 39–41, 44). There is a conspicuous variation in the number of brosse kineties (Tab. 1). I do not believe that this is due to confusion of different species because *P. caudata* shows a similar variation and transitions were found, viz. specimens having two and a half brosse kineties, i.e. a very small anterior row consisting of 2–5 dikinetids only (Figs. 29, 86).

Redescription of Prototrachelocerca caudata (Dragesco & Raikov, 1966) nov. comb. (Table 1, Figs. 45–52, 59–94)

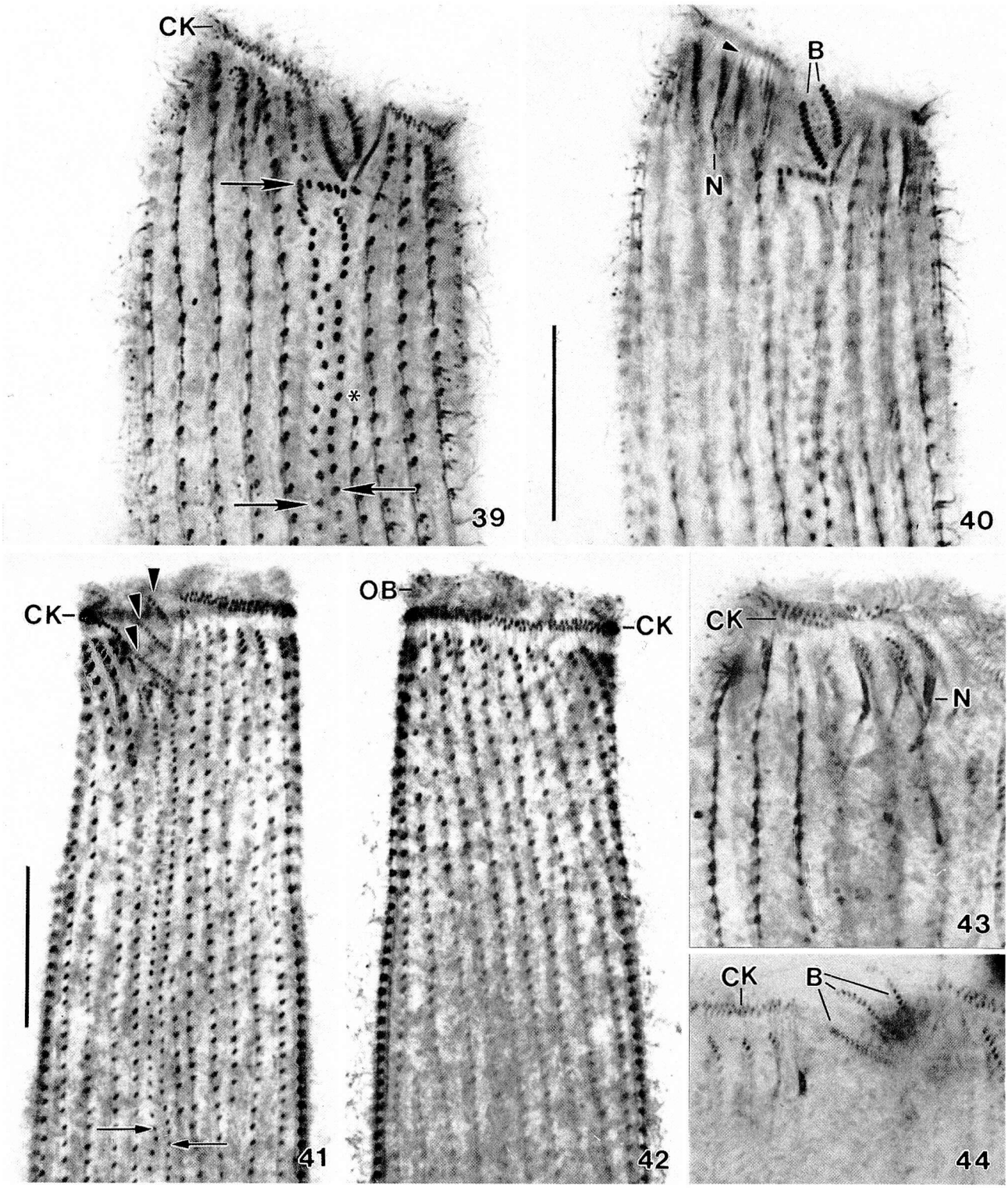
1966 *Tracheloraphis caudatus* Dragesco & Raikov, Arch. Protistenk., *109*, 105 (*Tracheloraphis caudata* nom. corr.; "raphis" has feminine gender!).

1986 *Tracheloraphis dogieli* Raikov, 1957 – Wilbert, Arch. Protistenk., *132*, 191 (misidentification).

History and identification. The species studied by Wilbert [31] occurred in the interstitial of the Red Sea near Eilat (Israel) and was, according to Wilbert (pers. comm.), identified by Raikov as *T. dogieli* in the protargol slides sent. However, *T. dogieli* is a rather broad species with nuclei individually arranged in a longitudinal strand [24, 26]. These characters are certainly not matched by Wilbert's specimens which have a slender shape (Figs. 50–52) and highly distinct nuclear rosettes, each comprising four macronuclei and two micronuclei (Figs. 61–64, 72). It is difficult to understand how Raikov, who described both species, could identify Wilbert's population as *T. dogieli*. Likewise, Wilbert's [31] description of the live cells is not based on his own observations (Figs. 50–52) but obviously on a summary of Raikov's [26] data on *T. dogieli*.

The characters recognizable in Wilbert's protargol slides and his notes on live specimens (published here for the first time, with permission) match *Tracheloraphis caudata* [7] well. This species is similar to *T. kahli* Raikov, 1962 [26] which is, however, smaller (600–1000 µm), has fewer ciliary rows (22–25), and more than four macronuclei per nuclear group. Another similar species is *Tracheloraphis angustivittata* Borror, 1963 [1] which has 67–100 ciliary rows, a very narrow (4 µm) glabrous stripe, and 28–78 ($\bar{x}$ 55, n = 8) irregularly distributed nuclear rosettes each comprising, as in *P. caudata*, four macronuclei and two micronuclei. However, *Tracheloraphis angustivittata* very likely belongs to *Prototrachelocerca* because Borror [1] states: "Anterior cilia extremely closely set in more than 60 radially arranged rows, and beat anteriorly (Fig. 54)". It is thus combined with the new genus: *Prototrachelocerca angustivittata* (Borror, 1963) nov. comb. (basionym: *Tracheloraphis angustivittatus* Borror, 1963; *T. angustivittata* nom. corr.).

Specimens investigated and type material. My description is based on Wilbert's notes on live cells (see



Figs. 39–44. *Prototrachelocerca fasciolata*, oral and somatic infraciliature after protargol impregnation. – Figs. 39, 40. Anterior region of left side at different focus level. This specimen has 2 brosse kineties, which are in the brosse pocket and thus out of focus when the anterior arch of the bristle kinety (arrows) is bought into focus. Arrowhead denotes nematodesmata originating from circumoral kinetids; asterisk marks first shortened somatic kinety of anterior secant system. – Figs. 41, 42. Left and right side of head and neck of specimen having 3 brosse kineties (arrowheads). Arrows mark bristle kinety bordering glabrous stripe, which is very narrow in this region. – Figs. 43, 44. Right and left side of head of squashed specimen with 3 brosse kineties. The circumoral ciliature consists of 2 rows of rather irregularly arranged dikinetids. B = brosse, CK = circumoral kineties (ciliature), N = nematodesmal bundles originating from anterior end of somatic kineties, OB = oral bulge. Scale bars = 20 μm.

above) and especially on his protargol slides, which contain about 50 specimens, 15 of which are excellently impregnated.

Dragesco & Raikov [7] did not mention any type material of *T. caudata*. Thus, I deposit, with permission, Wilbert's 3 protargol slides as neotypes in the Oberösterreichische Landesmuseum in Linz (LI). Relevant specimens are marked by a black ink circle on the cover glass.

Description of Wilbert's population. Length in vivo 800–1500 µm. Head, neck, tail and glabrous stripe brighter than darkly granulated trunk. Head conical and thus rather distinctly set off from neck; posterior third gradually narrowed and thus indistinctly separate from trunk, distal end of tail pointed. Cytoplasm with large food vacuoles and some fat globules (Figs. 50–52).

The structural and most morphometrical characteristics of *P. caudata* are rather similar to those of *P. fasciolata*. Thus, I restrict the description to features differing from those of that species and refer the reader to the figures, the morphometric characterization (Tab. 1), and the description of *P. fasciolata* for further details.

The macronuclei of *P. caudata* are about half the size of those of *P. fasciolata* and form highly characteristic rosettes, each usually comprising four macronuclei and two micronuclei (Figs. 63, 64, 72). The number of nuclei and rosettes is highly variable (Tab. 1), as also noted by Dragesco & Raikov [7]; they form a single strand in specimens with few nuclei (Fig. 63) and two more or less distinct rows in cells having many nuclei (Fig. 61). Intermediate configurations are common (Fig. 60), indicating that the variability is not caused by confusion of different species. This is supported by the lack of a directed variation in the infraciliature. For instance, specimens with 2, respectively, 3 brosse kineties occur in cells with few and many nuclei.

The glabrous zone of *P. caudata* is slightly narrower than that of *P. fasciolata* and corresponds to an area occupied by 4–7 kineties (Figs. 60, 67, 69, 70). All trunk kineties have both basal bodies ciliated, whereas the posterior cilium is lacking in the secant kineties of *P. fasciolata*. Furthermore, Wilbert's excellent slides show another peculiarity, seen also in *P. fasciolata*, very clearly, viz. that in the tail region the right branch of the bristle kinety has the posterior basal bodies of the dikinetids ciliated, in contrast to the dikinetids of the abutting somatic ciliary rows (posterior secant system), which have the anterior basal bodies ciliated (Figs. 93, 94). Thus, the bristle kinety is very likely not composed of segments from the ends of the somatic kineties, as it often appears, especially in the anterior secant system (Fig. 67).

The oral bulge of *P. caudata* is more distinct than that of *P. fasciolata* and higher on the right than on the left side of the cell (Figs. 76, 81, 91). The circumoral ciliature usually consists of 3 rather irregular rows of dikinetids, in contrast to the 2 rows present in *P. fasciolata*. One often gets the impression, as in *P. fasciolata*, that it is composed of many short, superimposed segments or, more rarely and as figured by Wilbert [31], of numerous minute, oblique radial rows (Figs. 76, 77, 79, 82, 83, 86, 87, 90, 91). The brosse pocket of *P. caudata* is deeper than that of *P. fasciolata* and contains 2–3, usually 2 brosse kineties, in contrast to *P. fasciolata*, which usually has 3 brosse kineties (Figs. 73, 76–78, 80, 82, 88, 89). Intermediate specimens having 2 long rows and 1 very short row have been found, indicating true variability (Figs. 86, 91). Note that brosse kinety 1 in Wilbert's [31] Figure 1 is the anterior arch of the bristle kinety.

Discussion

Prototrachelocerca as a New Genus and Family

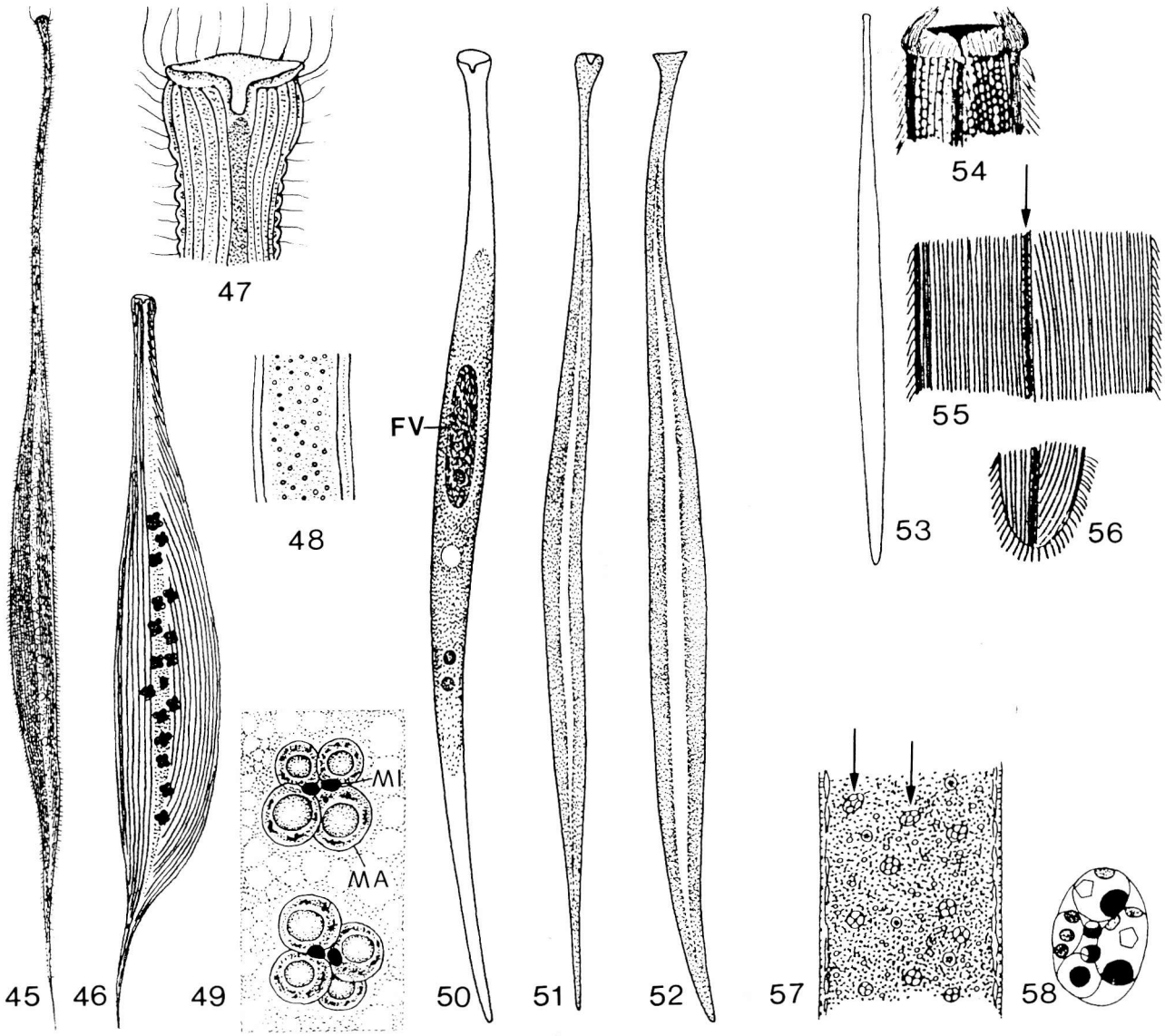
Foissner & Dragesco [14] reviewed the systematics of trachelocercid ciliates and based genus distinction on peculiarities of the somatic and oral infraciliature. *Prototrachelocerca* is unique in having a (compound) circumoral ciliature composed of several rows of dikinetids. All other known trachelocercids possess a (simple) circumoral kinety consisting of a single row of closely spaced dikinetids. The compound circumoral ciliature justifies separation at least at genus level.

The foundation of a new family for *Prototrachelocerca* might be questioned. It is partially based on evolutionary considerations. Foissner & Dragesco [14] suggested that trachelocercids and loxodids are sister groups, i.e. have a common ancestor, because they possess the same unique structure of the bristle kinety. Furthermore, loxodids have, like *Prototrachelocerca*, some sort of compound paroral ciliature, i.e. the paroral is associated with a kinety composed of oralized somatic kinetids [12, 13]. It is thus reasonable to consider the compound circumoral (paroral) ciliature of *Prototrachelocerca* as an ancient feature common to the mutual ancestor of both loxodids and trachelocercids. At first glance, this is contradicted by the complex brosse: *Trachelocerca*, which lacks a brosse, has a simple circumoral kinety [8, and unpubl. results by Foissner & Dragesco], i.e. appears less complexly organized than *Prototrachelocerca*. However, many members of this genus have the nuclei united to complex capsules, which is considered as a derived character [25]. It may thus be speculated that *Trachelocerca* lost the brosse and is the most highly evolved member of the family.

Admittedly, these are rather daring speculations which need to be proved by morphogenetic studies, which are unfortunately lacking.

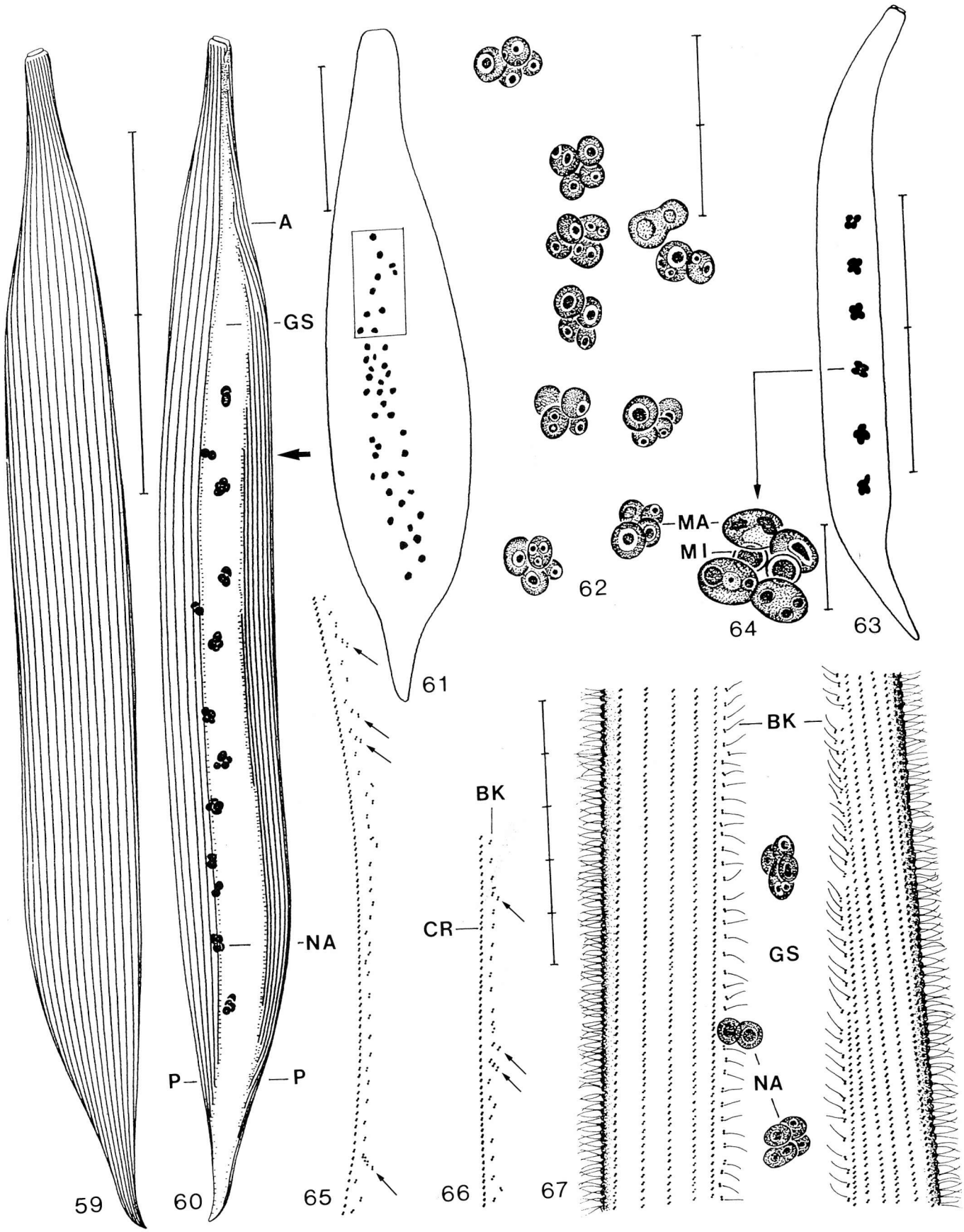
Rationale of Identifications Proposed

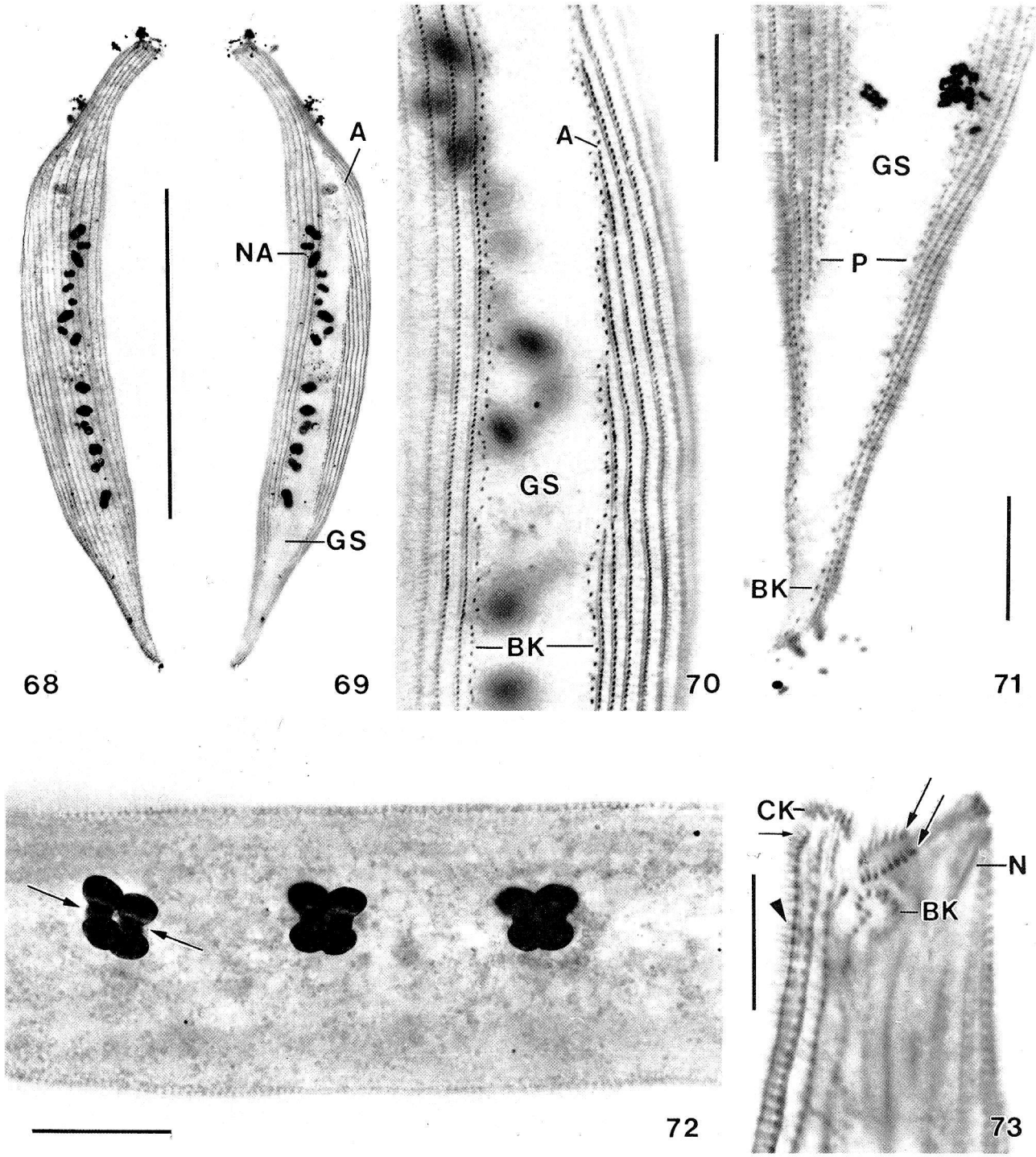
About 70 trachelocercids have been described [2]. Unfortunately, many of them are obviously poorly defined. For instance, not a single species has been adequately analyzed morphometrically. Thus, variability



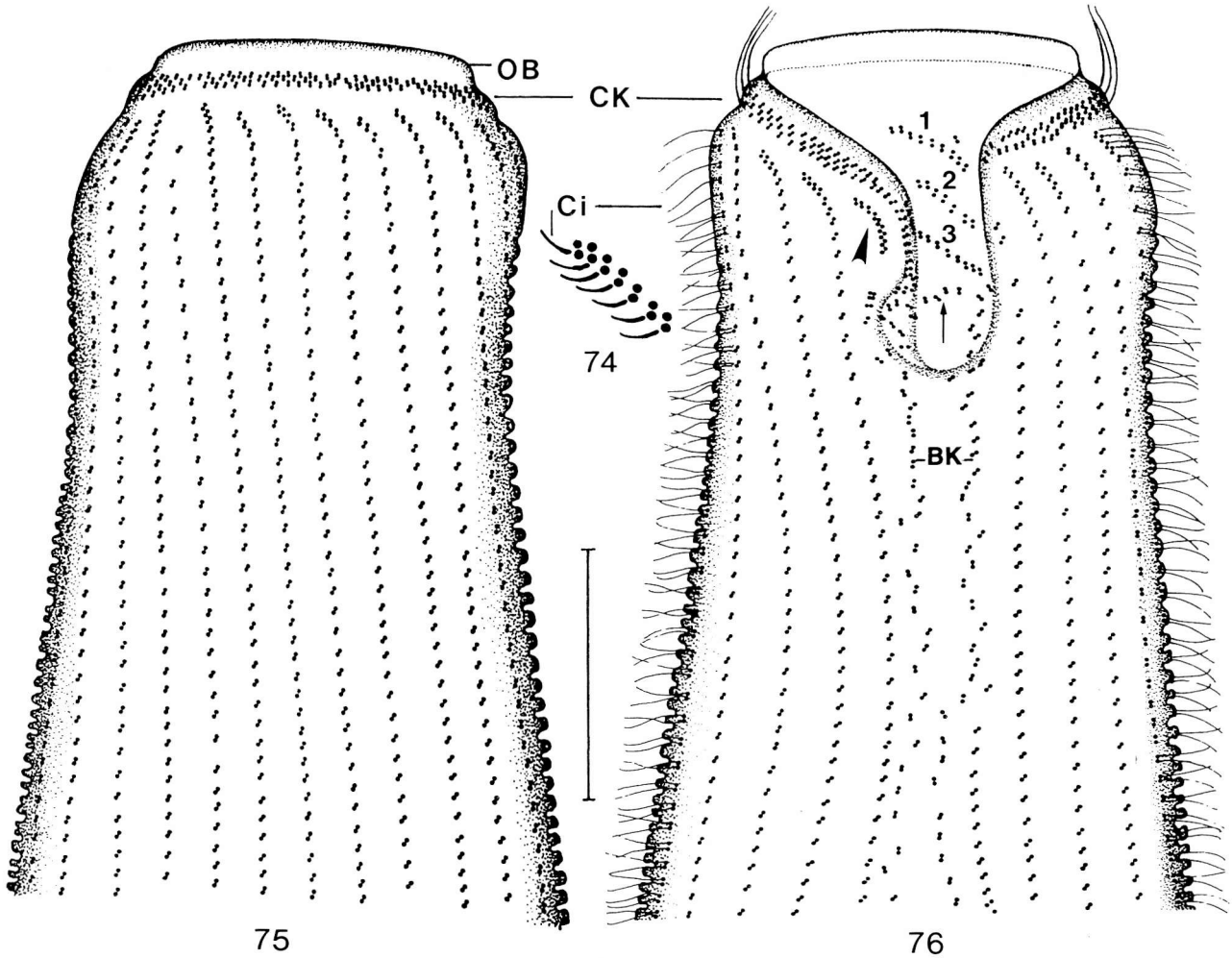
Figs. 45–52. Synonymy of *Prototrachelocerca caudata*. – Figs. 45–49. *Tracheloraphis caudata* (from [7]). – Fig. 45. General view from life, length 1000–2500 µm; Fig. 46. Schematic figure showing arrangement of ciliary rows and nuclear rosettes after protargol impregnation; Fig. 47. Left side of head in vivo; Fig. 48. Interkinetal protrichocysts in vivo; Fig. 49. Two nuclear rosettes, Feulgen stain. – Figs. 50–52. *Tracheloraphis* sp., redrawn from drafts made by Wilbert from live specimens (see text), length 800–1500 µm. FV = large food inclusion, MA = macronucleus, MI = micronucleus.
Figs. 53–58. *Tracheloraphis angustivittata*, method(s) not indicated (from [1]). – Fig. 53. Body shape, length 1500 µm. – Fig. 54. Left side of head. – Fig. 55. Left side of middle trunk region, width 80 µm. Note narrow glabrous stripe (arrow). – Fig. 56. Left side of posterior end. – Fig. 57. Optical section in trunk region, width 80 µm. Note numerous nuclear vesicles (arrows) and dense endoplasmic granulation. – Fig. 58. Nuclear vesicle, 11 × 8 µm, containing 4 macronuclei and 2 micronuclei.

Figs. 59–67. *Prototrachelocerca caudata*, somatic infraciliature and nuclear apparatus after protargol impregnation. – Figs. 59, 60. Somatic infraciliature of right and left side and nuclear apparatus of typical specimen. Arrow marks region shown at higher magnification in Fig. 67. – Figs. 61, 62. Specimen with many nuclear rosettes arranged in two indistinct rows. Framed area of Fig. 61 is shown at higher magnification in Fig. 62. – Figs. 63, 64. Specimen with few nuclear rosettes. Usually, a rosette comprises 4 macronuclei and 2 micronuclei (Fig. 64). – Figs. 65, 66. Details from right branch of trunk bristle kinety of two specimens. Arrows denote short, oblique kineties scattered within bristle kinety. – Fig. 67. Left side of anterior trunk region (cp. Fig. 60). Note that the dikinetids in the right branch of the bristle kinety have the posterior basal bodies ciliated, whereas the anterior ones are ciliated in the left branch. A = anterior secant system, BK = bristle kinety; CR = somatic ciliary row, GS = glabrous stripe, MA = macronuclei, MI = micronuclei, NA = nuclear apparatus, P = posterior secant system. Scale bar division 100 µm (Figs. 59–61, 63) and 10 µm (Figs. 62, 64, 67). ▶


A
GS
NA
P
P
MA
MI
BK
CR
BK
GS
NA
59
60
61
62
63
64
65
66
67



Figs. 68–73. *Prototrachelocerca caudata*, somatic and oral infraciliature and nuclear apparatus after protargol impregnation. – Figs. 68, 69. Infraciliature of right and left side of typical specimen. – Figs. 70, 71. Details from Fig. 69, showing trunk and tail infraciliature at higher magnification. – Fig. 72. *P. caudata* has highly characteristic nuclear rosettes each consisting of 4 macronuclei and 2 micronuclei (arrows). – Fig. 73. Left side of head from specimen having 2 brosse kineties (large arrows). Small arrow marks single cilia at anterior end of somatic kineties, arrowhead denotes paired cilia beyond. A = anterior secant system, BK = bristle kinety, CK = circumoral kineties (ciliature), GS = glabrous stripe, N = nematodesmal bundle, NA = nuclear apparatus, P = posterior secant system. Scale bars 200 μm (Figs. 68, 69) and 20 μm (Figs. 70–73).



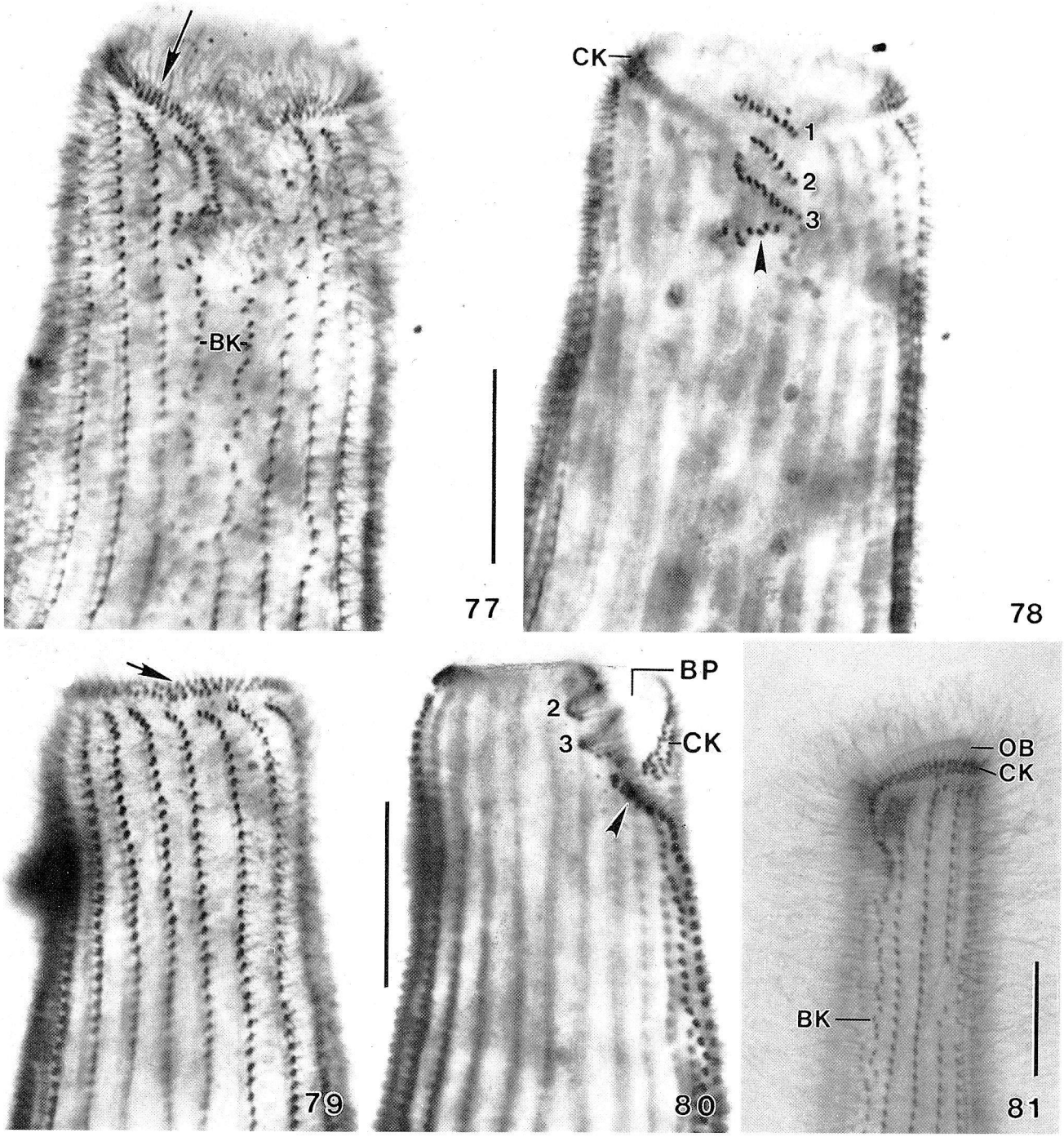
Figs. 74–76. *Prototrachelocerca caudata*, oral infraciliature after protargol impregnation. These drawings are from the type specimen shown in Wilbert's [31] Figure 1. – Fig. 74. The brosse kineties, here shown for kinety 2, have only the posterior basal bodies of the dikinetids ciliated. – Figs. 75, 76. Right and left side of head and neck. Numbers denote brosse kineties. Note that Wilbert's brosse kinety 1 is the anterior arch of the bristle kinety (arrow). Arrowhead marks small kinety fragment frequently found on right lip of oral bulge. BK = bristle kinety, Ci = cilia, CK = circumoral ciliature (kineties), OB = oral bulge. Scale bar = 20 μm.

is almost unknown and it would have been easy to describe the two forms investigated as new species. This is, however, not the philosophy I recommend – in agreement with views often expressed by Corliss [3, and references therein] – because it is senseless and injures the reputation of taxonomy in general to create one new species after the other without considering previous literature. Rather, I suggest that species be identified with poorly described ones if they match in at least one main character or, if appropriate, to reinterprete such characters [14]. This should create some stability, if forthcoming workers accept such identifications as "authoritative redescription" (see, e.g. [11]).

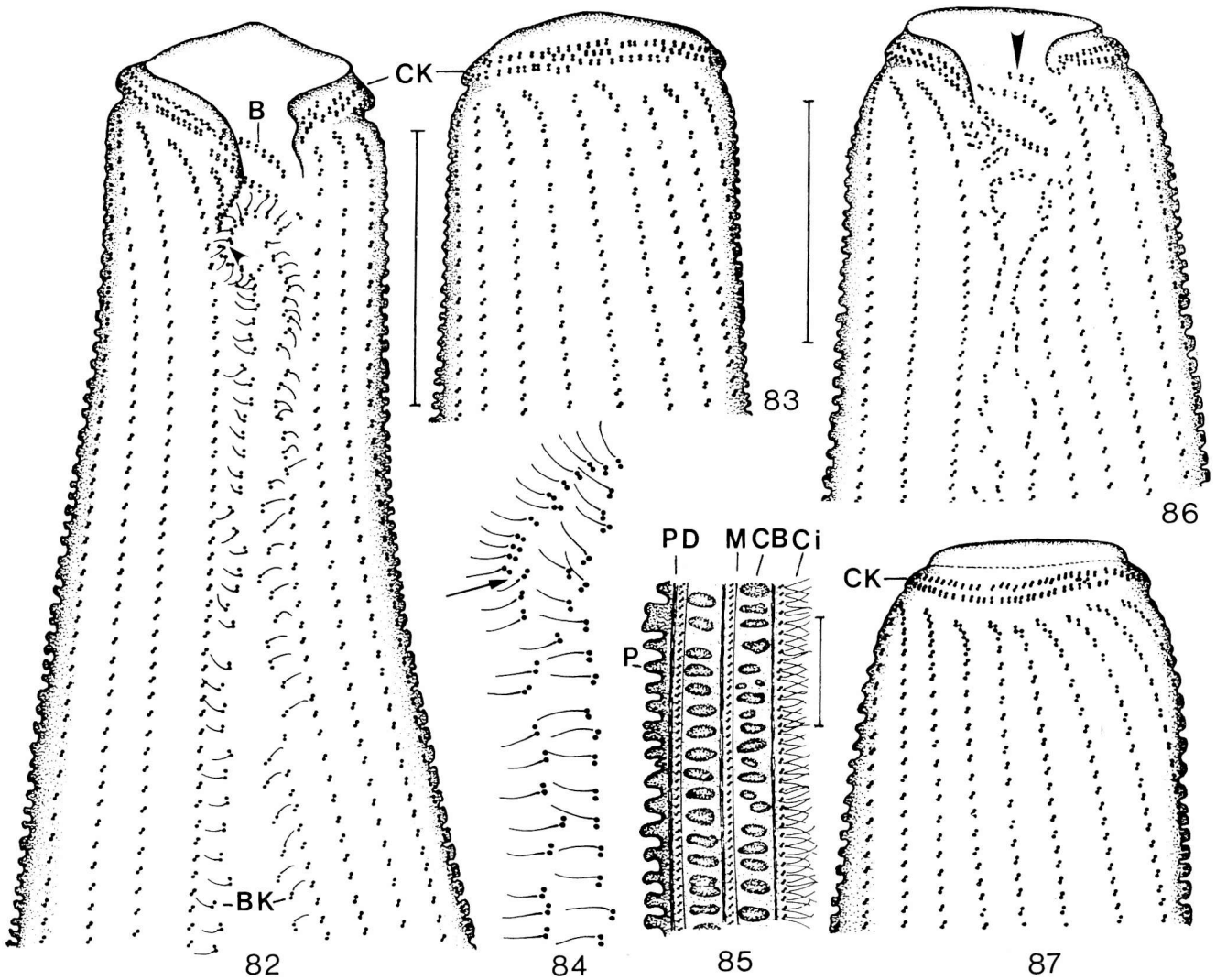
Furthermore, species and genus nomenclature, which is in poor condition in most protozoan groups, must be greatly improved if stability is to be attained. The international code of zoological nomenclature [16] has to be followed strictly, even if this sometimes requires saying good-bye to names and practices which we have grown accustomed to [12].

Acknowledgements

Supported by a grant from the University of Salzburg. I would like to thank Prof. Dr. André Toulmond, director of the Station Biologique de Roscoff (France), for providing working facilities, and Dr. Remigius Geiser (Salzburg) for advice on nomenclature. I am also deeply indebted to Prof. Dr. Jean Dragesco (Saint-Clément-de-Rivière, France), who stimulated this research, showed me how to collect sand ciliates, and helped with laboratory organization. The technical assistance of Dr. Eva Herzog and Mag. Eric Strobl is greatly ap-



Figs. 77–81. *Prototrachelocerca caudata*, oral infraciliature after protargol impregnation. – Figs. 77, 78. Left side of head and neck (at different focus level) of type specimen (cp. Figs. 74–76) shown in Wilbert's [31] Figures 2a, b. Arrow in Fig. 77 denotes the circumoral ciliature which, depending on the interpretation, consists of numerous small, oblique kineties, of many oblique kinety fragments, or of 3 superimposed circular rows of dikinetids (see also Fig. 79). The brosse and the anterior arch of the bristle kinety (arrowhead) are in a deep pocket (cp. Fig. 80). – Figs. 79, 80. Lateral view of head at different focus level. Arrow marks circumoral ciliature (cp. Fig. 77), arrowhead denotes anterior arch of bristle kinety which extends onto slope of brosse pocket. – Fig. 81. A darkly copied specimen to show prominent oral bulge, the base of which is surrounded by the circumoral ciliature. BK = bristle kinety, BP = brosse pocket CK = circumoral ciliature, OB = oral bulge. Numbers denote brosse kineties. Scale bars = 20 μm.



Figs. 82–87. *Prototrachelocerca caudata*, variability of somatic and oral infraciliature after protargol impregnation. – Figs. 82, 83. Left and right side of head and neck of specimen having 2 brosse kineties. Arrowhead marks point where ends of bristle kinety meet (cp. Fig. 84). – Fig. 84. Anterior portion of bristle kinety. The right branch has the posterior basal bodies of the dikinetids ciliated, whereas the anterior and left branch have the anterior basal bodies ciliated. Arrow marks "transition point", where ends of kinety meet. – Fig. 85. Somatic infraciliature. – Figs. 86, 87. Left and right side of head of specimen having 2.5 brosse kineties, i.e. with a very short brosse kinety 1 (arrowhead). The circumoral ciliature consists of 2 rather regular rows of dikinetids. B = brosse, BK = bristle kinety, CB = cortical blisters caused by contraction of cell, Ci = cilia, CK = circumoral kineties (ciliature), M = myoneme or subkinetal microtubule ribbon, P = side view of cortical blisters PD = postciliodesma. Scale bars = 20 μm (Figs. 82, 83, 86, 87) and 10 μm (Fig. 85).

preciated. Finally, my deep gratitude and respect to Dr. Norbert Wilbert (Bonn University) for the permission to re-evaluate his outstanding protargol slides of *P. caudata*.

References

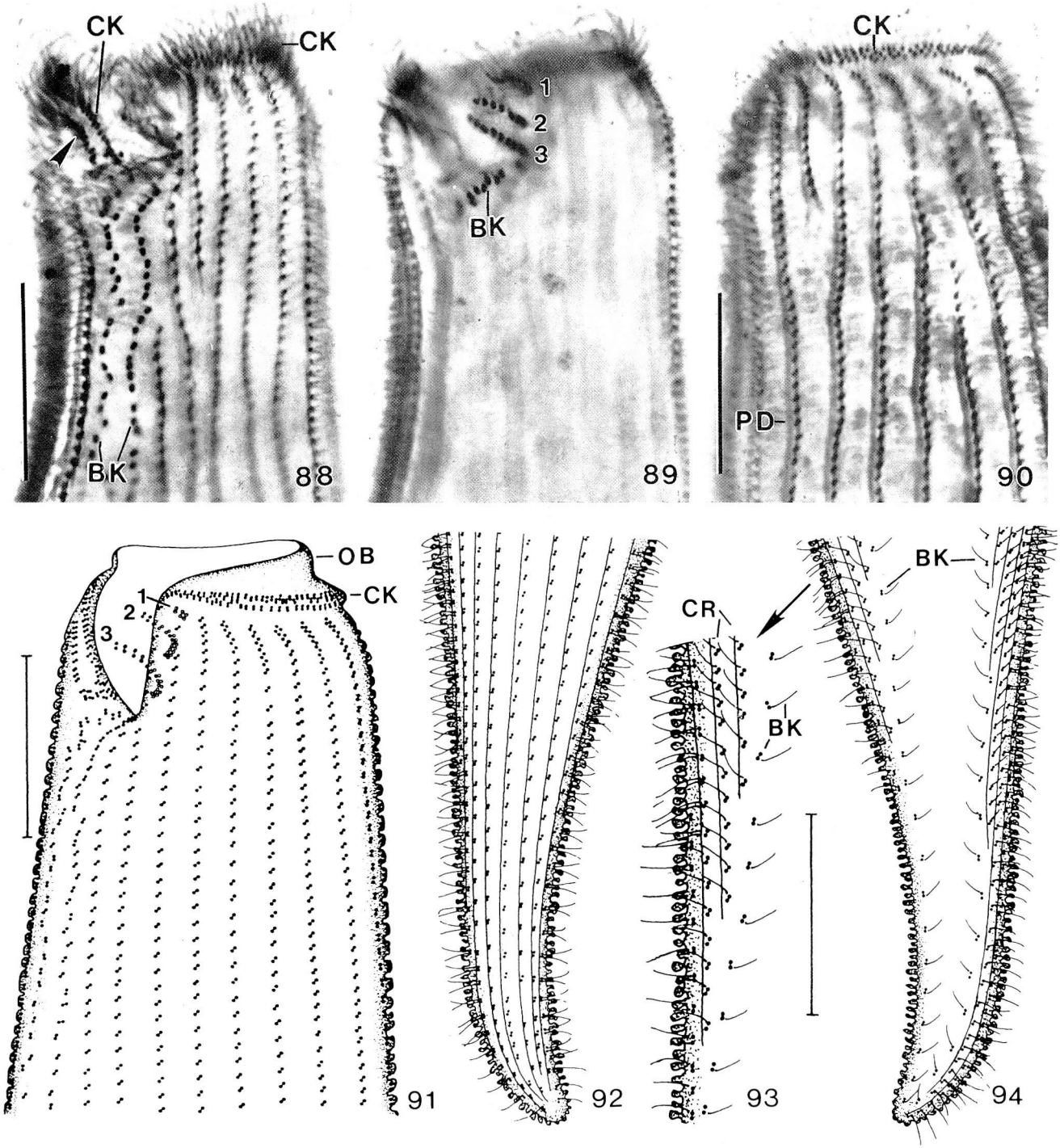
1 Borror A. C. (1963): Morphology and ecology of the benthic ciliated protozoa of Alligator Harbor, Florida. Arch. Protistenk., *106*, 465–534.

2 Carey P. G. (1992): Marine interstitial ciliates. Chapman & Hall, London, New York, Tokyo, Melbourne, Madras.

3 Corliss J. O. (1979): The ciliated protozoa. Characterization, classification, and guide to the literature. 2nd ed. Pergamon Press, Oxford.

4 Dragesco J. (1960): Ciliés mésopsammiques littoraux. Systématique, morphologie, écologie. Trav. Stn Biol. Roscoff (N.S.),*12*, 1–356.

5 Dragesco J. (1963): Compléments a la connaissance de ciliés mésopsammiques de Roscoff. I. Holotriches, II. Hétérotriches. Cah. Biol. mar., *4*, 91–119 and 251–275.



Figs. 88–94. *Prototrachelocerca caudata*, oral and somatic infraciliature after protargol impregnation. – Figs. 88, 89. Left side of head at different focus level. Arrowhead marks kinety fragment on right lip of oral bulge. – Fig. 90. Right side of head with circumoral ciliature seemingly composed of many short, oblique rows. – Fig. 91. Lateral view of head from specimen with minute brosse kinety 1. The brosse kineties insert in a distinct pocket. – Figs. 92–94. Right and left side of tail. Figure 93 is an enlarged portion of Fig. 94 and shows that the right branch of the bristle kinety has the posterior basal bodies of the dikinetids ciliated, whereas the dikinetids of the abutting somatic ciliary rows (posterior secant system) have the anterior basal bodies ciliated. Thus, the bristle kinety is very likely not composed of segments from the ends of the somatic kineties. BK = bristle kinety, CK = circumoral kineties (ciliature), CR = somatic ciliary rows, OB = oral bulge, PD = postciliodesma. Numbers denote brosse kineties. Scale bars = 20 μm.

6 Dragesco J. et Dragesco-Kernéis A. (1986): Ciliés libres de l'Afrique intertropicale. Faune tropicale, *26*, 1–559.
7 Dragesco J. et Raikov I. (1966): L'appareil nucléaire, la division et quelques stades de la conjugaison de *Trachelo-raphis margaritatus* (Kahl) et *T. caudatus* sp. nov. (Ciliata, Holotricha). Arch. Protistenk., *109*, 99–113.
8 Epstein S. S. (1994): A new marine interstitial ciliate from the Northwest Atlantic coast *Tracheloraphis primitarum* sp. n. (Ciliophora, Kinetofragminophora, Karyorelictida, Trachelocercidae). J. Euk. Microbiol.,*41*, 500–503.
9 Fauré-Fremiet E. (1951): The marine sand-dwelling ciliates of Cape Cod. Biol. Bull. mar. biol. Lab., Woods Hole, *100*, 59–70.
10 Foissner W. (1991): Basic light and scanning electron microscopic methods for taxonomic studies of ciliated protozoa. Europ. J. Protistol., *27*, 313–330.
11 Foissner W. (1993): Colpodea (Ciliophora). Protozoenfauna,*4/1*, I–X, 1–789.
12 Foissner W. (1995a): A redescription of *Remanella multinucleata* (Kahl, 1933) nov. gen., nov. comb. (Ciliophora, Karyorelictea), emphasizing the infraciliature and extrusomes. Europ. J. Protistol. *32*, 234–250.
13 Foissner W. (1995b): The infraciliature of *Cryptopharynx setigerus* Kahl, 1928 and *Apocryptopharynx hippocampoides* nov. gen., nov. spec. (Ciliophora, Karyorelictea), with an account on evolution in loxodid ciliates. Arch. Protistenk., *146*, 309–327.
14 Foissner W. and Dragesco J. (1996): Updating the trachelocercids (Ciliophora, Karyorelictea). I. A detailed description of the infraciliature of *Trachelolophos gigas* n. g., n. sp. and *T. filum* (Dragesco and Dragesco-Kernéis, 1986) n. comb. J. Euk. Microbiol., *43*, 12–25.
15 Foissner W. and Foissner I. (1988): The fine structure of *Fuscheria terricola* Berger et al., 1983 and a proposed new classification of the subclass Haptoria Corliss, 1974 (Ciliophora, Litostomatea). Arch. Protistenk., *135*, 213–235.
16 International Commission on Zoological Nomenclature (1985): International code of zoological nomenclature. 3rd ed. Univ. California Press, Berkeley & Los Angeles.
17 Jankowski A. W. (1975): A conspectus of the new system of subphylum Ciliophora Doflein, 1901 (in Russian). In: Balashov, U. S. (ed.): Account of scientific sessions on results of scientific work, year 1974: Abstracts of reports, pp. 26–27. Trudy zool. Inst., Leningrad.
18 Jankowski A. W. (1978): New higher taxa of ciliated protozoa (Ciliophora). Tezisy Dokl. Zool. Inst. Akad. Nauk SSSR, year 1978, 88–90 (in Russian).
19 Kahl A. (1930): Urtiere oder Protozoa I: Wimpertiere oder Ciliata (Infusoria) 1. Allgemeiner Teil und Prostomata. Tierwelt Dtl., *18*, 1–180.
20 Kahl A. (1935): Urtiere oder Protozoa I: Wimpertiere oder Ciliata (Infusoria) 4. Peritricha und Chonotricha. Tierwelt Dtl., *30*, 651–886.
21 Kent W. S. (1880–1882): A manual of the infusoria: including a description of all known flagellate, ciliate, and tentaculiferous Protozoa British and foreign, and an account of the organization and affinities of the sponges. Vols. I–III. David Bogue, London (Vol. I 1880: 1–432; Vol. II 1881: 433–720, 1882: 721–913; Vol. III 1882: Plates).
22 Kiesselbach A. (1936): Zur Ciliatenfauna der nördlichen Adria. Thalassia, *2*, 1–53.
23 Puytorac P. de (1994): Classe des Karyorelictea Corliss, 1974. Traité de Zoologie, *2(2)*, 21–34.
24 Raikov I. B. (1957): Nuclear apparatus and its reorganization during the fission cycle in the infusoria *Trachelocerca margaritata* (Kahl) and *T. dogieli*, sp. n. (Holotricha). Zool. Zh., *36*, 344–359 (in Russian with English summary).
25 Raikov I. B. (1958): Der Formwechsel des Kernapparates einiger niederer Ciliaten. I. Die Gattung *Trachelocerca*. Arch. Protistenk.,*103*, 129–192.
26 Raikov I. B. (1962): Les ciliés mésopsammiques du littoral de la Mer Blanche (U.R.S.S.) avec une description de quelques espèces nouvelles ou peu connues. Cah. Biol. mar., *3*, 325–361.
27 Raikov I. B. and Kovaleva V. G. (1968): Complements to the fauna of psammobiotic ciliates of the Japan Sea (Posjet gulf). Acta Protozool.,*6*, 309–333.
28 Raikov I. B., Gerassimova-Matvejeva Z. P., and Puytorac P. de (1975): Cytoplasmic fine structure of the marine psammobiotic ciliate*Tracheloraphis dogieli* Raikov. I. Somatic infraciliature and cortical organelles. Acta Protozool., *14*, 17–42.
29 Sauerbrey E. (1928): Beobachtungen über einige neue oder wenig bekannte marine Ciliaten. Arch. Protistenk., *62*, 355–407.
30 Small E. B. and Lynn D. H. (1985): Phylum Ciliophora. In: Lee J. J., Hutner S. J. and Bovee E. C. (eds.): Illustrated guide to the protozoa, pp. 393–575. Allen Press, Lawrence, Kansas.
31 Wilbert N. (1986): Die orale Infraciliatur von *Tracheloraphis dogieli* Raikov, 1957 (Ciliophora, Gymnostomata, Karyorelictida). Arch. Protistenk., *132*, 191–195.

Key words: Infraciliature – Evolution –*Prototrachelocerca* nov. gen. – Prototrachelocercidae nov. fam. – Trachelocercida

Wilhelm Foissner, Universität Salzburg, Institut für Zoologie, Hellbrunnerstrasse 34, A-5020 Salzburg, Austria