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Updating the Trachelocercids (Ciliophora, Karyorelictea). III. Redefinition of the Genera *Trachelocerca* EHRENBERG and *Tracheloraphis* DRAGESCO, and Evolution in Trachelocercid Ciliates

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Summary: The morphology and infraciliature of *Trachelocerca sagitta* (MÜLLER, 1786) EHRENBERG, 1840, *T. ditis* (WRIGHT, 1982) nov. comb., *Tracheloraphis phoenicopterus* (COHN, 1866) DRAGESCO, 1960, *T. aragoi* (DRAGESCO, 1954) DRAGESCO, 1960, *T. longicollis* (DRAGESCO, 1960) nov. comb., and *T. oligostriata* (RAIKOV, 1962) nov. comb. were studied in live and protargol impregnated specimens, as well as with the scanning electron microscope. Neotype slides with protargol impregnated specimens of each species have been deposited in (LI). The somatic and oral infraciliature of the species investigated basically agrees with that of *Trachelolophos* and *Prototrachelocerca.* Specifically, all have a glabrous stripe bordered by a peculiar (bristle) kinety composed of dikinetids having a unique ciliation and fibrillar system. Furthermore, all trachelocercids have specialized structures at the anterior end of the body, highly reminiscent of a prostome and/or gymnostome oral apparatus. Some of the species investigated represent the types of the genera *Trachelocerca* EHRENBERG, 1840 *(T. sagitta)*, *Tracheloraphis* DRAGESCO, 1960 *(T. phoenicopterus)*, and *Trachelonema* DRAGESCO, 1960 *(T. longicollis)*, three taxa often confused due to the vague original diagnoses. Our study provides accurate characteristics for distinguishing *Tracheloraphis* (with brosse) from *Trachelocerca* (without brosse), while the genus *Trachelonema* is synonymized with *Tracheloraphis* because of distinct similarities in the infraciliatures of the type species. Accordingly, three well-defined genera are recognized in the family Trachelocercidae KENT, 1881: *Trachelocerca* EHRENBERG, 1840, *Tracheloraphis* DRAGESCO, 1960, and *Trachelolophos* FOISSNER & DRAGESCO, 1996. The order Trachelocercida JANKOWSKI, 1978 is redefined using the glabrous stripe, the bristle kinety, and the apical location of the oral apparatus as unique character constellation. HENNIG's cladistic method suggests that the Trachelocercidae evolved from the Prototrachelocercidae and both have a common ancestor with the Loxodida. Some minor taxonomic changes (new combinations) and many nomenclatural emendations have been made.

Key Words: Evolution; Infraciliature; Taxonomy; *Trachelocerca* spp.; Trachelocercida; *Trachelonema* spp.; *Tracheloraphis* spp.

Introduction

Trachelocercid ciliates are very common in marine littoral sands. It is thus not surprising that the first species was described more than 200 years ago by one of the early scientific microscopists, the Danish zoologist OTTO FRIEDRICH MÜLLER (1786). Later, his *Vibrio sagitta* was made type of a new genus, *Trachelocerca,* by another giant, CHRISTIAN GOTTFRIED EHRENBERG (1840). The next 100 years brought little progress

although some new species were described, often, however, very incompletely and confusingly, still posing difficult taxonomic and nomenclatural problems (KAHL 1930, 1935). It was only in the sixties that DRAGESCO (1960, 1963) and RAIKOV (1958, 1969) published some fundamental studies showing not only that the diversity of trachelocercids was greatly underestimated by previous workers but also their particular nuclear structure, i.e. that they have non-dividing, diploid macronuclei generated by the micronuclei. This prompted CORLISS (1974) to establish a new order, Karyorelictida, which is now widely recognized (PUYTORAC 1994; SMALL & LYNN 1985).

The generic classification of trachelocercid karyorelictids was less successful and is still bewildering. Following a note from KAHL (1933), DELPHY (1939) split them into four genera, viz. *Trachelocerca* (distal end of tail curved), *Gruvelina* (whole tail extends in main body axis), *Nephrocerca* (with contractile vacuole), and *Protrichophora* (with mucocysts). Later, DRAGESCO (1960) split the trachelocercids again using, however, the absence (*Trachelocerca*) /presence (*Tracheloraphis*, *Trachelonema*) of a glabrous stripe and its relative width as sole characteristics. However, it soon becomes evident that the characters used by DELPHY (1939) and DRAGESCO (1960) are of very limited value because many transitions were found.

Later students did not improve the situation, but simply followed DRAGESCO's view and moved species from one genus to the other. Even when the first detailed studies on the infraciliature of some representative trachelocercids become available, concomitantly published by DRAGESCO & DRAGESCO-KERNÉIS (1986) and WILBERT (1986), the situation did not change. Thus, we commenced a project in 1994 to revise the entire group by reinvestigating the type species. This was, however, more complicated and time consuming than we had assumed because two new genera, which had to be published first (FOISSNER 1996a; FOISSNER & DRAGESCO 1996), were discovered and many taxonomic and nomenclatural problems delayed the work.

The present study, the third in the series, attempts to solve all the problems relating to the generic classification of the trachelocercids s. str., i.e. the genera *Trachelocerca*, *Tracheloraphis* and *Trachelonema*. To achieve this goal, we carefully redescribe the type species and related taxa, improve the generic diagnoses, fix neotypes, and correct the numerous nomenclatural mistakes that have accumulated over the years.

Finally, some comment is necessary regarding the presentation of the results because several reviewers of previous papers by the junior author complained that the descriptions were too detailed and the illustrations too numerous. Certainly, this would seemingly apply also to the present paper. However, we rigorously defend this style of description because it prevents the same species either being redescribed a few years later or even being described as a new species because the data were insufficient for a reliable identification. Many examples can be found in the literature; in fact, most synonymies are not caused by insufficient knowledge of the literature but by insufficient original descriptions! Thus, a description can hardly be too detailed.

Materials and Methods, Terminology

Trachelocerca sagitta, *T. ditis*, *Tracheloraphis phoenicopterus*, and *T. longicollis* were found in the mesopsammon, i.e. in the upper 0–4 cm sand layer, of the French Atlantic coast at Roscoff (W 4°, N 48°50′). *Tracheloraphis aragoi* and *T. oligostriata* occurred in the mesopsammon of the French Mediterranean coast (Gulf of Lions) at Sète (E 3°, N 43′), a small town about 140 km west of Marseille.

Samples were collected and treated as described by FAURÉ-FREMIET (1951). The upper 0–4 cm sand layer of shallow pools was taken with a small shovel during the tide, put into a 1 litre jar, and was allowed to settle for at least 24 hours. During this time many trachelocercids and other ciliates move upwards and enrich in the upper 1 cm of sand. About 20 ml sand and sea water from this layer were collected with a large-bore (5 mm) pipette and mixed with about 5 ml of a 12 % $MgCl_2$ solution to detach the ciliates. The mixture was then gently rotated in a Petri dish so that the sand collected in the centre and the detached 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 and bright-field or differential interference contrast (FOISSNER 1991). The infraciliature was revealed by protargol impregnation [FOISSNER 1991; protocol B (WILBERT's method)], using the fixative described by FOISSNER & DRAGESCO (1996): 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. This fixative preserves all karyorelictids very well, but does not prevent contraction in contractile species. Specimens were fixed for 10–15 min and washed three times in distilled water. The nuclear apparatus and the cortical granules of some species were also studied in transient preparations stained with methyl green-pyronin (FOISSNER 1991). Specimens for scanning electron microscopy were prepared as described in FOISSNER (1991) using the fixative mentioned above.

Counts and measurements on silvered specimens were performed at a magnification of X 1,000. In vivo measurements were conducted at a magnification of X 40–1,000. Although these provide only rough estimates, it is worth giving such data as specimens usually shrink in preparations and contract during fixation. Illustrations of live specimens were based on free-hand sketches and micrographs, those of impregnated cells were made with a camera lucida. If not stated otherwise, all figures are oriented with the anterior end of the organism directed to the top of the page.

Terminology is according to FOISSNER & DRAGESCO (1996), who discuss in detail the problems associated with the orientation of the trachelocercid cell. Briefly, we consider the surface bearing the glabrous stripe and the bristle kinety as left side, and the oral apparatus to be in a prostome position because there are distinct oral structures at the anterior end of all trachelocercids.

Results

Morphometric data shown in Tables 1, 3, 4 are repeated in this section only as needed for clarity. All observations are from field material. Thus, it cannot be excluded that similar, but different, species were mixed, although this is unlikely because we excluded specimens which deviated in at least one prominent character, e.g. with 6 instead of 4 macronuclei or a distinctly different number of somatic kineties. Certainly, this procedure must be applied cautiously because it can generate some bias in the data, i.e. underestimate variability. On the other hand, variability would be overestimated if specimens which possibly belong to another species or are malformed were included.

Genus *Trachelocerca* EHRENBERG, 1840

1840 *Trachelocerca* EHRENBERG, Ber. Verh. K. Preuss. Akad. Wiss. Berl., year 1840: 202. Type (by monotypy): *Vibrio sagitta* MÜLLER, 1786.

1939 *Trachelocerca* COHN – DELPHY, Bull. Lab. marit. Dinard, 20: 54. Type (invalid subsequent designation): *T. phaenicopterus* COHN, 1866.

1939 *Nephrocerca* DELPHY, Bull. Lab. marit. Dinard, 20: 54. Type (original designation): *Trachelocerca tenuicollis* QUENNERSTEDT, 1867.

1939 *Gruvelina* DELPHY, Bull. Lab. marit. Dinard, 20: 54. Type (original designation): *G. longissima* DELPHY, 1939.

1939 *Protrichophora* DELPHY, Bull. Lab. marit. Dinard, 20: 54. No type species given, thus invalid according to article 13b of the ICZN (1985).

1960 *Trachelocerca* EHRENBERG, 1840 – DRAGESCO, Trav. Stn biol. Roscoff, 12: 110. Type (invalid subsequent designation): *Trachelocerca entzi* KAHL, 1927.

Improved diagnosis: Trachelocercidae KENT, 1881 with continuous (uninterrupted) circumoral and bristle kinety, each composed of a single row of dikinetids.

Type species: *Vibrio sagitta* MÜLLER, 1786 (by monotypy).

Etymology: Composite of the Greek nouns *trachelos* (neck) and *kerkos* (tail). *Cerca* is latinized and of feminine gender.

Synonymy: *Trachelocerca tenuicollis* QUENNERSTEDT, 1867, on which DELPHY (1939) based the new genus *Nephrocerca*, is very likely a pleurostomatid ciliate, as indicated by the two globular macronuclei in the body centre and the contractile vacuole in the posterior end. However, KAHL (1930) mentioned that the shape of the anterior body end of *T. tenuicollis* is more similar to that found in trachelocercid than in pleurostomatid ciliates. This does not agree with our experience and literature data (e.g., FOISSNER et al. 1995), which show that the anterior end of *T. tenuicollis* is very similar to that found in amphileptid pleurostomes, for instance, *Amphileptus procerus*.

Gruvelina and *Trachelocerca* are distinguished solely by the shape of the posterior body end (DELPHY 1939): straight in the first and curved in the second. This is indeed a very weak character, at best useful to distinguish species (see following descriptions of *Trachelocerca sagitta* and *T. ditis*). Thus, we synonymize *Gruvelina* with *Trachelocerca* and transfer the type species to that genus: *Trachelocerca longissima* (DELPHY, 1939) nov. comb.

Remarks: EHRENBERG (1840) used MÜLLER's (1876) species diagnosis to characterize the genus: "*Trachelocerca Sagitta = Vibrio Sagitta* MÜLLERI: *T.* corpore fusiforme albo, collo longissimo, capitulo terminali niveo opaco, hinc pro nigro venditato. Magn. extensi corporis 1/10'''. E mari boreali et baltico". Later, KENT (1881) provided a refined diagnosis including, however, species from different genera, e.g. *Lacrymaria olor*. Likewise, the diagnosis provided by KAHL (1927) is vague: "Flask-shaped, extensible Holophryidae with usually roundish, seemingly opened pharyngeal aperture and tuberculate ectoplasm between ciliary rows". Later, KAHL (1930) even widened the diagnosis: "Elongate, more or less distinctly extensible, marine Holophryidae with filiform or flask-shaped body". In 1939, DELPHY restricted *Trachelocerca* to contractile species with distinct neck, curved tail, and lacking contractile vacuole. More recently, DRAGESCO (1960) made a new attempt to define *Trachelocerca* more properly: "This genus, type of the family, has a complete (holophryide) ciliature composed of meridional kineties. The body is circular, very rarely elliptical in transverse section". Specifically, DRAGESCO separated *Trachelocerca* from *Tracheloraphis* and *Trachelonema* by the lack of a glabrous stripe which is, however, disproved by the present and former investigations (FOISSNER 1996a; FOISSNER & DRAGESCO 1996). DRAGESCO's error was obviously caused by his use of the wrong type species, viz. *Trachelocerca entzi*, which is, in fact, not a trachelocercid because it lacks a glabrous stripe and the entire somatic infraciliature consists of monokinetids (FOISSNER, unpubl.).

Obviously, all previous diagnoses of *Trachelocerca* are vague and include characteristics from species belong-

ing to other genera, with the notable exception of STEIN (1859), who restricted *Trachelocerca* to the type species and recognized that it is different from *Lacrymaria*. Our definition is based on previous results (FOISSNER 1996a; FOISSNER & DRAGESCO 1996) and the reinvestigation of two species, one of which we believe represents the type of the genus, *T. sagitta*. *Trachelocerca* is unique among the trachelocercids by its simple oral apparatus, i.e. the lack of any brosse structures.

There is also much confusion on the type species of *Trachelocerca* because previous authors either did not know of or disregarded the contributions by MÜLLER (1786) and EHRENBERG (1840). Typical examples are COHN (1866), who was unable to obtain MÜLLER's book, and CLAPARÈDE & LACHMANN (1859), who did not recognize that EHRENBERG based the genus on MÜLLER's description of *Vibrio sagitta*. Others, e.g. ENTZ (1884), SCHEWIAKOFF (1896) and MORGAN (1926), incorrectly synonymized *V. sagitta* with *Trachelocerca phoenicopterus*, a species described much later by COHN (1866). Unfortunately, KAHL (1927, 1930) and DRAGESCO (1960), the first revisers of the genus, carried on with this tradition and did not even mention the type species. However, EHRENBERG (1840) founded the genus correctly and with a single species only, viz. *Vibrio sagitta* MÜLLER, 1786, which is thus type (fixation by monotypy, article 68d of the ICZN 1985). Accordingly, the subsequent designations of *Trachelocerca phoenicopterus* COHN, 1866 and *T. entzi* KAHL, 1927 as type of *Trachelocerca* by DELPHY (1939), respectively, DRAGESCO (1960) are invalid.

Redescription of *Trachelocerca sagitta* (MÜLLER, 1786) EHRENBERG, 1840, type of the genus (Figs. 1–27, Tables 1, 6)

1786 *Vibrio sagitta* MÜLLER, Animalcula Infusoria: 59.
1840 *Trachelocerca sagitta* – EHRENBERG, Ber. Verh. K. Preuss. Akad. Wiss., year 1840: 202.
1962 *Tracheloraphis striatus* RAIKOV, Cah. Biol. mar., 3: 345.
1982 *Tracheloraphis conformis* WRIGHT, Cah. Biol. mar., 23: 281.

Identification and synonymy: The description and illustrations (Figs. 4, 5) of *Vibro sagitta* indicate at least two characters which suggest that MÜLLER (1876) observed a trachelocercid ciliate, viz. a black head (very typical for some of the more common trachelocercids) and a long tail, both unusual in lacrymariids, some of which superficially resemble certain trachelocercids. Furthermore, MÜLLER (1786) mentioned that *V. sagitta* is highly contractile, filiform, and moves like a turbellarian worm, a character combination highly specific for trachelocercid ciliates. Thus, MÜLLER's species should not be disrespected, although we admit that it is impossible to know which species he saw. But this applies also to many other species described at that time and even to many recent descriptions of trachelocercids (see below).

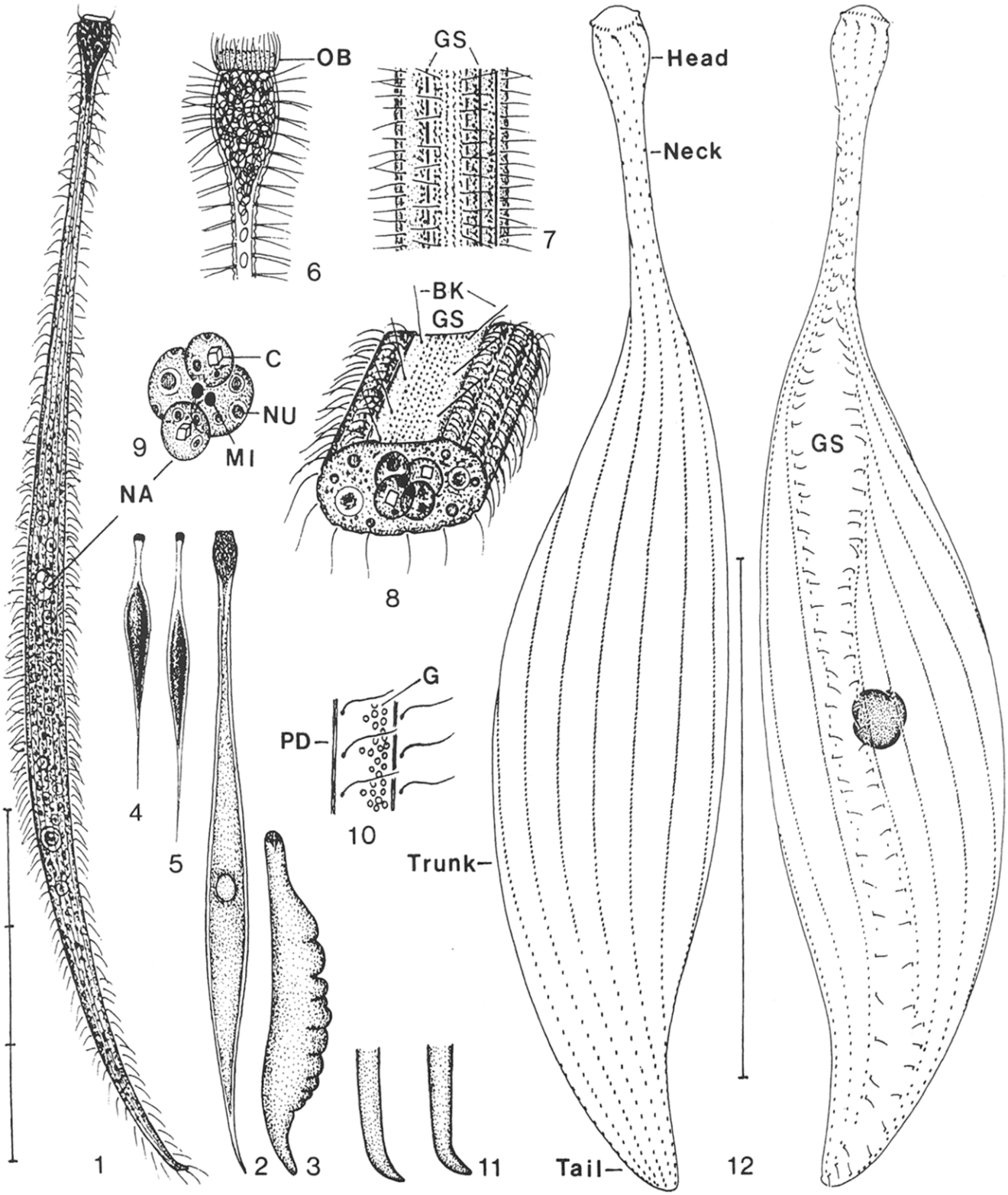
Considering that *V. sagitta* is type of *Trachelocerca*, it is unfortunate that later authors, especially KAHL (1927, 1930) and DRAGESCO (1960), did not identify any of the species they found with MÜLLER's form. Accordingly, the genus still lacks an unambiguous measure, i.e. a well-defined type species. Thus, we decided to fix one of our species, which has the main characteristics of *Vibrio sagitta*, as neotype and to provide a time honoured name with a precise meaning.

Both the species we synonymize with *V. sagitta* MÜLLER, 1786 were superficially described, i.e. from poorly preserved and stained specimens. Thus, no information is available on their natural shape, cortical granulation, and oral infraciliature. However, both match each other and our species in some main characters. All have 11–14 somatic kineties, a narrow glabrous zone 1–3 kineties wide, 4 macronuclei, 2 micronuclei, and are less than 500 µm long in preserved (contracted) condition (Figs. 28–33). Another species, *Tracheloraphis bodiani* DRAGESCO, 1963, is also rather similar to *V. sagitta*. However, it has 6 macronuclei and might thus be a different species. Likewise, *Trachelocerca gracilis* DRAGESCO, 1954b and *T. schulzei* DRAGESCO, 1960 highly resemble *T. sagitta* in size, shape, and nuclear apparatus, but have 25–26 somatic kineties.

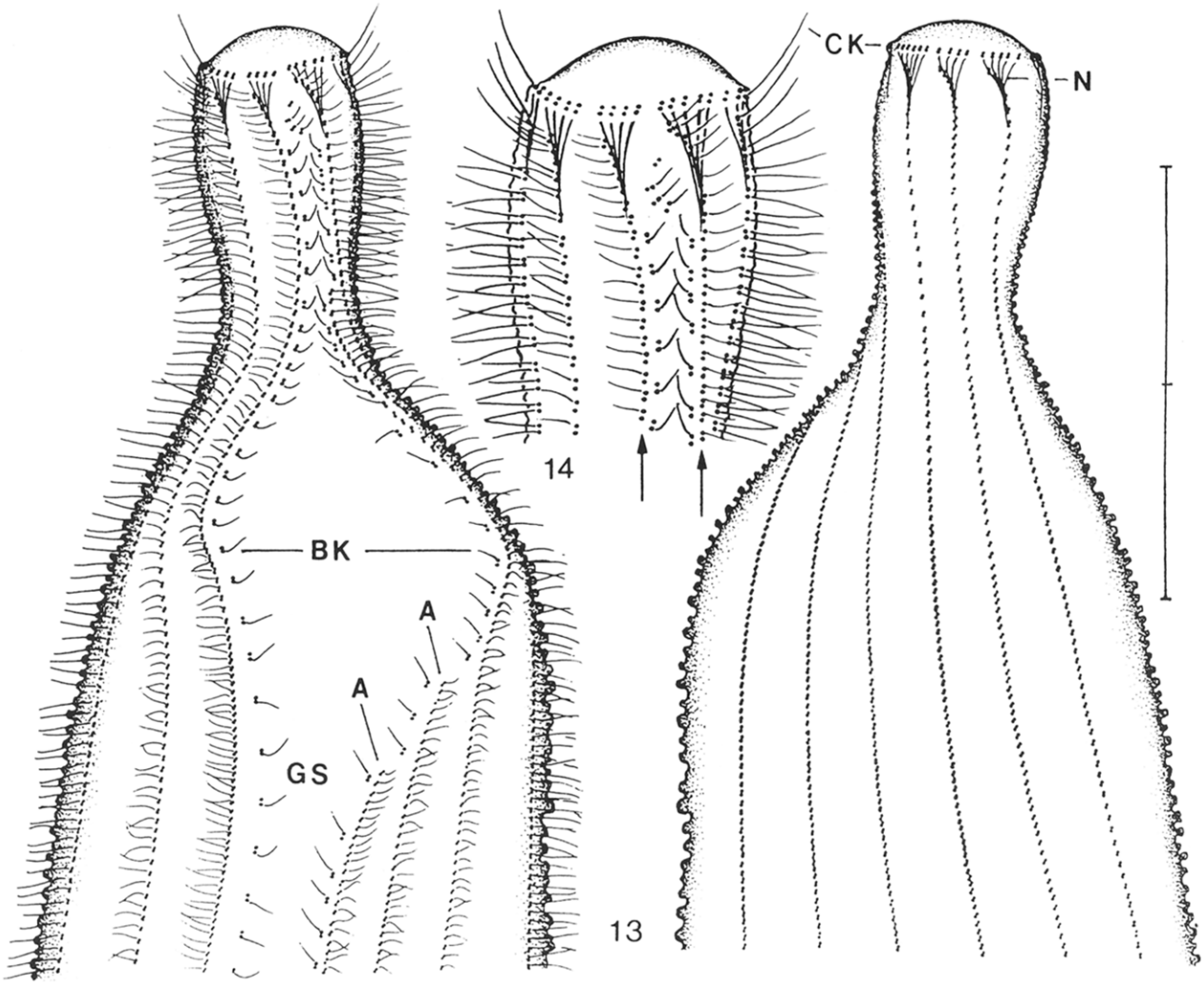
Specimens investigated and type material: The redescription is based on 15 well-impregnated specimens; some others were of usuable quality and served for completing morphometry. No type material from *T. sagitta* has been mentioned in the literature. Thus, we have deposited two neotype slides with specimens from Roscoff, prepared as described, in the Oberösterreichisches Landesmuseum in Linz (LI), Austria. Relevant specimens are marked by a black ink circle on the cover glass.

Improved diagnosis: Fully extended cells in vivo about 1,000 × 30 µm. Filiform, neck and tail indistinctly separate from trunk, head claviform and dark, distal end of tail curved. 4 macronuclei and 2 micronuclei forming tight cluster in centre of trunk. 11–14 somatic ciliary rows and 19–34 circumoral dikinetids; glabrous stripe distinct, about one third of body width. Cortical granules about 1 µm in diameter, colourless, form stripes between ciliary rows and narrowly spaced rows in glabrous zone.

Redescription (Figs. 1–27, Tables 1, 6): Size of fully extended specimens in vivo about 1,000 × 30 µm, highly flexible and contractile, size and shape thus poorly preserved and highly variable in protargol slides (Table 1; Figs. 1, 12, 15, 16, 20); trunk flattened up to



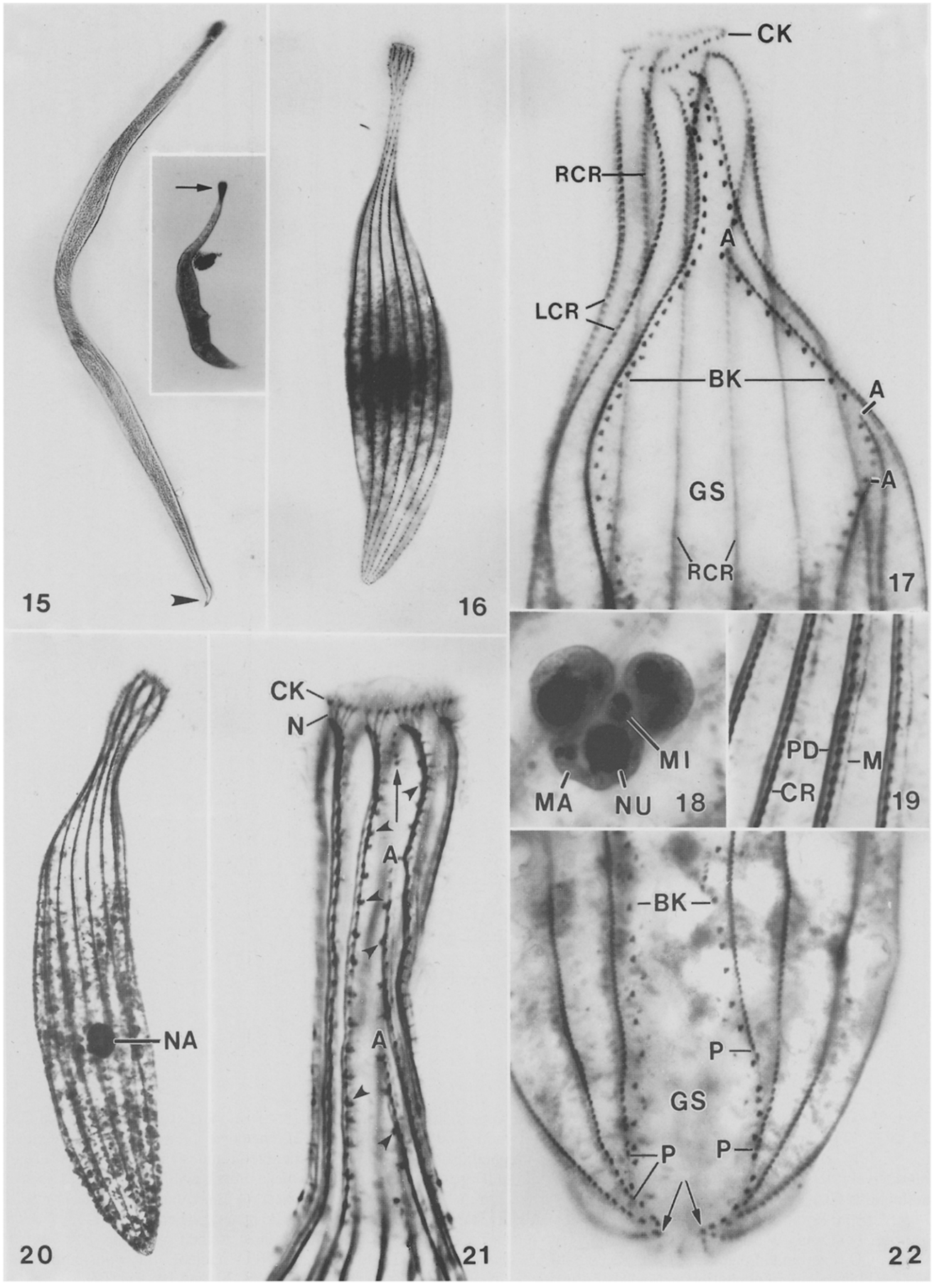
Figs. 1–12. *Trachelocerca sagitta* from life (Figs. 1–11) and after protargol impregnation (Fig. 12). **1.** Fully extended specimen. Scale bar division 100 μm. **2, 3.** Partially and fully contracted specimen. **4, 5.** MÜLLER's original figures of *T. sagitta*. Note distinct similarity to our Fig. 2. **6.** Head with many ellipsoid inclusions causing dark colour at low magnification (cp. Figs. 1, 15). **7.** Surface view of left side in trunk region. **8.** Transverse section of trunk. **9.** Nuclear apparatus. **10.** Surface view of right side cortex. **11.** Tail variability. **12.** Infraciliature of right and left side; for details see following figures. Bar 100 μm. BK = bristle kinety, C = (protein?) crystal, G = cortical granules, GS = glabrous stripe, MI = micronuclei, NA = nuclear apparatus, NU = nucleolus, OB = oral bulge, PD = postciliodesma.



Figs. 13, 14. *Trachelocerca sagitta*, somatic and oral infraciliature in left and right anterior body region after protargol impregnation. Note that ciliary rows (arrows) alongside bristle kinety only have the anterior basal body of the dikinetids ciliated, whereas all other kineties have ciliated dikinetids in the anterior neck region. A = anterior secant system, BK = bristle kinety, CK = circumoral kinety, GS = glabrous stripe, N = nematodesmata. Scale bar division 20 µm (Fig. 13).

2:1 (Fig. 8). Greyish in dissecting and bright-field microscope (Figs. 1, 15). Fully extended specimens filiform with anterior and posterior third gradually tapering, neck and tail thus indistinctly separate from trunk (Fig. 1). Head claviform, conspicuous because distinctly wider than neck and dark to black at low magnificaton (≤ X 100) due to many about 3 × 2 µm sized, refractile (crystalline ?) inclusions; oral bulge hyaline,

Figs. 15–22. *Trachelocerca sagitta* from life (Fig. 15) and after protargol impregnation (Figs. 16–22). **15.** Extended and contracted (inset) specimen. Note dark head (arrow) and curved tail (arrowhead). **16, 20.** Infraciliature of right side. **17, 22.** Somatic infraciliature of left side in anterior and posterior body region (cp. Figs. 13, 23). The posterior arch of the bristle kinety has slightly separated (arrows) due to the great inflation of the tail (cp. Fig. 15) caused by the preparation procedure. Note triangular shape of bristle kinetids (cp. Fig. 27). **18.** Nuclear apparatus; three of the four macronuclei and one of the two micronuclei are recognizable. **19.** Somatic fibrillar system. **21.** Left side view showing oral infraciliature, anterior secant system and anterior end of bristle kinety (arrow). Arrowheads mark bristle kinety. A = anterior secant system, BK = bristle kinety, CK = circumoral kinety, CR = ciliary row, GS = glabrous stripe, LCR = ciliary rows of left side, M = myoneme, MA = macronucleus, MI = micronucleus, N = nematodesmata, NA = nuclear apparatus, NU = nucleolus, P = posterior secant system, PD = postciliodesma, RCR = ciliary rows of right side.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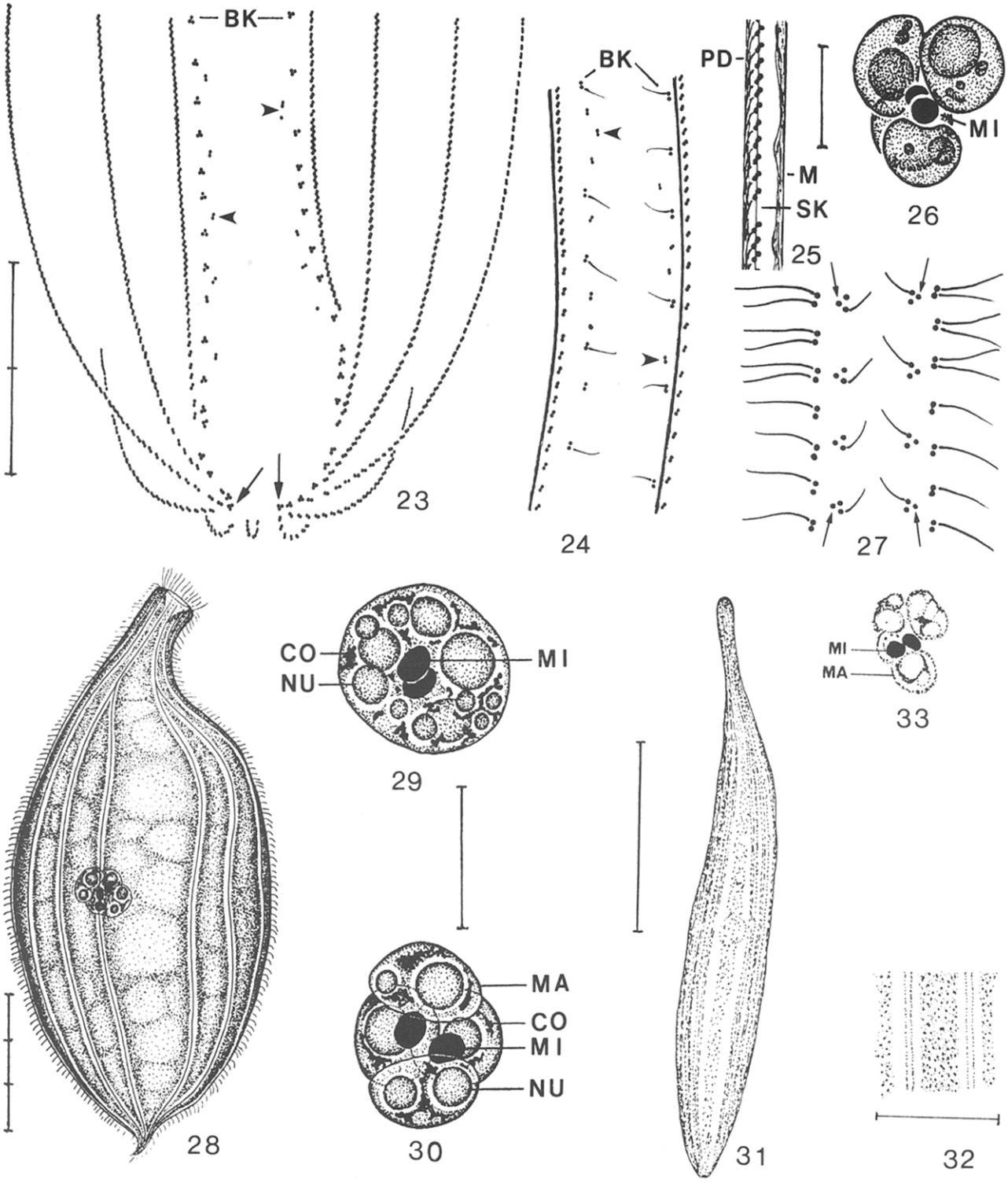


Figs. 23–33. *Trachelocerca sagitta*, details of left lateral somatic infraciliature (Figs. 23–25, 27) and synonymy (Figs. 28–33). **23, 24, 27.** Fine structure of bristle kinety after protargol impregnation (cp. Figs. 17, 22). The posterior arch of the bristle kinety has slightly separated (arrows in Figs. 23) due to the preparation. Arrows in Fig. 27 denote granules (parasomal sacs?) right, respectively, left of the bristle dikinetids, emphasizing their opposed polarity. Arrowheads mark unciliated granules (barren dikinetids? extrusomes?). **25, 26.** Somatic fibrillar system and nuclear apparatus after protargol impregnation. **28–30.** *Trachelo-raphis striata* RAIKOV, 1962, left lateral view of hematoxylin stained specimen and nuclear apparatus (Feulgen). **31–33.** *Trache-loraphis conformis* WRIGHT, 1982, left lateral view, nuclear apparatus and cortex of fuchsin stained specimen. BK = bristle kinety, CO = chromatin patches, M = myoneme, MA = macronuclei, MI = micronuclei, NU = nucleoli, PD = postciliodesma, SK = subkinetal microtubule ribbon. Scale bar division 5 μm (Fig. 32), 10 μm (Figs. 23, 26, 28–30) and 100 μm (Fig. 31).

Table 1. Morphometric characteristics from *Trachelocerca sagitta* (upper line) and *Trachelocerca ditis* (lower line).

Character[1])	$\bar{x}$	M	SD	$SD_{\bar{x}}$	CV	Min	Max	n
Body, length[2])	221.2	200.0	58.1	13.7	26.3	147	320	18
	350.7	335.0	118.3	25.2	33.7	210	660	22
Body, width at head	14.3	15.0	3.2	0.7	22.2	9	20	18
	20.3	20.0	5.9	1.3	29.1	10	35	22
Body, (maximum) width at trunk[3])	52.1	50.0	11.8	2.8	22.7	37	83	18
	82.2	82.0	18.8	4.0	22.9	50	120	22
Glabrous stripe, width in	14.2	13.5	4.6	1.1	32.7	7	24	18
mid-body[3])	13.5	12.5	4.3	0.9	31.6	6	19	22
Anterior end to nuclear capsule,	212.1	108.5	38.4	9.0	31.7	81	200	18
distance	176.0	157.0	63.6	13.6	36.2	97	350	22
Nuclear capsule, length	13.4	13.0	1.6	0.4	11.8	11	18	18
	17.7	18.0	2.3	0.5	12.7	12	22	22
Nuclear capsule, width	11.7	11.0	1.6	0.4	14.1	10	16	18
	16.0	17.0	2.6	0.5	16.1	10	20	22
Macronuclei, number	4.0	4.0	0.0	0.0	0.0	4	4	12
	4.0	4.0	0.0	0.0	0.0	4	4	8
Micronuclei, number	2.0	2.0	0.0	0.0	0.0	4	4	12
	2.0	2.0	0.0	0.0	0.0	2	2	8
Somatic kineties, number on head	7.7	8.0	0.7	0.2	8.9	6	8	18
	13.1	13.0	1.1	0.2	8.3	11	16	22
Somatic kineties, (maximum)	12.5	13.0	0.9	0.2	7.4	11	14	18
number on trunk	28.1	28.0	2.2	0.5	7.9	24	33	22
Dikinetids, number in 10 µm in	7.6	7.0	3.0	0.7	38.9	3	12	18
neck region	8.3	8.0	2.7	0.6	32.9	4	13	22
Dikinetids, number in 10 µm in	11.5	10.5	3.8	0.9	32.7	7	19	18
trunk region	10.9	10.0	3.6	0.8	33.1	5	18	22
Circumoral kinetids, number	24.9	24.0	3.8	0.9	15.4	19	34	18
	67.4	70.0	16.3	3.5	24.2	40	100	22

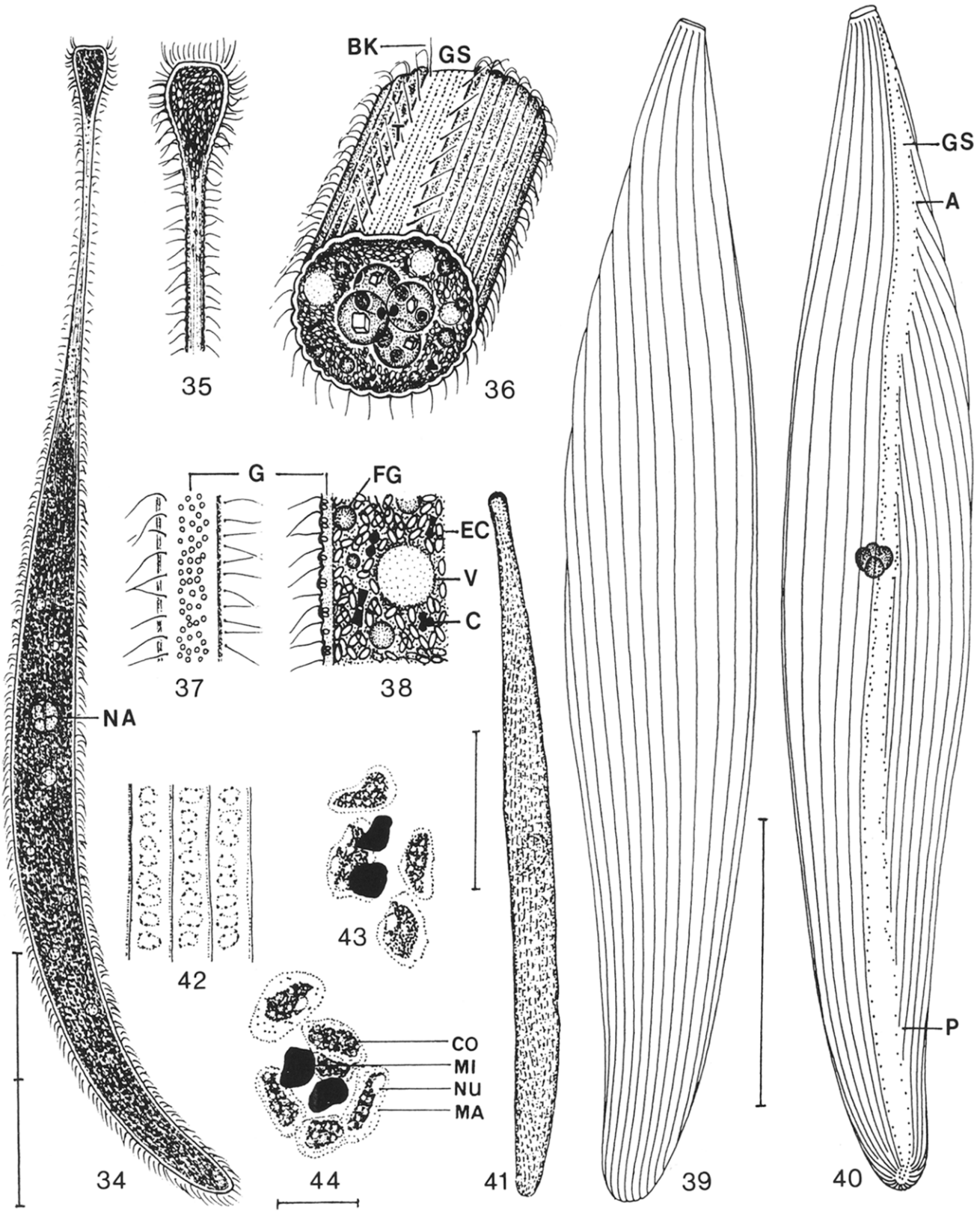
[1]) Data based on protargol impregnated and mounted morphostatic specimens from field. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of specimens investigated, SD – standard deviation, $SD_{\bar{x}}$ – standard deviation of arithmetic mean, $\bar{x}$ – arithmetic mean.

[2]) Values distinctly different from those of live specimens which strongly contract when fixed for preparation.

[3]) Data of very limited value because specimens are highly contractile and trunk often becomes inflated due to preparation procedures.

about 3 µm high, surface flat or slightly depressed in centre (Figs. 1, 6). Distal end of tail pointed and distinctly curved, sometimes almost rectangularly bent (Figs. 1, 11, 15). Fully contracted specimens about 250 × 50 µm in vivo, banana-shaped, convex side with glabrous stripe distinctly protruding and tuberculate (Fig. 3); partially contracted cells elongate-fusiform (Fig. 2), highly resembling MÜLLER's figures (Figs. 4, 5). Macronuclei globular, form distinct cluster, possibly a capsule, in centre of cell (Figs. 1, 2, 9, 12, 18, 26); contain small and large nucleoli and often a tetragonal protein crystal which does not stain with protargol (Figs. 9, 26). Micronuclei globular, in centre of macronuclear cluster. No contractile vacuole. Cortex highly flexible, about 1 µm thick, forms columnar tubercles in contracted specimens. Cortical granules globular, about 1 µm in diameter, colourless, arranged in narrow stripes right of ciliary rows and tightly spaced rows in glabrous zone (Figs. 7, 10). Movement like in other trachelocercids, i.e. elegantly gliding and winding between sand grains and organic debris.

Somatic infraciliature (Figs. 12–14, 16–27). The surface of *T. sagitta* is densely ciliated, leaving blank a rather wide zone, the glabrous stripe, extending the whole body length in the midline of the left side (Figs. 8, 12, 13, 17, 22, 23). The cilia, which are rather stiff and can be spread, are about 10 µm long and arranged in longitudinal rows which are distinctly separate from the circumoral ciliature and extend between flat cortical crests. The anterior end of the ciliary rows has condensed, i.e. more narrowly spaced dikinetids and is slightly curved to the right. The ciliary rows are gradu-



Figs. 34–44. *Trachelocerca ditis*, general morphology of life (Figs. 34–38) and stained specimens (Figs. 39–44). **34.** Fully extended specimen. **35.** The head is slightly asymmetrical. **36.** Transverse section of trunk. **37, 38.** Surface view and optical section of cortex. **39, 40.** Infraciliature of right and left side after protargol impregnation; for details see following figures. **41–44.** General view, cortex and nuclear apparatus of hematoxylin stained specimens (from WRIGHT 1982). A = anterior secant system, BK = bristle kinety, C = crystal, CO = chromatin, EC = ellipsoid (crystalline?) inclusions,

ally 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 and posterior secant system are formed on the left surface of the neck and tail where 5–6 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 (Table 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.

The entire infraciliature consists of dikinetids which, however, have a highly specialized ciliation (Figs. 13, 14). The dikinetids are rotated 20–30° counter-clockwise to the kinety axis and associated with conspicuous, overlapping postciliary microtubule ribbons, which originate from the posterior basal body of the dikinetids and form a thick, strongly impregnated postciliodesma right of each ciliary row. A thin, sharply impregnated fibre, very likely a subkinetal microtubule ribbon (RAIKOV et al. 1975), extends underneath each ciliary row (Figs. 19, 25). Only the anterior basal body of the dikinetids is ciliated, except in the distal neck region of the right side, where both are ciliated. In other words, the posterior cilium is lacking in the dikinetids of all kineties neighbouring the bristle kinety, in the condensed dikinetids at the anterior end of the head kineties, and in all trunk and tail dikinetids (Figs. 13, 14).

The contractile apparatus of *T. sagitta* consists of a myoneme close to the left of each kinety (Figs. 19, 53). The distinctiveness of the myonemes varies highly, depending on preparation conditions; frequently, they are partially or completely unstained. The myonemes are flattened ribbon-like and extend the whole length of the kineties, but are wider (thicker) in the trunk than in the tail and head region. No myonemes were found in the glabrous stripe in any of the species investigated. Likewise, all myonemes observed were unbranched, i.e. did not contact each other.

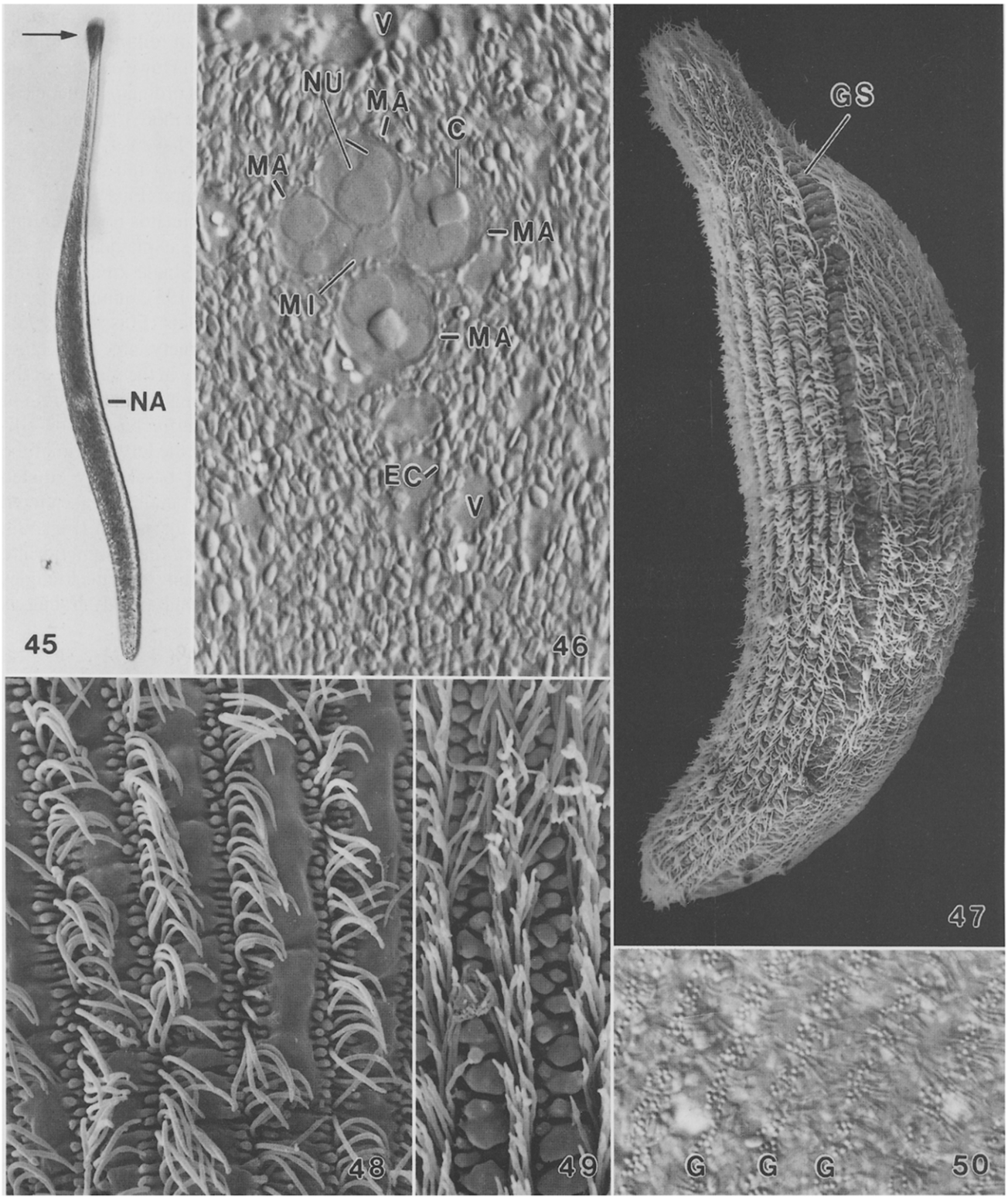
The glabrous stripe, which extends along the whole length of the body, is narrow in the head region and widens, respectively narrows, gradually on the neck and tail. Its full width on the trunk corresponds to an area occupied by 1–2 kineties, i.e. approximately one third of body width. The glabrous stripe is rather flabby and becomes tuberculate when the cell contracts (Figs. 3, 12). It is bordered by the bristle kinety which consists, like the ordinary ciliary rows, of dikinetids having about 15 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. 12, 13, 17, 22, 27). Furthermore, the bristle kinetids have a unique ciliation, most parsimoniously explained by the assumption that they belong to a single kinety extending along the stripe margins (Fig. 195), quite similar to the left lateral kinety of the loxodids (FOISSNER 1996b, c). Both ends of the bristle kinety are very close together subapically and terminally in the midline of the glabrous stripe. The dikinetids along the right margin of the glabrous stripe have the *posterior* basal body ciliated, whereas the dikinetids along the left margin of the glabrous stripe have the *anterior* basal body ciliated (Figs. 14, 24, 27). Nonciliated granules are scattered within the bristle kinety in the trunk region (Figs. 23, 24). In the best preparations, the *ciliated* dikinetids are composed of three granules forming minute triangles (Figs. 17, 22, 23, 27). The additional (third) granule is directed to the somatic kineties.

Oral infraciliature (Figs. 6, 12–14, 17, 21). The oral infraciliature of *T. sagitta* is very simple and consists of a single, dikinetidal circumoral kinety extending in the flat furrow separating the oral bulge from the head. The circumoral kinety is very likely composed of about 8 small fragments, as indicated by small gaps, 1–2 dikinetids wide, and the bundled arrangement of the nematodesmata. The dikinetids have, very likely, only the posterior basal body ciliated and are associated with a distinct nematodesma. The nematodesmata of each dikinetidal fragment unite to small bundles extending posteriorly underneath the anterior end of the somatic kineties (Figs. 13, 14, 21).

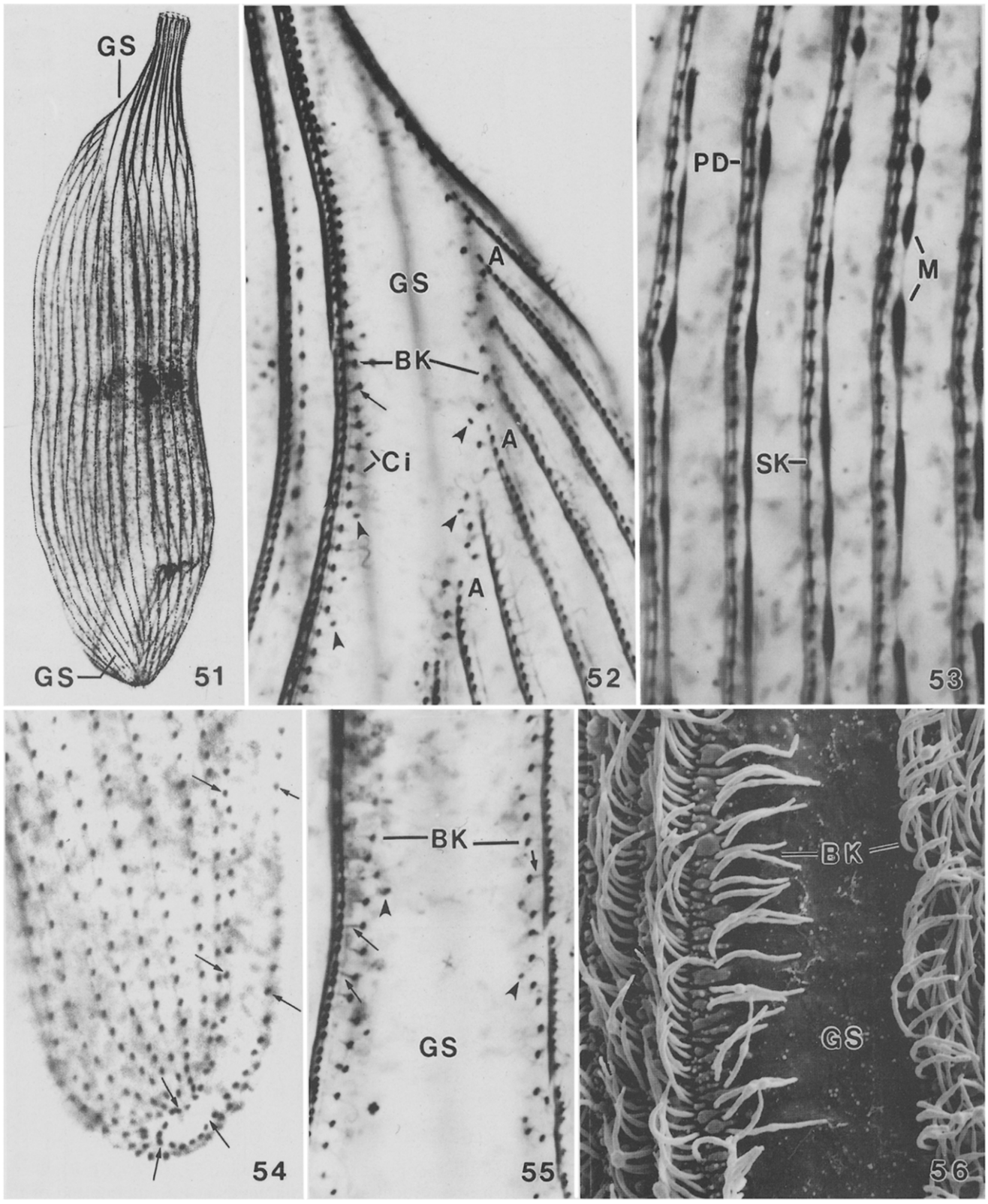
Redescription of *Trachelocerca ditis* (WRIGHT, 1982) nov. comb. (Figs. 34–69, Tables 1, 6)

Identification and taxonomy: There are several *Trachelocerca* and *Tracheloraphis* species known which are similar to our population in size, shape, and nuclear apparatus. However, none matches perfectly (main deviating characters in brackets): *Trachelocerca incaudata* KAHL, 1933 (6–8 macronuclei according to DRAGESCO 1960, RAIKOV & KOVALEVA 1968, WRIGHT 1982, and our unpubl. observations), *T. grisea* KAHL,

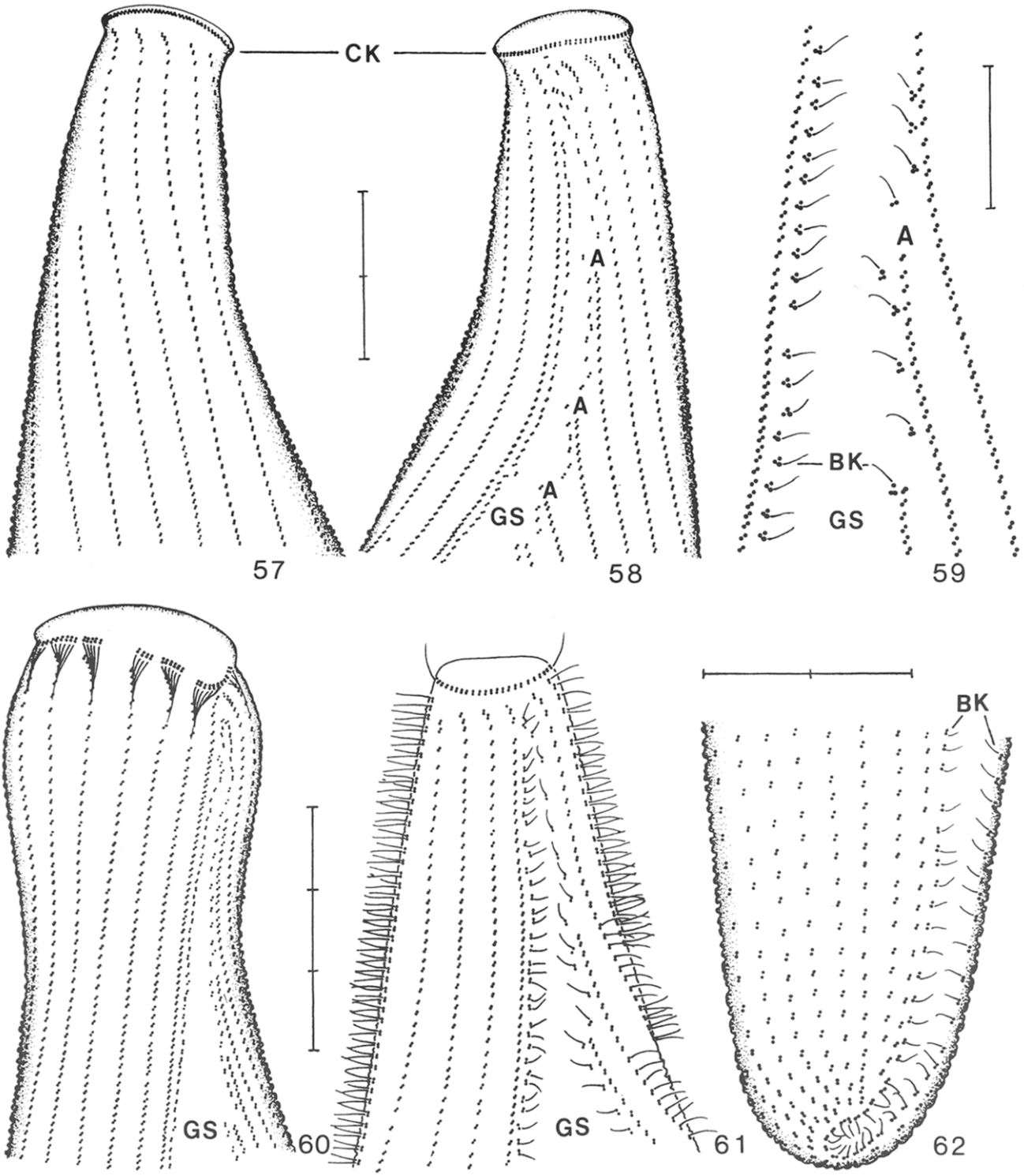
FG = fat globule, G = cortical granules, GS = glabrous stripe, MA = macronuclei, MI = micronuclei, NA = nuclear apparatus, NU = nucleolus, P = posterior secant system, V = vacuole. Scale bar division 10 μm (Figs. 43, 44) and 100 μm (Figs. 34, 39, 40, 41).



Figs. 45–50. *Trachelocerca ditis* from life (Figs. 45, 46, 50) and in the scanning electron microscope (Figs. 47–49). **45.** Slightly contracted specimen. Arrow marks dark head. **46.** Nuclear apparatus and cytoplasmic inclusions. Four macronuclei form a cluster with two micronuclei in centre. **47.** Contracted specimens are banana-shaped. Note narrow glabrous stripe. **48, 49.** The cortex forms columnar blisters in contracted specimens, especially in the neck region (Fig. 49). **50.** Stripes of cortical granules extend between ciliary rows. C = protein crystal, EC = ellipsoid (crystalline?) inclusions, G = cortical granules, GS = glabrous stripe, MA = macronuclei, MI = micronuclei, NA = nuclear apparatus, NU = nucleoli, V = vacuoles.



Figs. 51–56. *Trachelocerca ditis*, somatic infraciliature after protargol impregnation (Figs. 51–55) and in the scanning electron microscope (Fig. 56). **51.** Right side view with kineties and glabrous stripe of left side shining through. **52, 55, 56.** Fine structure of bristle kinety. Arrows mark fibre extending centrifugally from bristle dikinetids. Arrowheads denote granules without cilia. **53.** Somatic fibrillar system. **54.** The bristle kinety (arrows) is continuous at the posterior end of the glabrous stripe (cp. Fig. 62). A = anterior secant system, BK = bristle kinety, Ci = cilia, GS = glabrous stripe, M = myoneme, PD = postciliodesma, SK = subkinetal microtubule ribbon.



Figs. 57–62. *Trachelocerca ditis*, somatic and oral infraciliature after protargol impregnation. **57, 58, 60, 61.** Right and left side views of anterior body region. Note lack of any brosse structures. The dikinetids at the anterior end of the somatic kineties have only the anterior basal body ciliated. The wide gaps in the circumoral kinety of the specimen shown in Fig. 60 are very likely caused by the preparation procedure. **59.** The dikinetids of the bristle kinety are associated with a granule (parasomal sac?) at the right, respectively, left side, emphasizing their opposed polarity. **62.** The bristle kinety curves around the posterior end of the glabrous stripe (cp. Fig. 54). Thus, the dikinetids in the right branch of the bristle kinety have the posterior basal bodies ciliated, whereas those in the left branch have the anterior basal bodies ciliated. A = anterior secant system, BK = bristle kinety, CK = circumoral kinety, GS = glabrous stripe. Scale bar division 10 μm.

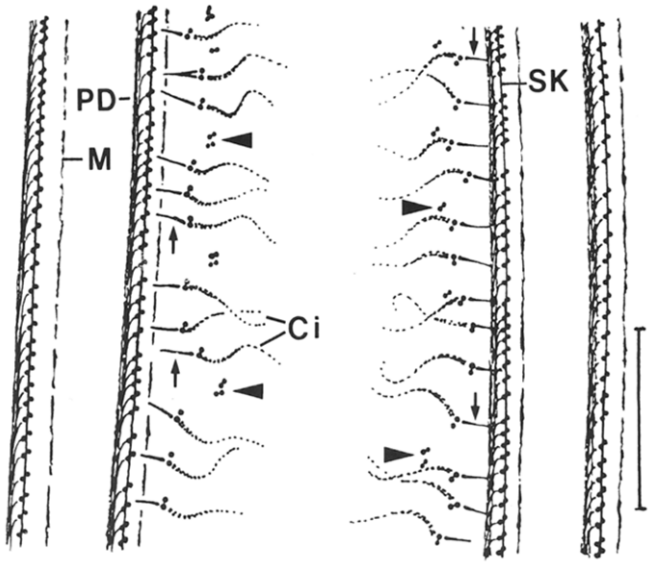


Fig. 62a. *Trachelocerca ditis*, fine structure of the somatic infraciliature and the bristle kinety after protargol impregnation. A short fibre (arrows) is associated with the ciliated basal body of the bristle dikinetids and extends towards the somatic ciliary rows, emphasizing the opposed polarity of the right and left branch of the bristle kinety. Arrowheads mark barren granules, possibly unciliated dikinetids and/or a special kind of cortical granules (extrusomes?). Ci = cilia, M = myoneme, PD = postciliodesma, SK = subkinetal microtubule ribbon. Bar 10 µm.

1933 (a flat species having a brosse and a wide glabrous zone according to DRAGESCO 1960 and DRAGESCO & DRAGESCO-KERNÉIS 1986), *T. geopetiti* DRAGESCO, 1954 (50–60 somatic kineties; see also KOVALEVA & GOLEMANSKY 1979), *Tracheloraphis gracilis* DRAGESCO, 1960 (12–13 somatic kineties, head disk-shaped, glabrous zone rather wide), *T. enigmatica* DRAGESCO, 1960 (oral bulge annulated, glabrous zone wide), *T. primitarum* EPSTEIN, 1994 (3 macronuclei), *T. monocaryon* DRAGESCO, 1965 (40 somatic kineties), *T. stephani* DRAGESCO, 1965 (16–20 somatic kineties), *T. swedmarki* DRAGESCO, 1960 (head with distinct trichites and two types of cilia; see also RAIKOV & KOVALEVA 1968), *T. lactea* RAIKOV & KOVALEVA, 1968 (40 somatic kineties, 8 macronuclei and 4 micronuclei, single row of conspicuous cortical granules between each two kineties), *T. nivea* WRIGHT, 1982 (43 somatic kineties, head white), *T. ditis* WRIGHT, 1982 (18–22 somatic kineties).

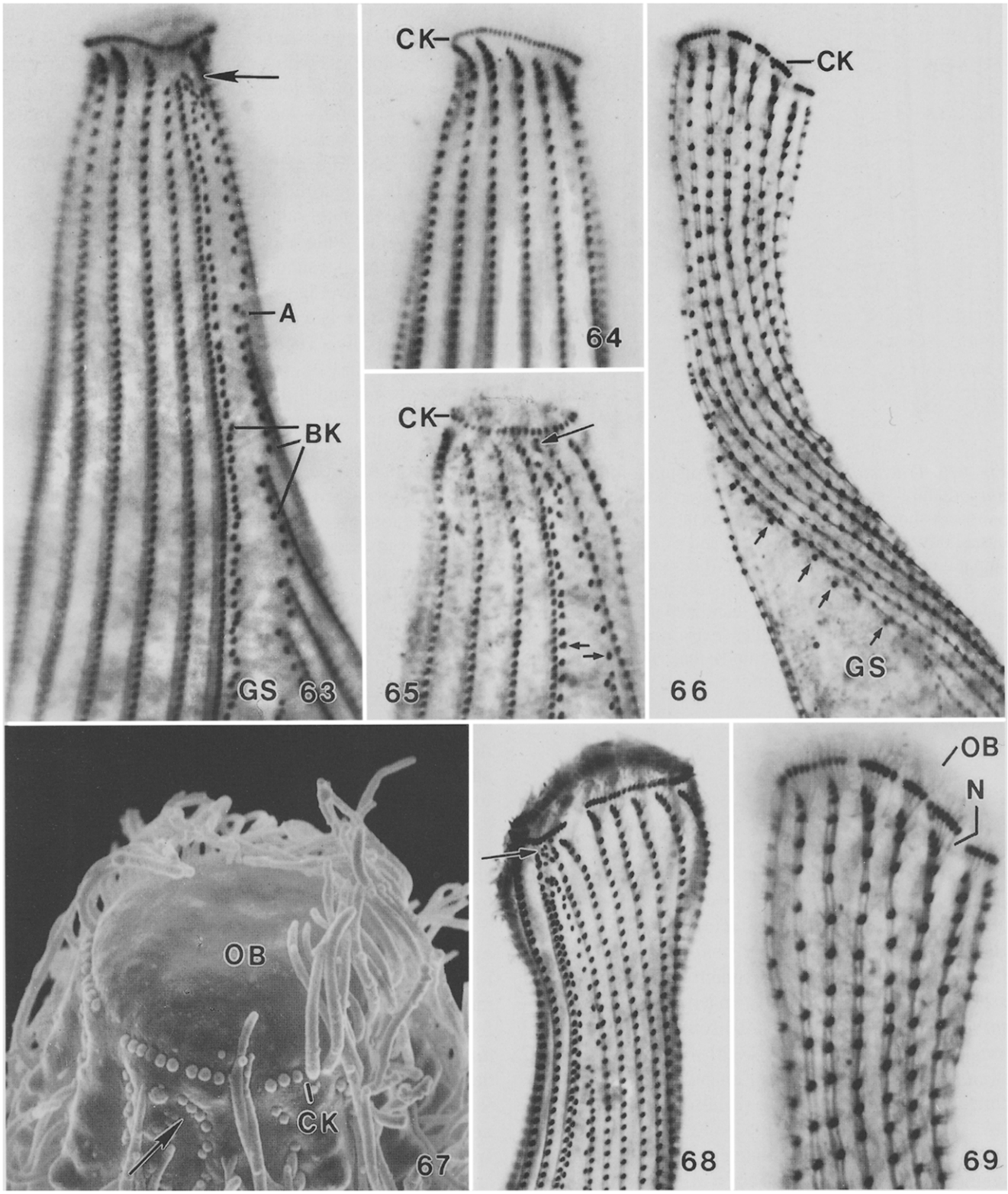
Most of these species have been described so incompletely that any identification is more or less arbitrary. Thus, we decided – instead of making a new species – to fill one of the names with a more precise content, viz. *Tracheloraphis ditis*, for which WRIGHT (1982) provided some poor illustrations from prepared material (Figs. 41–44) and a rather general description: "This ciliate is colourless with a slightly swollen apical region and a rounded posterior end. The cytostome is simple, without a slit and is occasionally obscured by inclusions. Length between 300 and 800 µm, average 450 µm. There are between eighteen and twenty-two kineties; the globerulus zone very narrow and occupying the equivalent of one kinety. The interkinetic spaces and globerulus zone are occupied by plications which have small mucocysts on their surface. The globerulus zone had, on average, eight kineties that terminated against it. There is a loosly associated group of nuclei located centrally. The macronuclei vary in number between four and six, more usually four. They vary in size between 6 and 8 µm. They have an irregular outline, contain a large amount of chromatin and may contain one or two small nucleoli. There are two micronuclei, although on one occasion only a single micronucleus was observed. They are large, measuring 5 µm across the longest axis and are ovoid in outline."

There is only one character in WRIGHT's description which does not match our specimens, viz. the number of somatic kineties. However, we doubt that WRIGHT (1982) could count them accurately, considering his illustration (Fig. 41). Another species close to our population is *Tracheloraphis primitarum* EPSTEIN, 1994 which, however, has only three macronuclei. We restudied EPSTEIN's slides and cannot confirm the macronuclear number. All specimens, when focused appropriately, have four to six macronuclei. Thus, it is very likely a junior synonym of *T. ditis*.

Tracheloraphis ditis lacks any brosse structures, as also evident from WRIGHT's description ("The cytostome is simple, without a slit..."). Thus, it has to be transferred to *Trachelocerca*, according to our classification (Table 5): *Trachelocerca ditis* (WRIGHT, 1982) nov. comb.

Specimens investigated and type material: The redescription is based on 20 well-impregnated specimens; some others were of usuable quality and served for completing morphometry. No type material of *T. ditis* has been mentioned in the literature. Thus, we have deposited two neotype slides with specimens from Roscoff, prepared as described, at the same site as mentioned for *T. sagitta*.

Improved diagnosis: Fully extended cells in vivo about 1,000 × 40 µm. Slender, neck rather distinctly separate from cylindroid trunk, head claviform and dark, posterior end rounded. 4 macronuclei and 2 micronuclei forming tight cluster in centre of trunk. 24–33 somatic ciliary rows and 40–100 circumoral dikinetids; glabrous stripe narrow, about one quarter or less of body width. Cortical granules about 0.6 µm in diameter, colourless, form stripes between ciliary rows and narrowly spaced rows in glabrous zone.



Figs. 63–69. *Trachelocerca ditis*, infraciliature after protargol impregnation (Figs. 63–66, 68, 69) and in the scanning electron microscope (Fig. 67). **63, 64.** Left and right side view of same specimen. Arrow marks anterior end of bristle kinety. **65, 68.** Left side views of anterior region. The dikinetids of the bristle kinety (small arrows) are rather irregularly arranged underneath the circumoral kinety (large arrow). **66, 69.** Distinct nematodesmata are associated with the circumoral dikinetids. Arrows mark left branch of bristle kinety. **67.** The surface of the oral bulge is smooth. The cilia of the circumoral kinety and the anterior end of the somatic kineties (arrow) are frequently lost due to preparation. A = anterior secant system, BK = bristle kinety, CK = circumoral kinety, GS = glabrous stripe, N = nematodesmata, OB = oral bulge.

Redescription (Figs. 34–40, 45–69, Tables 1, 6): Size of fully extended specimens in vivo about 800–1,000 × 40–50 µm, highly flexible and contractile, size and shape thus poorly preserved and highly variable in protargol slides (Table 1; Figs. 34, 39, 45, 47, 51); only slightly flattened laterally (Fig. 36). Grey to blackish in dissecting and bright-field microscope due to innumerable, 4 × 2 µm sized, refractile (crystalline ?) inclusions in head and trunk (Figs. 34, 38, 45, 46). Shape of fully extended specimens slenderly fusiform with neck distinctly separate from head and cylindroid trunk; no tail, i.e. posterior region only slightly tapering and narrowly rounded. Head about 30 µm wide, claviform, at one side obliquely truncate, conspicuous because distinctly wider and darker than neck due to many ellipsoid inclusions described above; oral bulge inconspicuous, about 3 µm high, difficult to recognize because indistinctly separate from head and also filled with ellipsoid inclusions, surface flat or slightly depressed in centre (Figs. 34, 35, 45, 67). Slightly contracted cells fusiform (Fig. 39), fully contracted specimens about 350 µm long in vivo, ampulliform (Fig. 51) or banana-shaped (Fig. 47) and with distinct (Figs. 60, 68) or indistinct (Figs. 47, 51, 61) head; glabrous stripe neither protruding nor distinctly tuberculate (Fig. 47). Macronuclei globular, form conspicuous, about 20 µm sized cluster in vivo, possibly a capsule, in centre of trunk (Figs. 34, 36, 40, 45, 46); each nucleus usually contains two large nucleoli and one or two cuboid or hexagonal protein crystals, which do not stain with protargol (Fig. 46). Micronuclei globular, in centre of macronuclear cluster. No contractile vacuole. Cortex highly flexible, about 1–2 µm thick, forms large columnar tubercles between and many small claviform blisters along ciliary rows in contracted specimens (Figs. 38, 48, 49). Cortical granules about 0.6 µm in diameter, colourless, arranged in broad stripes between kineties and in narrowly spaced rows in glabrous stripe (Figs. 36–38, 50); stain red with methyl green-pyronin but are not extruded. Cytoplasm packed with ellipsoid inclusions as described above, many fat globules and clear vacuoles, and some 2–3 µm sized irregular crystals (Figs. 36, 38, 46). Movement like in other trachelocercids, i.e. elegantly gliding and winding between sand grains and organic debris.

Infraciliature (Figs. 39, 40, 51–69). The somatic and oral infraciliature of *T. ditis* is very similar to that of *T. sagitta*. All important differences concern morphometric characteristics, compiled in Table 1, and features recognizable only in live specimens as described above, emphasizing the need for morphometry and live observation for a correct identification of trachelocercid ciliates. Thus, we refrain from a complete description of the infraciliature, which would be a repetition of that given for *T. sagitta*, and refer to the detailed figures and figure explanations. Nevertheless, a few features are different or were seen clearly only in this species, and are thus described in some detail.

The somatic ciliation of *T. ditis* is highly variable. In some specimens it is very similar to that described for *T. sagitta*, while others have both basal bodies of the dikinetids ciliated throughout, especially in the kineties right of the glabrous stripe (Fig. 61). The anterior end of the somatic kineties is distinctly curved (Figs. 57, 58, 60, 63, 64) or almost straight, bearing only 1–3 more narrowly spaced (condensed) dikinetids (Figs. 61, 65, 68, 69). These dikinetids lack the posterior cilium, as in all other trachelocercids (Fig. 61).

The glabrous stripe is relatively narrower in *T. ditis* than in *T. sagitta*, i.e. occupies only one quarter or less of the body width, corresponding to an area occupied by 1–2 kineties (Figs. 36, 40, 47, 51, 56). Highly interesting specializations were found in the bristle kinety bordering the glabrous stripe. In three specimens it was clearly recognizable, obviously because this species lacks a tail, that the bristle kinety curves around the posterior end of the organism, emphasizing our interpretation that it is a single row extending around the glabrous stripe (Figs. 54, 62). Furthermore, a special fibre, associated with the ciliated basal body of the dikinetids and directed laterally towards the somatic kineties, was observed in some excellently prepared specimens (Figs. 52, 55, 62a). Accordingly, this fibre shows the same peculiar polarity as the ciliation of the bristle dikinetids, i.e. it originates from the posterior basal body along the right side of the glabrous stripe and from the anterior basal body along its left side.

The number of dikinetids comprising the circumoral kinety is much more variable in *T. ditis* than in *T. sagitta* (Table 1). Likewise, their arrangement is more variable which is, however, possibly a preparation artifact. In most specimens the dikinetids form a continuous row (Figs. 57, 58, 61, 63–65), while more or less distinct fragments are recognizable in others (Figs. 60, 68, 69). Scanning electron micrographs revealed that the oral dikinetids have only one basal body ciliated, possibly the posterior. Interestingly, the circumoral cilia and those at the anterior end of the somatic kineties are frequently partially or completely lost by the preparation procedure (Fig. 67).

Genus *Tracheloraphis* DRAGESCO, 1960

1960 *Tracheloraphis* DRAGESCO, Trav. Stn biol. Roscoff, 12: 120.
Type (original designation): *Trachelocerca phoenicopterus* COHN, 1866.

1960 *Trachelonema* DRAGESCO, Trav. Stn biol. Roscoff, 12: 135.
Type (original designation): *Trachelonema longicolle* DRAGESCO, 1960.

Improved diagnosis: Trachelocercidae KENT, 1881 with circumoral kinety interrupted at brosse cleft. Bristle kinety often composed, at least in trunk region, of many minute, oblique kineties, each comprising 2–5 dikinetids. One or more oblique or straight brosse kineties.

Type species: *Trachelocerca phoenicopterus* COHN, 1866 (original designation).

Etymology: Composite of the Greek nouns *trachelos* (neck) and *raphis* (needle). *Raphis* has feminine gender. Unfortunately, many nominal *Tracheloraphis* species were supplied with a masculine termination, obviously because most describers assumed a masculine gender of *raphis* from the termination *us* in *phoenicopterus*, the type species. However, *phoenicopterus* (Flamingo), originally written *Phoenicopterus*, is a noun in apposition, which retains the same ending, whatever the gender of the generic name with which it is combined (article 31b (ii) of the ICZN 1985). This requires many emendations, undertaken in the last chapter of the Results.

Remarks and synonymy: There are no nomenclatural problems because the subsequent designation of *T. phoenicopterus* as type of *Trachelocerca* by DELPHY (1939) is invalid and thus cannot preoccupy DRAGESCO's typification (see genus *Trachelocerca*).

Tracheloraphis differs from *Trachelocerca* mainly by the distinct brosse. Furthermore, the glabrous zone is usually considerably wider and the body more distinctly flattened. The brosse of *Trachelolophos* is unstructured and near the centre of the oral cavity, i.e. *within* the area bordered by the circumoral kinety, which is not interrupted (FOISSNER & DRAGESCO 1996). The second character contained in our diagnosis, viz. the structure of the bristle kinety, is somewhat ambiguous because the minute kineties are inconspicuous in one (*T. aragoi*) of the four species investigated. Thus, this character should possibly be removed from the diagnosis. However, we prefer it as an additional diagnostic, at least at the present state of knowledge, because it is very conspicuous when compared with the single row found in *Trachelocerca* (Figs. 12, 13, 52, 55, 58, 59), *Trachelolophos* (FOISSNER & DRAGESCO 1996) and *Prototrachelocerca* (FOISSNER 1996a).

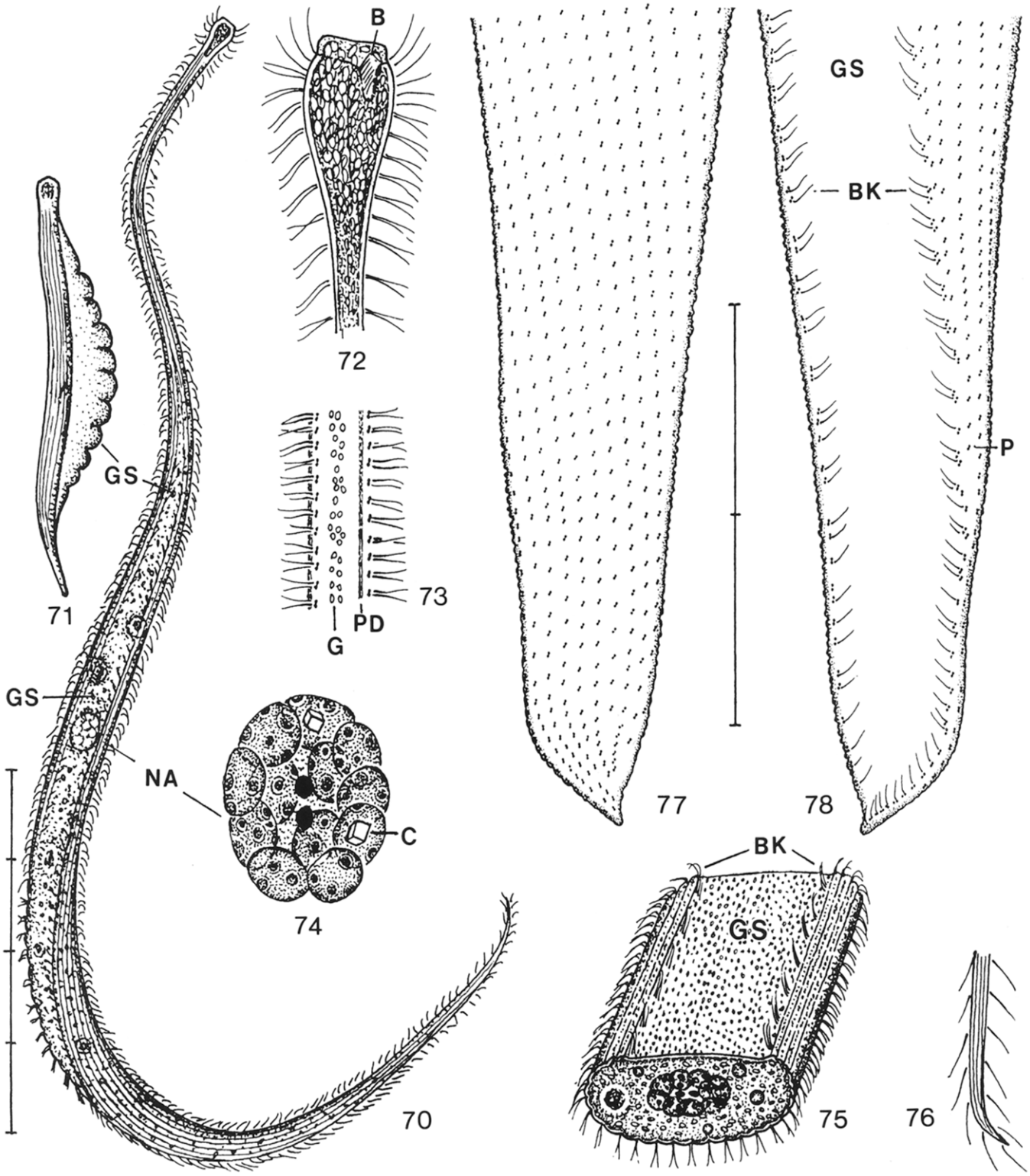
Trachelonema differs from *Tracheloraphis* in that it is flattened leaf-like and the glabrous stripe extends the whole body width, causing the ciliature to be restricted to the right surface (DRAGESCO 1960). We rediscovered the type species, *T. longicolle*, at the locus classicus and can confirm DRAGESCO's observations. This species is indeed very flat and ciliated only on the right side (Figs. 153, 170). However, the somatic and oral infraciliature of *T. longicolle* is very similar to that of *Tracheloraphis phoenicopterus* and *T. aragoi*. Furthermore, there are distinct transitions in body flattening and width of the glabrous stripe, as evident from a comparison of *T. aragoi* (Figs. 112, 132), *T. phoenicopterus* (Figs. 75, 84) and *T. longicollis* (Figs. 151, 153, 170). Other species, e.g. *Tracheloraphis grisea*, are also very flat and have a broad glabrous stripe (DRAGESCO & DRAGESCO-KERNÉIS 1986). Obviously, there is no distinct border between *Tracheloraphis* and *Trachelonema*, suggesting synonymy. Both genera were established in the same paper. We suggest preserving *Tracheloraphis* because it contains more species and has page priority.

The following nominal species of *Trachelonema* are transferred to *Tracheloraphis*: *T. binucleata* (AGAMALIEV, 1966) nov. comb., *T. grassei* (DRAGESCO, 1960) nov. comb., *T. lanceolata* (RAIKOV, 1962) nov. comb., *T. longicollis* (DRAGESCO, 1960) nov. comb., *T. minima* (DRAGESCO, 1960) nov. comb., *T. oligostriata* (RAIKOV, 1962) nov. comb., *T. sulcata* (KOVALEVA, 1966) nov. comb.

Description of a species of the *Tracheloraphis phoenicopterus* complex (COHN, 1866) DRAGESCO, 1960, type of the genus (Figs. 70–101, Tables 2, 3, 6)

Identification and taxonomy: The identity of *T. phoenicopterus* poses many problems because COHN (1866) described and figured three specimens, each obviously belonging to a particular species. RAIKOV (1958, 1962) considered the form with a single nuclear complex as typical, while DRAGESCO (1960) chose the form with a strand of isolated nuclei, later described by RAIKOV (1962) as a distinct species, *T. kahli*. We suggest considering RAIKOV's (1962) study as authoritative redescription because he was the first to bring some order into the chaos.

RAIKOV (1962) also synonymized *T. prenanti* DRAGESCO, 1960 with *T. phoenicopterus*, obviously because of distinct similarities in size, shape, nuclear structure and kinety number. Later, however, RAIKOV & KOVALEVA (1968) recognized *T. prenanti* as a distinct species and even split it into two formae which CAREY (1992) raised to species level, without, however, new evidences. Likewise, RAIKOV & KOVALEVA (1968) did not provide any discussion as to how *T. prenanti* and *T. phoenicopterus* could be distinguished. Accordingly, BORROR (1973) suggested uniting several apparently closely related forms to a "*phoenicopterus* complex", a view consistent with our data. We found two interlacing varieties in our slides, with characters similar to those known from literature (Table 2). The most common form, described in detail below, matches *T. prenanti multicineta* in kinety number, micronuclei number and size of the nuclear capsule, but not in the number of macronuclei which is closer to that of *T. prenanti oligostriata* and RAIKOV's *T. phoenicopterus* (Table 2).



Figs. 70–78. *Tracheloraphis phoenicopterus* from life (Figs. 70–76) and after protargol impregnation (Figs. 77, 78). **70.** Extended specimen. **71.** Fully contracted specimen with glabrous stripe distinctly protruding. **72.** Head with brosse and many ellipsoid inclusions. **73.** Surface view of cortex. **74.** Nuclear apparatus consisting of about 12 macronuclei and 2 micronuclei in centre of cluster. **75.** Transverse section in trunk region. **76.** Tail. **77, 78.** Infraciliature of right and left side in posterior body region. B = brosse, BK = bristle kinety, C = (protein) crystal, G = cortical granules, GS = glabrous stripe, NA = nuclear apparatus, P = posterior secant system, PD = postciliodesma. Scale bar division 50 µm.

Table 2. Some main characteristics of the *Tracheloraphis phoenicopterus/prenanti* complex. Mean or common values, if available, in brackets.

Taxon[1])	Authors[2])	Number				Length (µm)	
		somatic kineties	macro-nuclei	micro-nuclei	brosse kineties	nuclear capsule	body
T. phoenicopterus	1	22–26 (24)	6	5-8 (6)	?	20	600–1300
T. phoenicopterus	2	23–27 (25)	6–12 (12)	2	2–4 (3)	20–30 (25)	1000–1300
T. phoenicopterus	3	19–21 (20)	4–18 ?	2	2–3 (2)	16–30 (22)	?
T. prenanti	4	20–25	6-8	2-3	?	?	400–2000
T. prenanti	5	20–26 (22)	6	2	3	12–13	400–750
T. prenanti oligocineta	6	14–18 (16)	6–8	2	?	15	500–1000
T. prenanti oligocineta	7	15–18	6–8	2	?	14–17	700–1200
T. prenanti oligocineta	8	15–17	6	2	?	?	500–1000
T. prenanti multicineta	6	20–26 (24)	16–20	2	?	25	800–1600

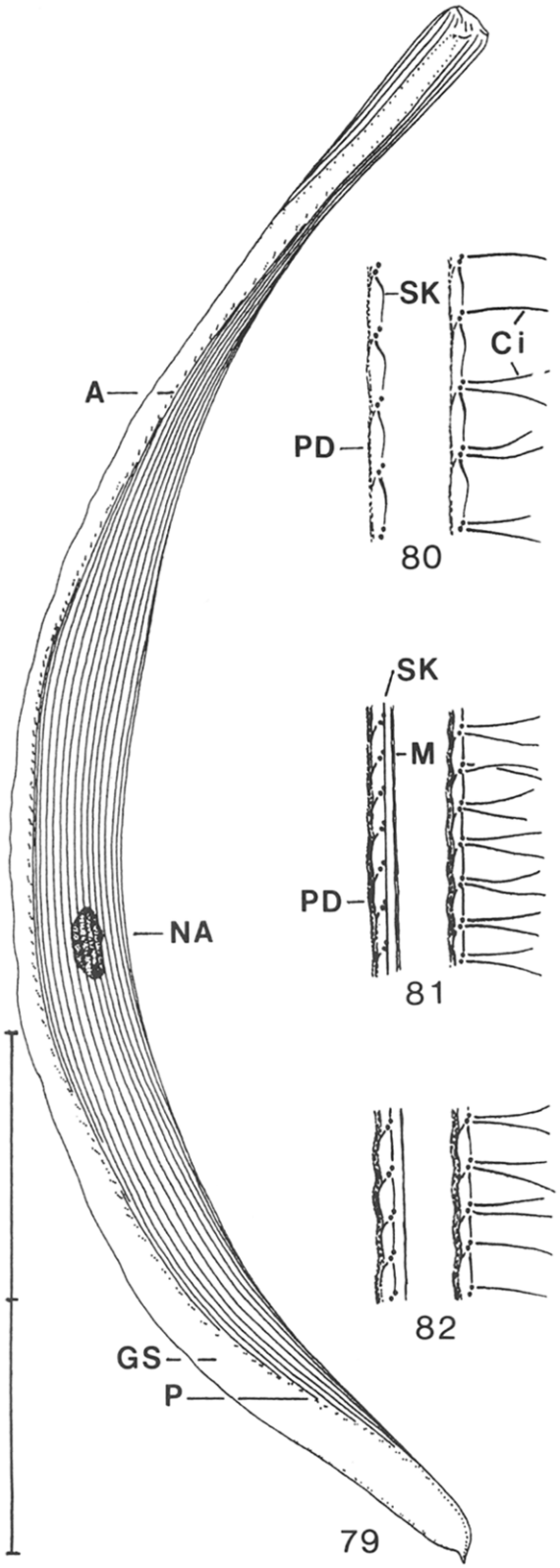
[1]) All populations are filiform and have a wide glabrous zone, corresponding to 6 - 8 kineties.
[2]) 1 – RAIKOV (1958, 1962), 2 – population described in this paper, 3 – this study, 10 specimens of another population not studied in detail, 4 – DRAGESCO (1960), 5 – DRAGESCO & DRAGESCO-KERNÉIS (1986), 6 – RAIKOV & KOVALEVA (1968), 7 – WRIGHT (1983), 8 – AGAMALIEV (1983).

Whether the *phoenicopterus* complex consists of a single, highly variable species, of several distinct, still insufficiently characterized morphospecies or, as we believe, of a set of sibling species, needs further investigation. At the present state of knowledge, the populations listed in Table 2 and some other species assigned to the complex by BORROR (1973) are hardly distinguishable. Further studies should thus try to characterize such populations in more detail, i.e. apply at least the methods we used and, if feasible, molecular techniques.

Specimens investigated and type material: The description is based on 10 well-impregnated specimens; some others were of usuable quality and served for completing morphometry. No type material of *T. phoenicopterus* has been mentioned in the literature. Thus, we declare the Roscoff population described below as neotype and deposit two slides with neotype specimens, prepared as described, in the Oberösterreichisches Landesmuseum in Linz (LI), Austria. Relevant specimens are marked by a black ink circle on the cover glass.

Description (Figs. 70–101, Tables 2, 3, 6): Size of fully extended specimens in vivo about 1,000–1,500 × 30–50 µm, highly flexible and contractile, size and shape thus poorly preserved, but better than in *Trachelocerca* spp., in protargol slides (Table 3; Figs. 70, 79); trunk distinctly, i.e. 2–3:1 flattened (Fig. 75). Greyish and opaque in dissecting and bright-field microscope. Fully extended specimens filiform with anterior and posterior third gradually tapering, neck and tail thus indistinctly separate from trunk (Fig. 70). Head slenderly claviform, dark to black at low magnification (≤ X 100) due to many about 4 × 2 µm sized, refractile (crystalline ?) inclusions; oral bulge inconspicuous but easy to recognize because distinctly set off from head, about 3 µm high, surface slightly depressed in centre, contains, like the head, ellipsoid inclusions; brosse cleft difficult to recognize (Figs. 70, 72). Distal end of tail pointed and distinctly curved (Figs. 70, 76). Fully contracted specimens banana-shaped in vivo, convex side with glabrous stripe distinctly protruding and tuberculate (Fig. 71); partially contracted cells sometimes spiral and with glabrous stripe indistinctly tuberculate (Fig. 79). Nuclear apparatus (capsule) in centre of trunk, surrounded by voluminous layer of pale, 2–3 µm sized granules faintly stained with protargol (Fig. 85); nuclei form tight, distinctly ellipsoid cluster, possibly a capsule, their number thus difficult to recognize, 6–12 macronuclei and 2 micronuclei are common. Macronuclei 6–8 µm in vivo, with small and medium-sized nucleoli, two of them contain a cubiform protein crystal which does not stain with protargol (Figs. 70, 74, 75, 85). Micronuclei about 4 µm in vivo, in centre of macronuclear cluster. See RAIKOV & KOVALEVA (1978) for a detailed transmission electron microscope account of the nuclear apparatus of *T. phoenicopterus*. No contractile vacuole. Cortex very flexible, about 1 µm thick, forms tubercles in contracted specimens. Cortical granules ellipsoid to fusiform, minute (about 1.2 × 0.6 µm), yellowish, form narrow stripes between ciliary rows and rather dense layer in cortex of glabrous stripe (Figs. 73, 75). Glides and winds elegantly between sand grains and organic debris.

Somatic infraciliature (Figs. 77, 78–97, 100, 101). The surface of *T. phoenicopterus* is densely ciliated, leaving



Figs. 79–82. *Tracheloraphis phoenicopterus*, infraciliature after protargol impregnation. **79.** Total left lateral view. Bar division 100 µm. **80–82.** Somatic fibrillar system and ciliation in head/neck, trunk, and tail region. A = anterior secant system, Ci = cilia, GS = glabrous stripe, M = myoneme, NA = nuclear apparatus, P = posterior secant system, PD = postciliodesma, SK = subkinetal microtubule ribbon.

blank a rather wide zone, the glabrous stripe, extending the whole body length in the midline of the left side (Figs. 70, 75, 78, 79, 84). The cilia, which are rather stiff and can be spread, are about 10 µm long and arranged in longitudinal rows which are distinctly separate from the circumoral ciliature and extend between flat cortical crests. The anterior end of the ciliary rows has condensed, i.e. more narrowly spaced dikinetids and is curved to the right. Usually, the condensation is inconspicuous or even lacking in some kineties (Figs. 87–91, 98, 99); rarely, it is absent in most kineties (Fig. 93). 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 and posterior secant system are formed on the left surface of the neck and tail where some kineties abut to the bristle kinety. Thus, the head, neck, and tail have about one third less kineties than the trunk (Table 3). The ciliary rows neighbouring the right branch of the bristle kinety are unshortened anteriorly and thus extend alongside 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. 83–86).

The entire infraciliature consists of dikinetids which have, however, a highly specialized ciliation and fibrillar system (Figs. 80–82, 87, 92, 94–96). The dikinetids are rotated about 20–30° counter-clockwise to the kinety axis and have both basal bodies ciliated, except the condensed kinetids at the anterior and the widely spaced kinetids at the posterior end of the somatic kineties, where only the anterior basal bodies are ciliated (Figs. 80–82, 90, 93). Likewise, the kinetids at the ends of the secant kineties lack the posterior cilium. The dikinetids are associated with various distinct fibres, all very likely originating from the posterior basal bodies (Figs. 80–82, 87, 88, 92). Our observations largely agree with the transmission electron microscopic investigations of Raikov & Kovaleva (1995) and Raikov et al. (1975) who, however, did not recognize the oralized somatic kinetids and some site-specific differences. On the other hand, the transverse microtubule ribbons and kinetodesmal fibres did not stain in our preparations. The most conspicuous fibres are the postciliary microtubule ribbons, several of which overlap to form a distinct bundle (postciliodesma) right of each kinety. The postciliodesmata are thinner in the head and neck region than in the trunk and tail. The subkinetal microtubules form a very thin, but sharply impregnated bundle underneath or close to the left of the kineties. They do not or hardly overlap in the head, neck and tail region, where their comma-like shape can thus be recognized. All head and neck dikinetids have associated a thin, rather irregular fibre, very likely a nematodesma,

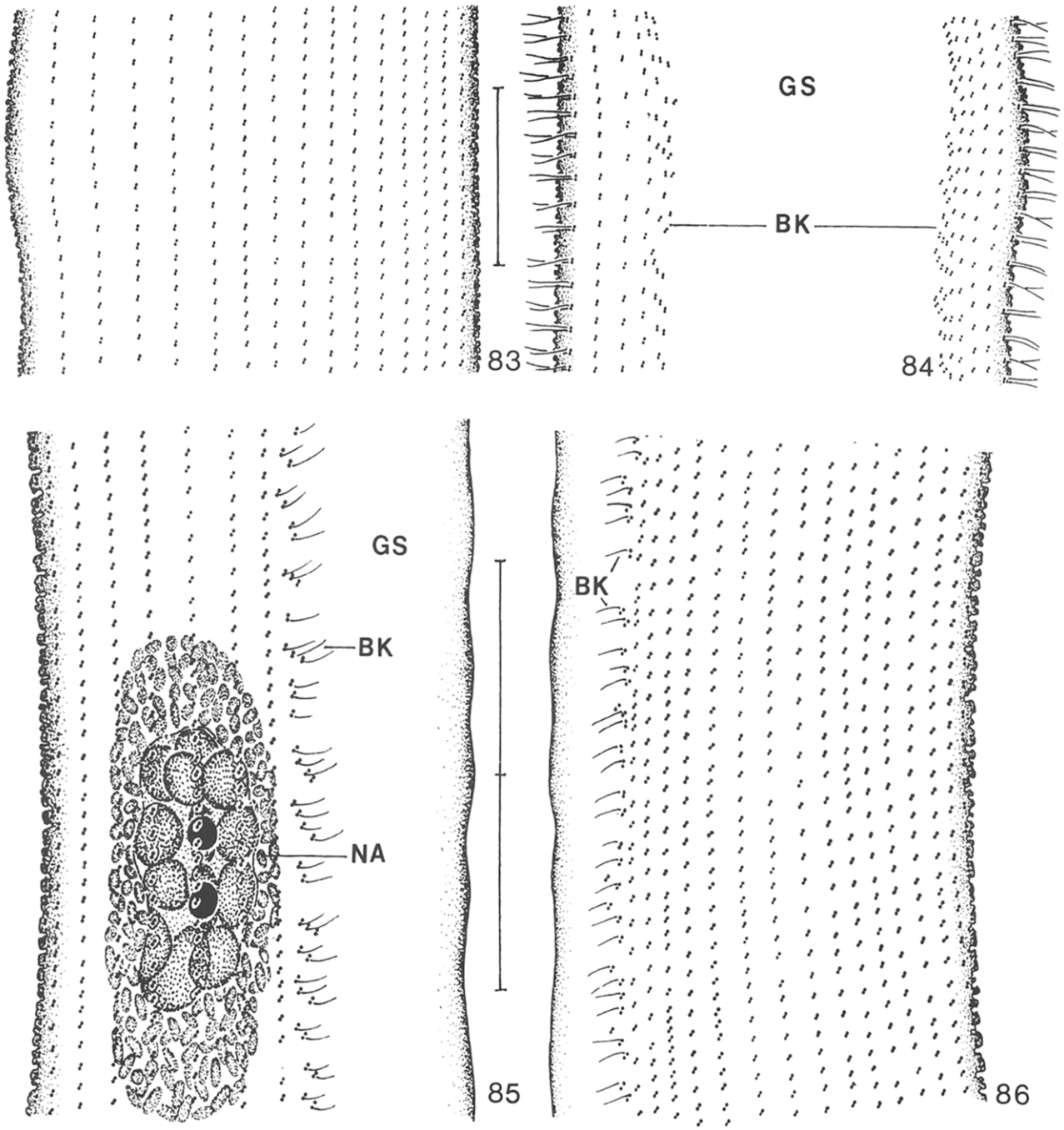
Table 3. Morphometric characteristics from *Tracheloraphis phoenicopterus* (upper line) and *T. aragoi* (lower line).

Character[1])	$\bar{x}$	M	SD	$SD_{\bar{x}}$	CV	Min	Max	n
Body, length[2])	571.4	570.0	105.5	28.2	18.5	400	730	14
	971.0	950.0	169.0	36.1	17.4	600	1400	22
Body, width at head	25.4	25.5	3.8	1.0	14.8	19	32	14
	28.8	29.0	3.0	0.6	10.5	21	34	30
Body, (maximum) width at trunk[3])	53.2	54.5	8.4	2.2	15.7	40	67	14
	85.4	90.0	16.9	3.8	19.7	60	120	21
Glabrous stripe, width in mid-body[3])	43.1	45.0	11.7	3.9	27.2	30	68	9
	9.9	10.0	1.8	0.5	18.1	7	13	12
Anterior end to nuclear capsule,	322.9	312.5	90.5	24.2	28.0	190	500	14
distance	389.8	392.5	62.8	14.0	16.1	250	520	20
Nuclear capsule, length	24.9	25.0	2.8	0.8	11.3	20	30	14
	31.9	33.0	4.0	1.0	12.5	25	38	16
Nuclear capsule, width	13.6	14.0	1.3	0.4	9.8	11	15	14
	18.5	18.5	2.2	0.6	12.2	14	22	16
Macronuclei, length	not measured because often not distinctly stained							
	10.1	10.0	1.8	0.3	17.5	6	15	32
Macronuclei, width	not measured because often not distinctly stained							
	6.6	7.0	0.8	0.2	12.9	5	8	26
Anterior brosse kinety, length	2.4	2.5	0.8	0.2	33.3	1	3.5	11
	2.7	2.7	1.8	0.6	66.6	0.5	6	10
Middle brosse kinety, length	3.5	3.5	0.8	0.2	23.9	2	5	12
	3.9	4.0	1.5	0.4	39.5	2	7.5	15
Posterior brosse kinety, length	3.9	4.0	1.0	0.3	26.3	2	5.5	12
	7.1	7.0	0.7	0.2	10.4	5.5	8	15
Somatic kineties, number on head	17.9	18.0	1.6	0.4	9.0	14	20	14
	20.6	20.0	1.9	0.4	9.2	12	24	20
Somatic kineties, (maximum)	24.7	24.5	1.2	0.3	4.9	23	27	14
number on trunk	38.2	38.0	1.9	0.4	5.0	36	42	20
Dikinetids, number in 10 µm in	3.6	3.5	1.3	0.3	35.5	2	6	14
neck region	7.2	7.0	0.6	0.2	8.4	6	8	13
Dikinetids, number in 10 µm in	7.3	7.0	1.8	0.5	24.9	5	11	14
trunk region	8.8	9.0	1.4	0.5	15.5	7	11	10
Bristle kinety, (maximum) number	3.4	3.0	0.6	0.2	19.0	3	5	14
of kinetids in oblique row	indistinct							
Brosse kineties, number	2.9	3.0	0.5	0.1	17.8	2	4	12
	2.6	3.0	_	_	_	2	3	20
Dikinetids in anterior brosse kinety,	4.1	4.0	1.0	0.3	25.5	3	6	11
number	5.6	4.5	4.0	1.3	72.0	1	11	10
Dikinetids in middle brosse kinety,	6.7	7.0	1.8	0.5	26.3	3	9	12
number	9.9	10.0	4.4	1.1	44.4	3	19	16
Dikinetids in posterior brosse	6.8	7.0	2.2	0.6	32.5	3	10	12
kinety, number	16.1	15.5	3.2	0.8	20.0	11	23	16
Macronuclei, number in capsule	about 6–12							
	8.7	9.0	1.9	0.4	21.7	5	12	20
Micronuclei, number in capsule	about 2–6, usually 2							
	2.0	2.0	0.0	0.0	0.0	2	2	20

[1]) Data based on protargol impregnated and mounted morphostatic specimens from field. 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 which strongly contract when fixed for preparation.

[3]) Data of very limited value because species are highly contractile and trunk often becomes inflated due to preparation procedures.

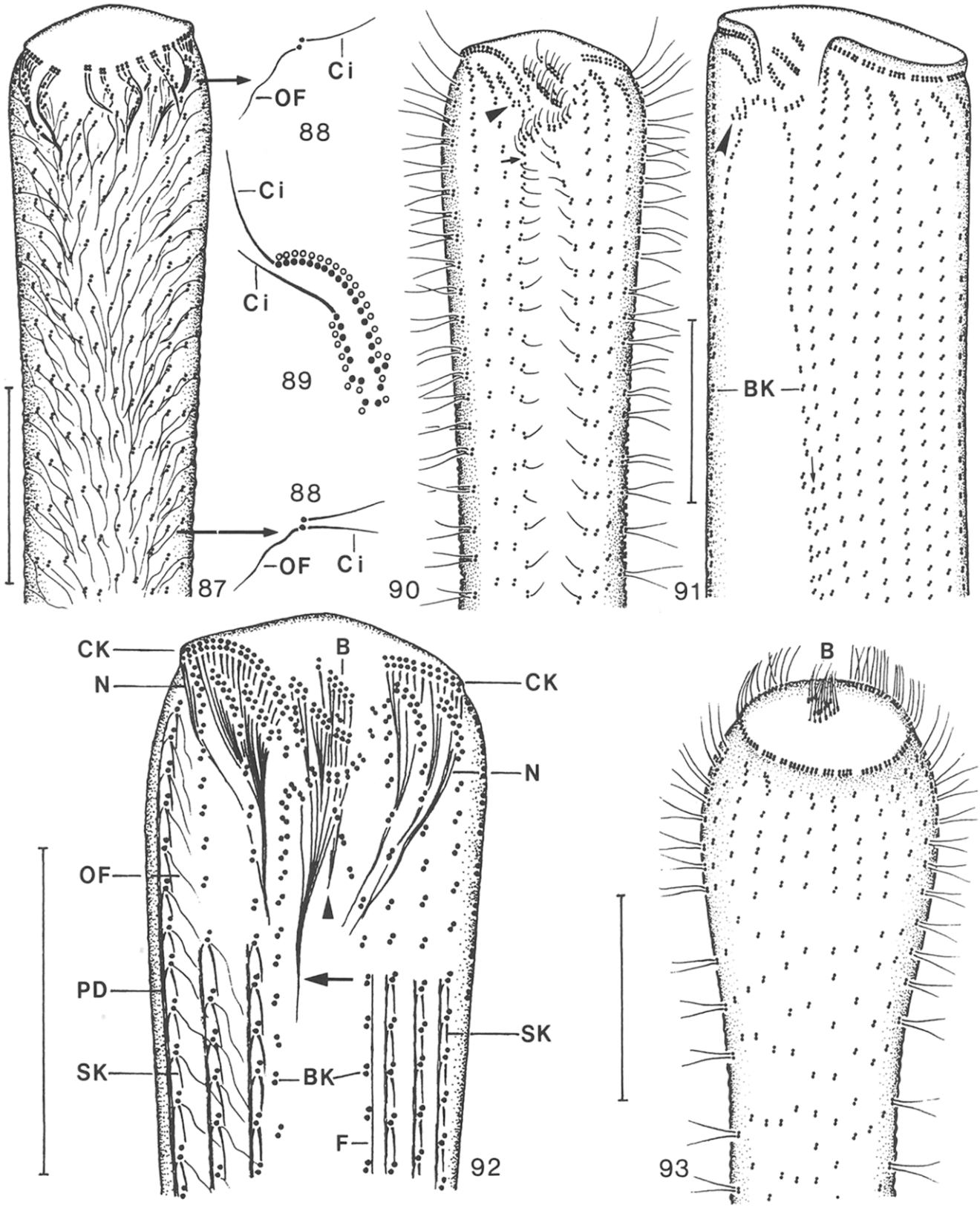


Figs. 83–86. *Tracheloraphis phoenicopterus*, trunk infraciliature after protargol impregnation. **83, 84.** Right and left side view of same specimen. Note broad glabrous stripe. **85, 86.** Lateral views of same specimen. The nuclear capsule is surrounded by a thick layer of ellipsoid structures. BK = bristle kinety, GS = glabrous stripe, NA = nuclear apparatus. Scale bar division 20 µm.

extending obliquely to the centre (Figs. 87, 88). Thus, they are oralized somatic kinetids as defined by FOISSNER & FOISSNER (1988).

The contractile apparatus of *T. phoenicopterus* is very similar to that described in *Trachelocerca sagitta* and *T. ditis*. However, the myonemes appear thinner and string-like and are lacking or unstained in the head and neck region (Figs. 80–82, 92).

The glabrous stripe, which extends 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



Figs. 87–93. *Tracheloraphis phoenicopterus*, head and neck infraciliature after protargol impregnation. **87–90, 92.** All from same, especially well-impregnated specimen (cp. Figs. 94–96), right and left lateral views. Figure 88 shows oralized somatic dikinetids. Figure 89 shows curved right end of circumoral kinety, marked by arrowhead in Fig. 90, at high magnification (open circles = barren basal bodies). Arrow in Fig. 90 marks site where right end and anterior arch of bristle

by about 10 kineties, i.e. approximately two thirds of body width (Figs. 70, 75, 78, 79, 84, 90, 94). The glabrous stripe is bordered by the bristle kinety which consists, like the ordinary ciliary rows, of dikinetids having about 12 µm long, rather stiff cilia. However, the bristle kinety is easily distinguished from ordinary somatic ciliary rows because its dikinetids are more widely spaced and more irregularly arranged and either lack or have very inconspicuous postciliary microtubule ribbons, too small to be recognized with the light microscope (Figs. 75, 78, 79, 84–86, 90–92, 94, 97, 98, 100, 101); there is, however, a very faintly stained fibre along its left branch (Fig. 92). The bristle kinety is continuous at the posterior end of the cell (Fig. 78), whereas its anterior end appears covered by a short, oblique kinety ("anterior arch of bristle kinety") composed of about 10–15 rather irregularly arranged dikinetids. The dikinetids of this segment might belong to the oral ciliature because they have, like the circumoral kinety and the brosse kineties, associated nematodesmata-like fibres extending posteriorly near the cell surface (Figs. 90–92, 94, 98, 195). The ciliation of the bristle dikinetids is the same as described in *Trachelocerca sagitta*, i.e. those along the right margin of the glabrous stripe have the posterior basal bodies ciliated, whereas the dikinetids along the left stripe margin have the anterior basal bodies ciliated (Figs. 78, 85, 86, 90).

The bristle kinety of *T. phoenicopterus* and some other species mentioned below is unique in being composed of many minute, oblique kineties, consisting of 2–5 dikinetids, in the trunk region (Figs. 85, 86, 97, 101). The proximal (inner) granule (rarely two) of the oblique kineties frequently appears unciliated and unpaired, indicating that it is not a kinetid but a special type of cortical granule, possibly an extrusome (KOVALEVA 1974). The oblique kineties become gradually shorter and more vertically arranged towards the ends of the cell, where the bristle kinety is of usual structure, i.e. composed of single, rather widely spaced dikinetids (Figs. 94, 98, 100). We cannot exclude that this peculiar pattern is caused by a particular mode of contraction of the cell during fixation. However, *Tracheloraphis aragoi* and *Trachelocerca sagitta*, which are also highly contractile, lack such kineties. On the other hand, the glabrous stripe is much more narrow in *T. aragoi* and *T. sagitta* than in the other species, which certainly influences its shape in contracted cells. This could also explain the lack of minute kineties in the neck and tail region of *T. phoenicopterus*, *T. longicollis* and *T. oligostriata*, where the glabrous stripe is as narrow as in the trunk region of *T. aragoi*. Furthermore, the bristle kinetids are more widely spaced in the neck and tail than in the trunk region, i.e. have enough space to arrange one behind the other when the cell contracts.

Oral infraciliature (Figs. 87–96, 98, 99). The oral infraciliature of *T. phoenicopterus* consists of a circumoral kinety and a distinct brosse, both associated with conspicuous fibres, very likely nematodesmata, clearly recognizable, however, only in perfectly impregnated specimens (Figs. 94–96). The circumoral kinety extends in the flat furrow separating the oral bulge from the head and is composed of a single row of vertically orientated dikinetids having, very likely, only the posterior basal body ciliated. Each circumoral dikinetid is associated with a distinct fibre (nematodesma) obliquely extending into the head. The nematodesmata of neighbouring dikinetids unite to conspicuous bundles, forming a cone-shaped oral basket (Figs. 87, 92, 95, 96). The circumoral kinety is very likely composed of rather many fragments, as indicated by small gaps, 1–2 dikinetids wide, and the bundled arrangement of the nematodesmata. The circumoral kinety is interrupted where the brosse kineties are inserted. Its left end simply abuts to the margin of the brosse cleft, i.e. to the left lip of the oral bulge. The right end is more complicated. It extends along the oblique margin of the brosse cleft and curves back at the cleft vertex in such a steep angle that a loop-like structure, or a small oblique segment, is formed paralleling the descending portion of the circumoral kinety and the anterior end of the neighbouring somatic kinety (Figs. 89, 90, 92, 94, 98). This peculiar configuration becomes evident, as in the bristle kinety, from the ciliation of the dikinetids: those in the bulge furrow have the posterior basal body ciliated, whereas the anterior basal bodies are ciliated in the curved segment (Fig. 89).

The brosse is located in a rather deep cavity, the brosse pocket, just above the arch of the bristle kinety, and intersects the circumoral kinety (Figs. 90–96, 98). The cilia of the brosse emerge through the brosse cleft, which divides the oral bulge and the circumoral cilia-

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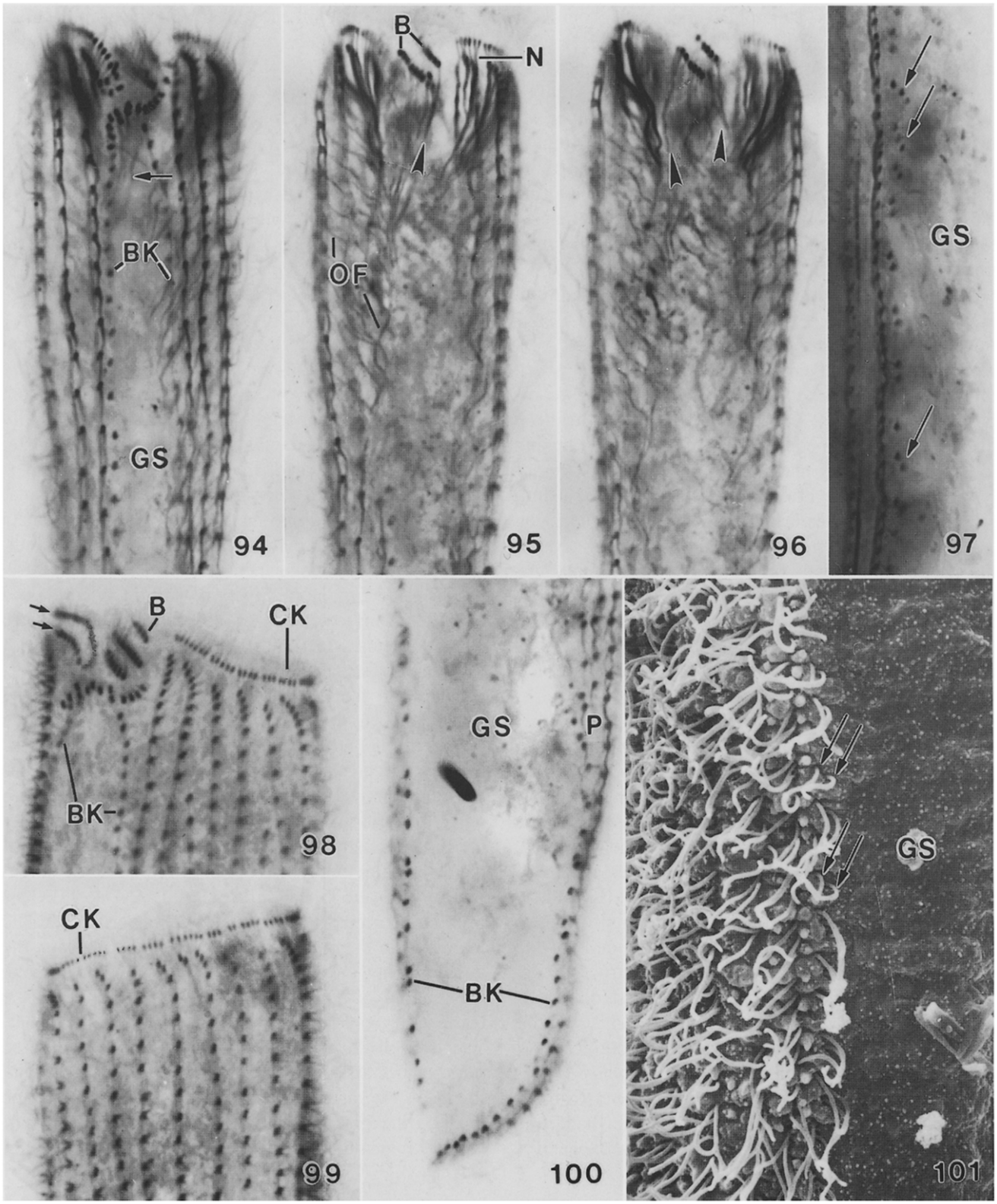
kinety abut and ciliation of bristle kinetids is opposed by about 180°. Arrow in Fig. 92 marks fibre bundle originating from anterior arch of bristle kinety; arrowhead denotes fibre bundle originating from brosse kinety 2. **91.** Specimen with three brosse kineties. The anterior ends of the bristle kinety are covered by a transverse arch (arrowhead), very likely belonging to the circumoral ciliature. Arrow marks first kinety of anterior secant system. **93.** Oblique view showing that brosse extends deeply into head. B = brosse, BK = bristle kinety, Ci = cilia, CK = circumoral kinety, F = fibre, N = nematodesmata, OF = oblique fibre, PD = postciliodesma, SK = subkinetal microtubule ribbon. Scale bars 20 µm.



Figs. 94–101. *Trachelorapbis phoenicopterus*, oral and somatic infraciliature after protargol impregnation (Figs. 94–100) and in the scanning electron microscope (Fig. 101). **94– 96.** Head and neck of specimen shown in Figs. 87–90, 92. Arrow in Fig. 94 marks fibre bundle originating from anterior arch of bristle kinety. Arrowheads mark fibres originating from brosse kineties. **97, 101.** In the trunk region, the bristle kinety consists of short, oblique rows (arrows). **98, 99.** Left and right side view of specimen with three brosse kineties. Arrows mark curved right end of circumoral kinety. **100.** Left side view of tail. B = brosse, BK = bristle kinety, CK = circumoral kinety, GS = glabrous stripe, N = nematodesmata, OF = oblique fibres (nematodesmata of oralized somatic dikinetids), P = posterior secant system.

ture into a right and left half (Fig. 72). The brosse consists of 2–4, usually 3, oblique kineties composed of closely spaced dikinetids having only the posterior basal body ciliated (Figs. 90–92, 95–98). The variation in the number of brosse kineties is not caused by a mixture of different species because the specimens with 2 or 4 kineties match those with 3 kineties very well in all other characteristics. Furthermore, a similar variation has been observed in *T. aragoi* (Table 3) and *Prototrachelocerca* (FOISSNER 1996a). The brosse kineties are arranged in parallel one behind the other and their dikinetids are associated with distinct fibres extending, like the circumoral nematodesmal bundles, into the head (Figs. 92, 95, 96).

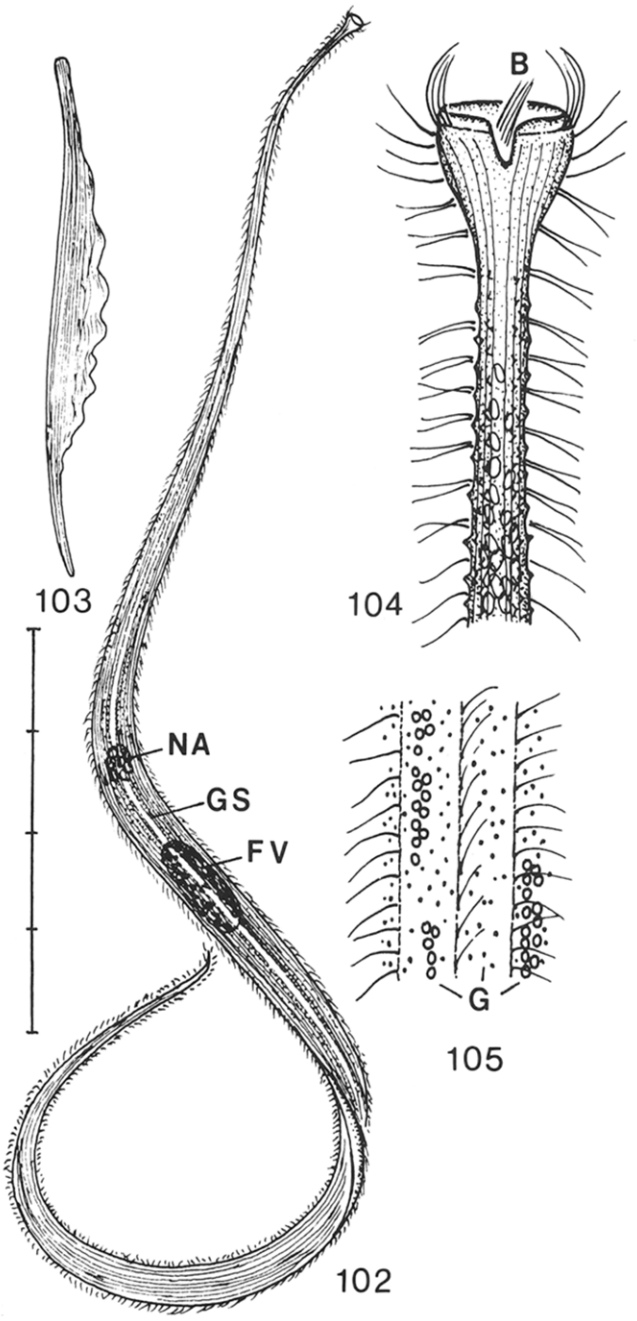
Redescription of *Tracheloraphis aragoi* (DRAGESCO, 1954) DRAGESCO, 1960 (Figs. 102–147, Tables 3, 6)

Identification: The populations from Sète and Roscoff match the type population from Banyuls sur Mer (France) in most main characters, particularly the unique cortical granulation, the narrow glabrous stripe, the nuclear apparatus, and the shape and size of the body. The only significant difference concerns the number of ciliary rows, 26–28 in the type population and 36–42 in the specimens from Sète and Roscoff. However, it is reasonable to assume that DRAGESCO (1954b, 1960), lacking the advantage of silver impregnation, underestimated the kinety number; he also did not recognize the brosse. An other difference concerns the size of the cortical granule clusters which are much larger in the Sète than in the Banyuls and Roscoff specimens (Figs. 105, 110, 116, 130–132, 135, 137).

The populations from Roscoff and Sète agree well in all main characteristics, especially the number of somatic kineties (36–39, $\bar{x}$ 37.4, n 5; 36–42, $\bar{x}$ 38.2, n 20), the nuclear apparatus (6 macronuclei, 2 micronuclei, n 4; 5–12 macronuclei, 2 micronuclei, n 20), the narrowness of the glabrous stripe, and the cortical granule clusters which, however, are larger in the Sète than in the Roscoff population.

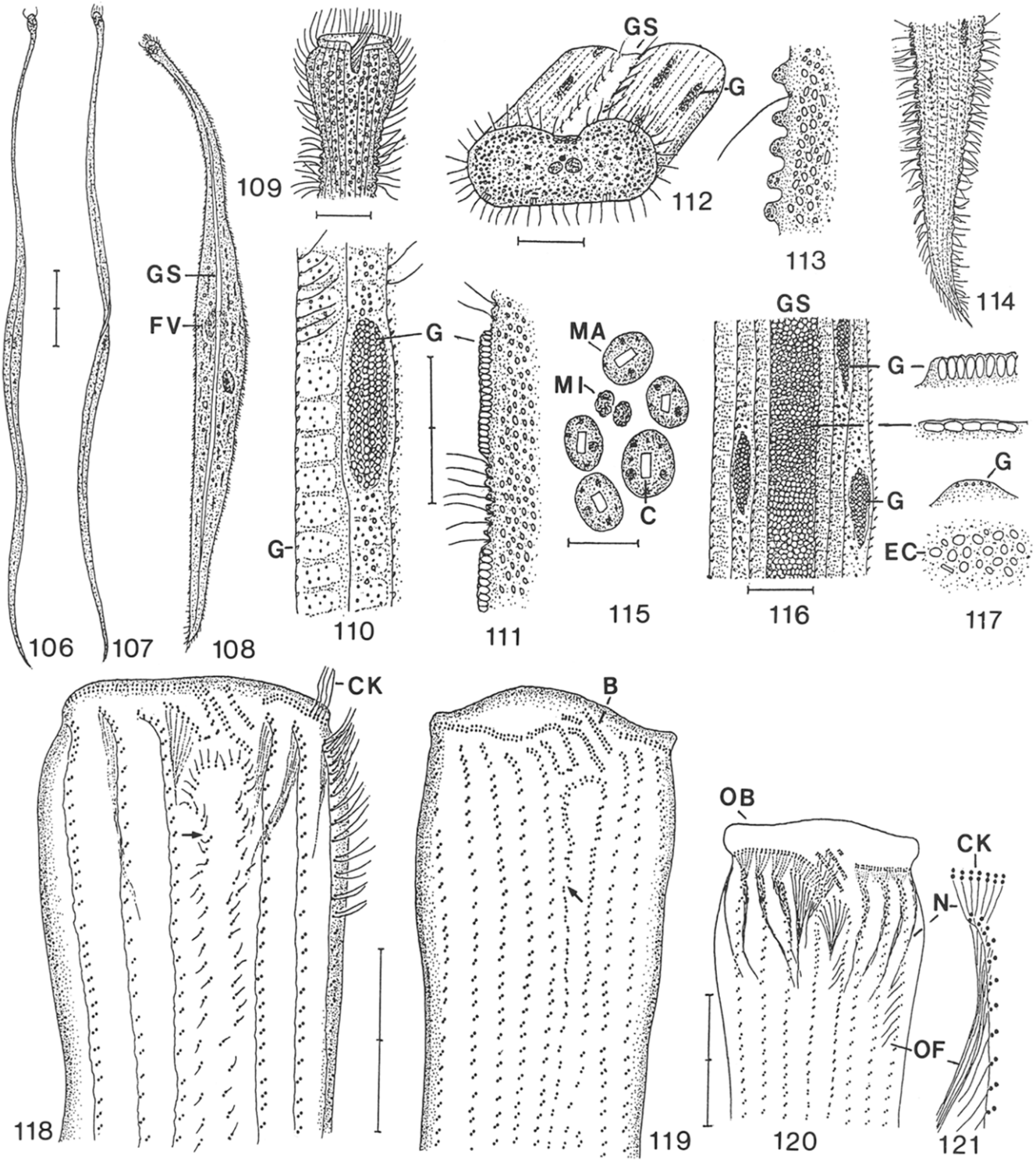
Specimens investigated and type material: The redescription is based on 20 well-impregnated specimens from Sète. The few specimens from Roscoff, briefly described above and illustrated in Figs. 102–105, 129–131, served for comparison only. No type material of *T. aragoi* is available. Thus, we declare the Sète population described below as neotype and deposit two slides with neotype specimens, prepared as described, in the Oberösterreichisches Landesmuseum in Linz (LI). Relevant specimens are marked by a black ink circle on the cover glass.

Improved diagnosis (based on the present investigations and literature data discussed above): Fully extended cells in vivo about 1,100–2,300 × 50–60 µm.

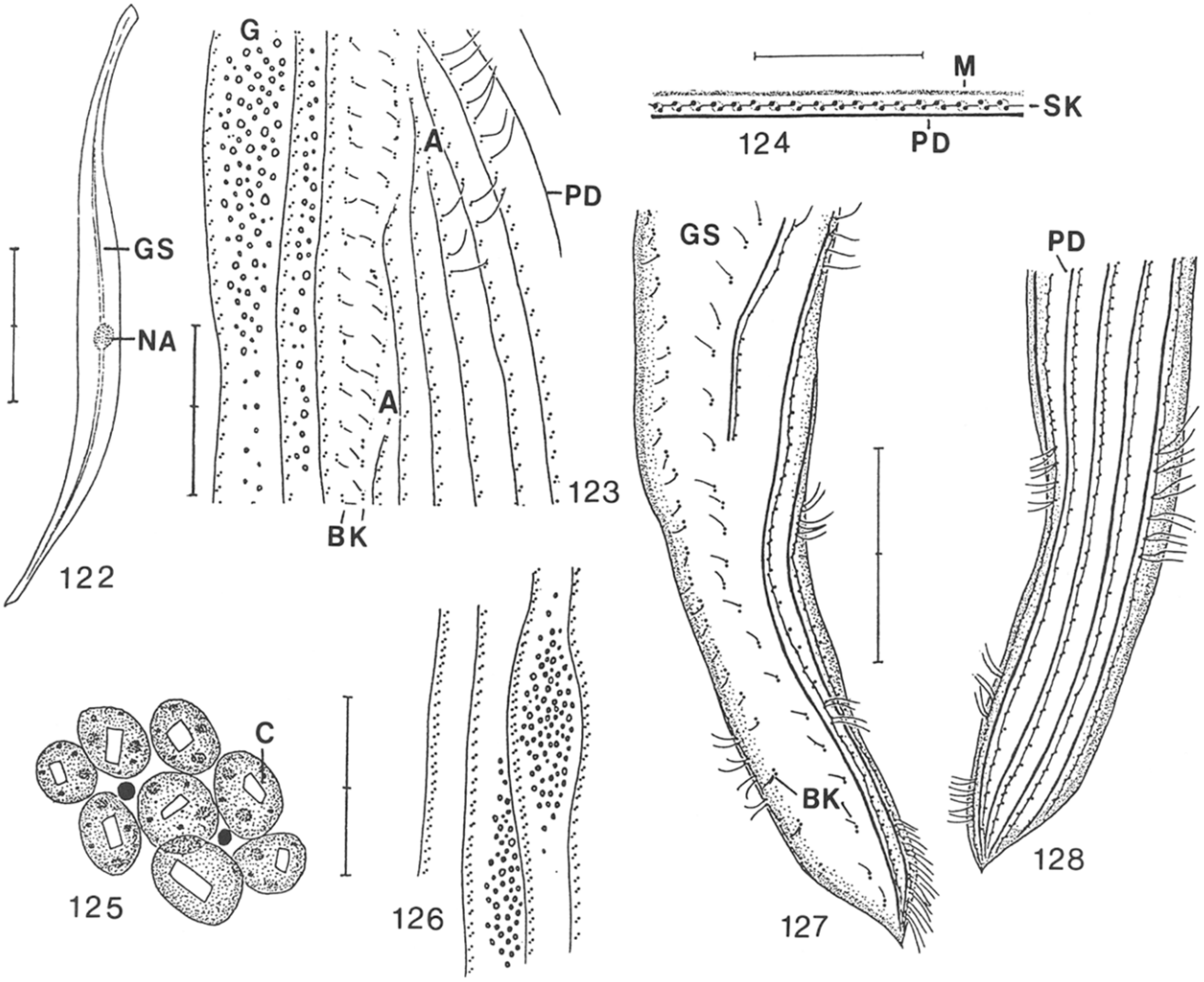


Figs. 102–105. *Tracheloraphis aragoi* (Roscoff population) from life. **102.** Fully extended specimen. Bar division 100 µm. **103.** Contracted specimen with margins of glabrous stripe distinctly folded. **104.** Fully extended head. Note minute cortical spines on neck surface. **105.** Surface view showing two types of cortical granules. B = brosse, FV = food vacuole, G = cortical granules, GS = glabrous stripe, NA = nuclear apparatus.

Filiform and 2–3:1 flattened laterally, neck and tail indistinctly separate from trunk, head claviform to calciform, distal end of tail distinctly narrowed and curved. 5–12 macronuclei and 2 micronuclei forming



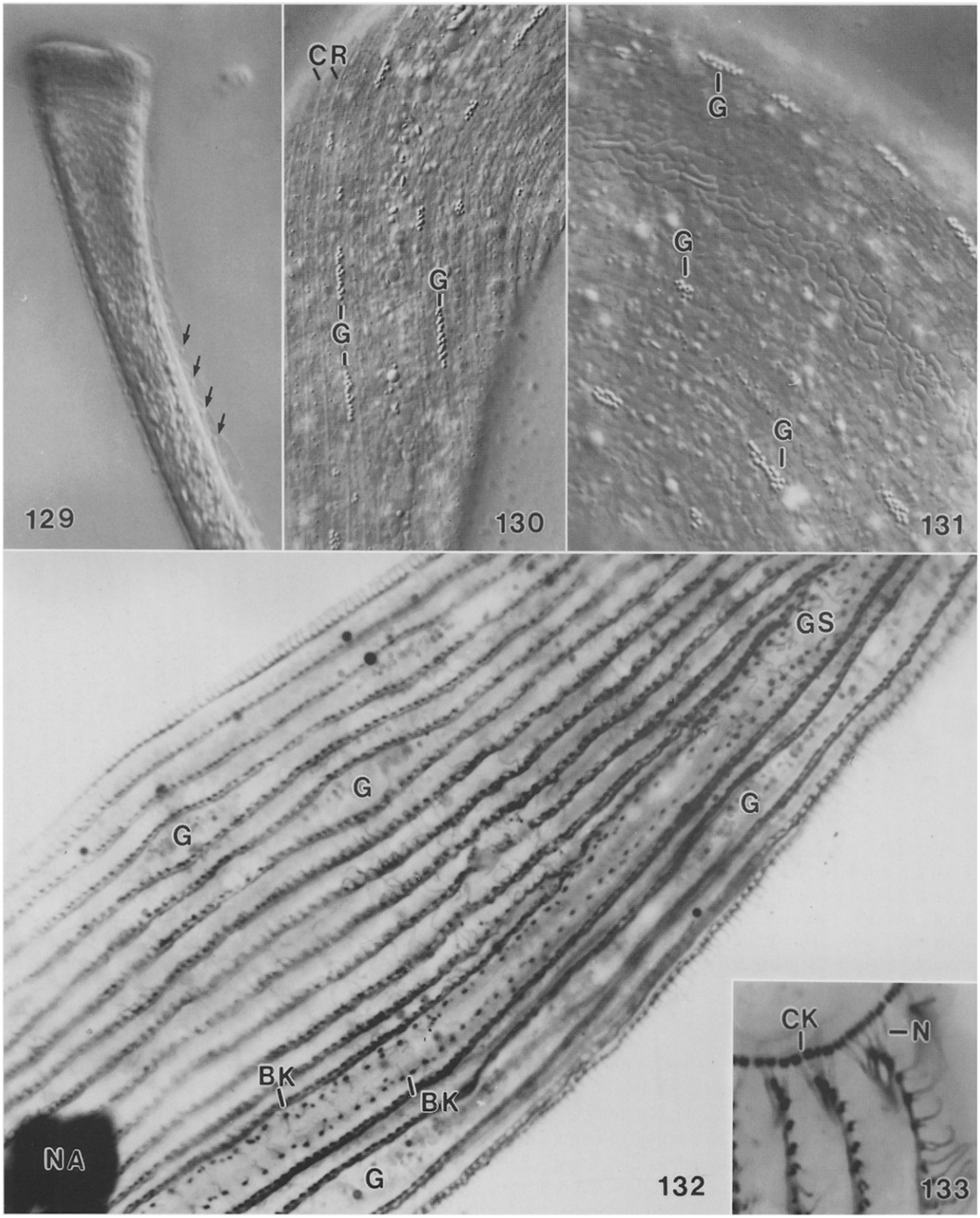
Figs. 106–121. *Tracheloraphis aragoi* (Sète population) from life (Figs. 106–117) and after protargol impregnation (Figs. 118–121). **106, 107.** Fully extended specimens. **108.** Slightly squeezed and contracted specimen. **109.** Head. **110, 111.** Surface view and optical section of cortex showing two types of cortical granules. **112.** Transverse section of trunk. **113.** Cortex in neck region. **114.** Tail. **115.** Nuclear apparatus. **116, 117.** Left side surface view and transverse section of cortex in trunk region. The glabrous stripe is underlain by a dense layer of yellowish structures. **118 - 120.** Left side views of head infraciliature. Arrows mark site where right end and anterior arch of bristle kinety abut and ciliation of bristle dikinetids is opposed by 180°. **121.** Oral fibre system. B = brosse, C = (protein) crystal, CK = circumoral kinety, EC = ellipsoid (crystalline?) inclusions, FV = food vacuole, G = cortical granules, GS = glabrous stripe, MA = macronucleus, MI = micronucleus, N = nematodesmata, OB = oral bulge, OF = oblique fibres of oralized somatic dikinetids. Scale bar division 10 µm (Figs. 116, 118 - 120), 20 µm (Figs. 109 - 115) and 100 µm (Figs. 106 - 108).



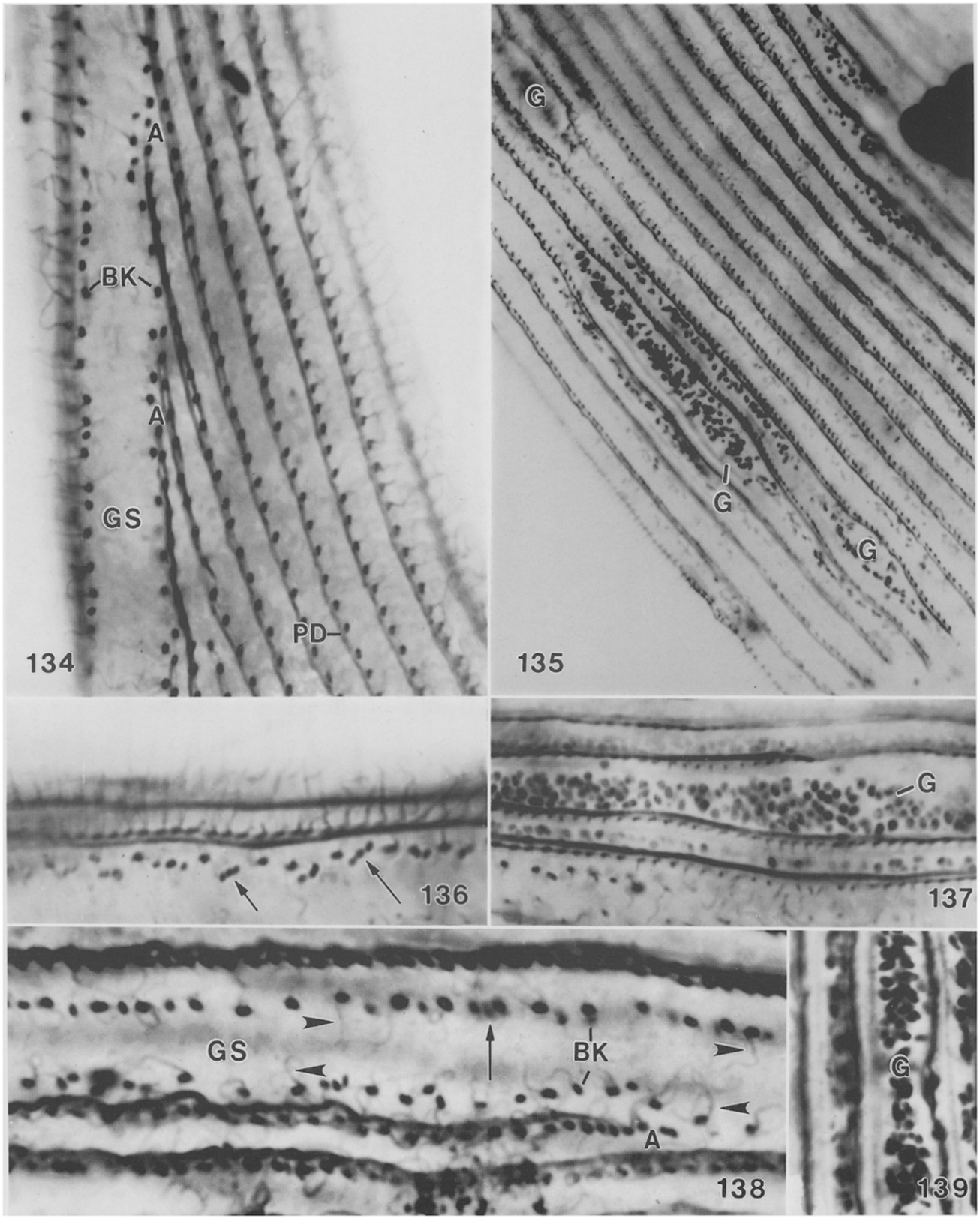
Figs. 122–128. *Tracheloraphis aragoi*, somatic infraciliature and nuclear apparatus after protargol impregnation. **122.** General left side view. Note comparatively well-preserved body shape and narrow glabrous stripe. **123.** Left side view at neck base. **124.** Somatic fibrillar system. **125.** Nuclear apparatus. **126.** Granule clusters frequently bulge ciliary rows. **127, 128.** Left and right side view of tail region. A = anterior secant system, BK = bristle kinety, C = (protein) crystal, G = cortical granule clusters, GS = glabrous stripe, M = myoneme, NA = nuclear apparatus, PD = postciliodesma, SK = subkinetal microtubule ribbon. Scale bar division 10 μm (Figs. 123–128) and 100 μm (Fig. 122).

loose cluster in centre of trunk. 36–42 somatic ciliary rows; glabrous stripe narrow, corresponds to an area occupied by 1–2 kineties. Bristle kinety composed of longitudinal row of dikinetids containing some minute kineties each comprising 2–4 dikinetids. 2–4, usually 3, oblique brosse kineties. Two types of yellowish cortical granules: type 1 about 2 μm across, highly refractile, forms distinct, widely spaced clusters between ciliary rows; type 2 inconspicuous, 0.2–0.5 μm across, scattered.

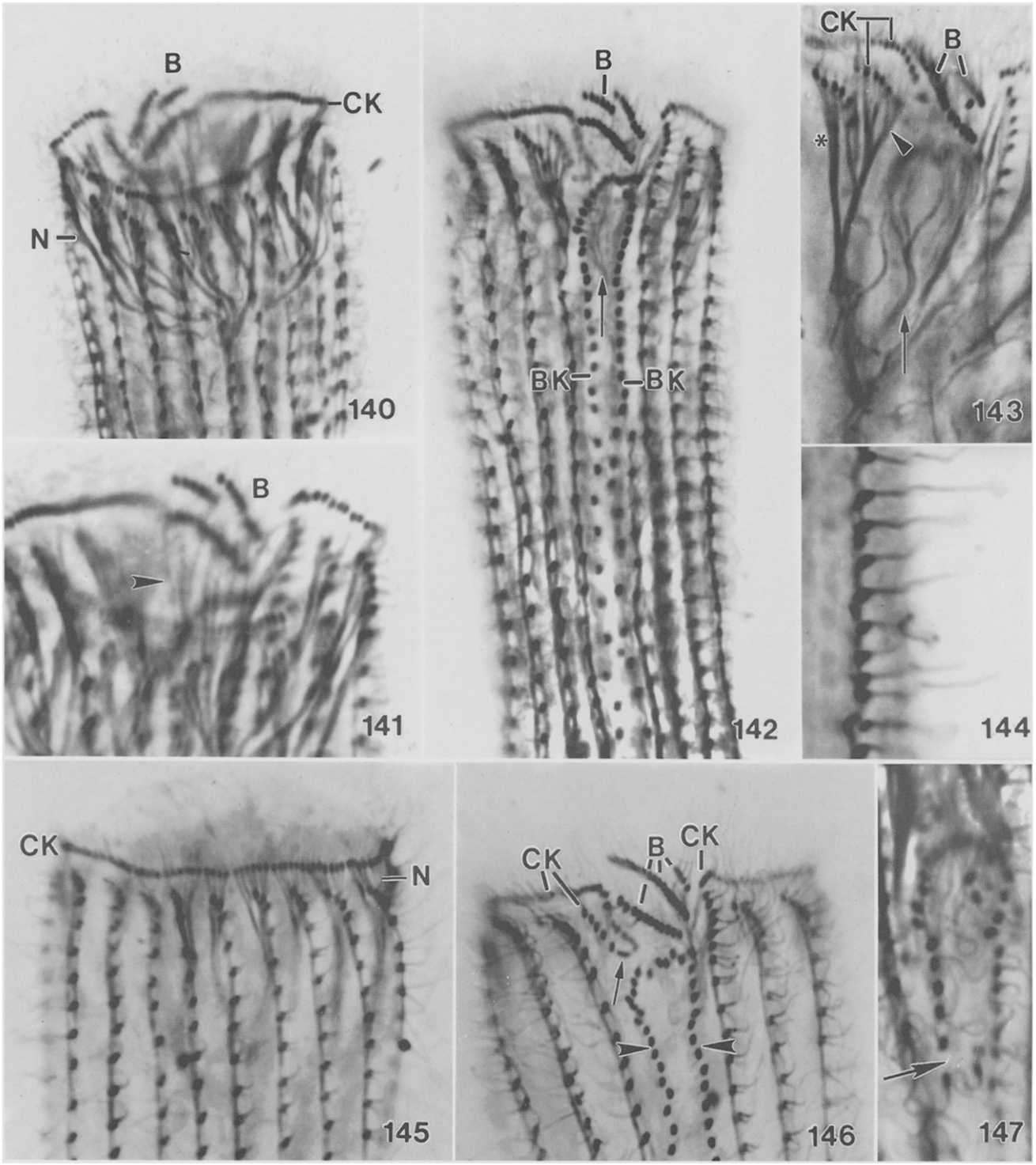
Description (Figs. 102–147, Tables 3, 6): Extended specimens in vivo about 1,100–2,300 × 50–60 μm, usually 1500–2000 μm long, very flexible but less contractile than many other trachelocercids, size and shape thus comparatively well preserved in protargol slides (Figs. 122, Table 3); trunk distinctly, that is 2–3:1 flattened. Greyish in dissecting and bright-field microscope, glabrous stripe appears as light, narrow band. Fully extended specimens filiform with anterior and posterior third gradually tapering, neck and tail thus indistinctly separate from trunk (Figs. 102, 106, 107). Glabrous stripe narrow, corresponds to an area occupied by 1–2 kineties, distinctly indented, not tuberculate, underlain by conspicuous, yellowish, discoidal structures, possibly mitochondria (Fig. 117). Head claviform to calciform and thus distinctly set off from neck, bright



Figs. 129–133. *Tracheloraphis aragoi*, Roscoff population from life (Figs. 129–131) and Sète population after protargol impregnation (Figs. 132, 133). **129.** Head and anterior neck region. Arrows mark minute cortical spines. **130, 131.** Surface views of cortex showing conspicuous granule clusters. **132.** Infraciliature of left side in trunk region. Note very narrow glabrous stripe and granule clusters bulging ciliary rows. **133.** Oral infraciliature. BK = bristle kinety, CK = circumoral kinety, CR = ciliary rows, G = cortical granule clusters, GS = glabrous stripe, N = nematodesmata, NA = nuclear apparatus.



Figs. 134–139. *Tracheloraphis aragoi*, Sète population, somatic infraciliature after protargol impregnation. **134.** Left side of neck region. **135, 137, 139.** Cortical granule clusters bulging ciliary rows. **136, 138.** Fine structure of bristle kinety. Arrows mark small, oblique granule rows, possibly dikinetids and/or a special sort of cortical granules. Arrowheads mark cilia of bristle dikinetids, which have the posterior basal body ciliated in the right branch and the anterior in the left branch of the bristle kinety. A = anterior secant system, BK = bristle kinety, G = cortical granule clusters, GS = glabrous stripe, PD = postciliodesma.



Figs. 140–147. *Trachelorаphis aragoi*, Sète population, oral and somatic infraciliature after protargol impregnation. **140–142.** Same specimen in three focus levels. The nematodesmata originating from the circumoral dikinetids form a distinct basket. Arrow in Fig. 142 marks fibres originating from anterior arch of bristle kinety (cp. Fig. 143). Arrowhead in Fig. 141 denotes fibres originating from brosse kineties. **143.** The right end of the circumoral kinety is curved loop-like (cp. Fig. 146) and its dikinetids have distinct nematodesmata associated (arrowhead). Arrow marks fibres originating from anterior arch of bristle kinety. Star denotes nematodesmata originating from the condensed dikinetids at the anterior end of the first ciliary row right of the bristle kinety. **144.** The trunk dikinetids have only the anterior basal bodies ciliated. **145, 146.** Same specimen, right and left lateral view. Arrow marks loop-like curved right end of circumoral kinety. Arrowheads border bristle kinety. Note that neck dikinetids have both basal bodies ciliated. **147.** Anterior arch of bristle kinety. Arrow marks site where right end and anterior arch of kinety meet and ciliation of dikinetids is opposed by 180°. B = brosse, BK = bristle kinety, CK = circumoral kinety, N = nematodesmata.

because not filled with ellipsoidal inclusions; oral bulge inconspicuous, distinctly set off from head, about 5 µm high, surface flat; brosse cleft distinct (Figs. 104, 109, 129). Distal end of tail pointed and curved (Figs. 102, 106, 107, 114). Fully contracted live specimens with *margins* of glabrous stripe distinctly folded and protruding (Fig. 103); fixed specimens, however, not banana-shaped but elongate, curved, or sigmoidal (Fig. 122). Nuclei in centre of trunk, form distinct, ellipsoid cluster; macronuclei globular to ellipsoid, contain many small nucleoli, some chromatin patches and, in Sète specimens, usually a colourless, oblong protein crystal which does not stain with protargol; micronuclei globular, 2–2.6 µm in protargol impregnated, 3.5–5.2 µm in methyl green-pyronin stained specimens, scattered within macronuclear group (Figs 102, 115, 125). No contractile vacuole. Cortex very flexible, with spiny projections between ciliary rows (Fig. 104, 129), rather distinctly set off from granular endoplasm (Fig. 113). Two types of yellowish cortical granules (Figs. 105, 108, 110–112, 116, 117, 130–132, 135, 137, 139): type 1 ellipsoid, 1.5–2.2 × 1–1.5 µm, forms conspicuous, widely spaced clusters protruding above cell surface between ciliary rows, highly refractile, stains red with methyl green-pyronin, impregnates faintly to intensely with protargol, depending on bleaching conditions, granule clusters in Sète specimens usually so large that somatic kineties become bulged; type 2 about 0.2–0.5 µm across, scattered between ciliary rows, does not stain with methyl green-pyronin and protargol. Cytoplasm conspicuously vacuolated, colourless, packed with brightly shining fat globules and innumerable, 2–4 µm sized ellipsoidal (crystalline ?) inclusions, becoming inflated and blueish when stained with methyl green-pyronin. Food vacuoles with greenish and brownish content, possibly from ingested algae; a specimen from Roscoff contained a huge (120 × 50 µm) vacuole with a decaying ciliate, possibly a *Condylostoma* (Fig. 102). Glides and winds elegantly between sand grains and organic debris.

Infraciliature (Figs. 118–128, 132–147): The somatic and oral infraciliature of *T. aragoi* is very similar to that of *T. phoenicopterus*. Most important differences concern morphometric characteristics, compiled in Table 3, and features recognizable only in live specimens, as described above. Thus, we refrain from a complete description of the infraciliature and refer to the description of *T. phoenicopterus*, the detailed figures and figure explanations. Nevertheless, a few features are different and will be thus described in detail.

The right somatic ciliation of *T. aragoi* is much more differentiated than that of *T. phoenicopterus*. Each kinety commences with a few condensed dikinetids having only the anterior basal body ciliated. The following head and neck dikinetids have both basal bodies of the dikinetids ciliated (Fig. 133). All trunk kinetids have only the anterior basal body ciliated (Fig. 144). The tail dikinetids have both basal bodies ciliated, except in the distalmost region, where only the anterior basal bodies bear a cilium.

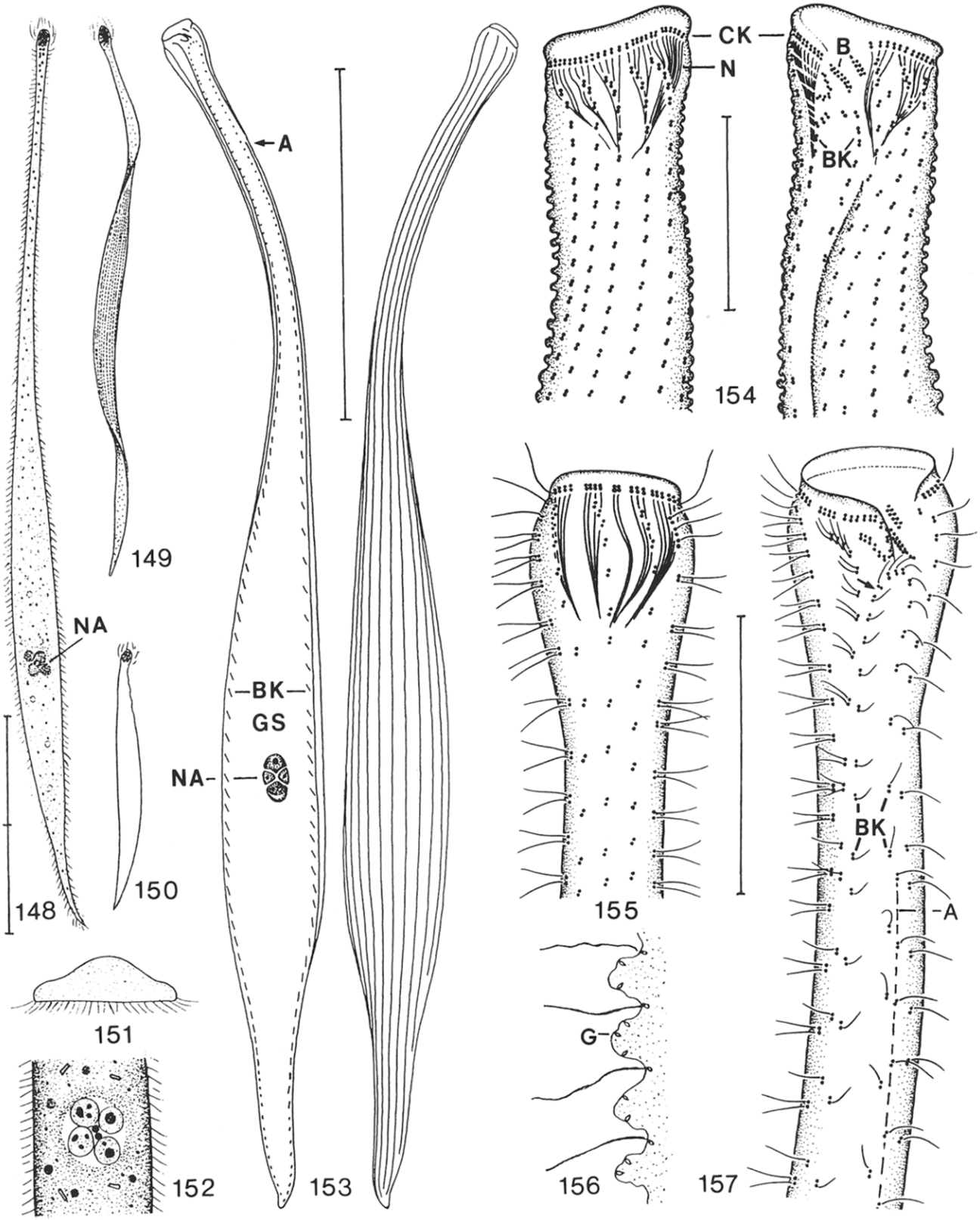
The bristle kinety of *T. aragoi* consists of a single row of loosely and rather irregularly arranged dikinetids (Fig. 132), unlike in *T. phoenicopterus* (Figs. 85, 97), *T. longicollis* (Figs. 153, 166, 169) and *T. oligostriata* (Figs. 184, 189), which have oblique kineties in the trunk region. Oblique, kinety-like structures are also found in the bristle kinety of *T. aragoi*, albeit rarely and irregularly scattered (Figs. 136, 138). However, only the granules (dikinetids) neighbouring the somatic kineties are ciliated; thus the other granules, which are often slightly smaller and unpaired, are very likely a special sort of cortical granules (extrusomes ?). This is supported by the observation that such granules are also scattered between the bristle kinetids in regions where the kinetids form a single line.

Nematodesmata-like fibres originating from the anterior arch of the bristle kinety were seen also in this species (Figs. 120, 142, 143). The contractile system of *T. aragoi* is either weakly developed, as indicated by the comparatively weak contractility of the species, or of different chemical composition because myonemes impregnated only very rarely and faintly (Fig. 124).

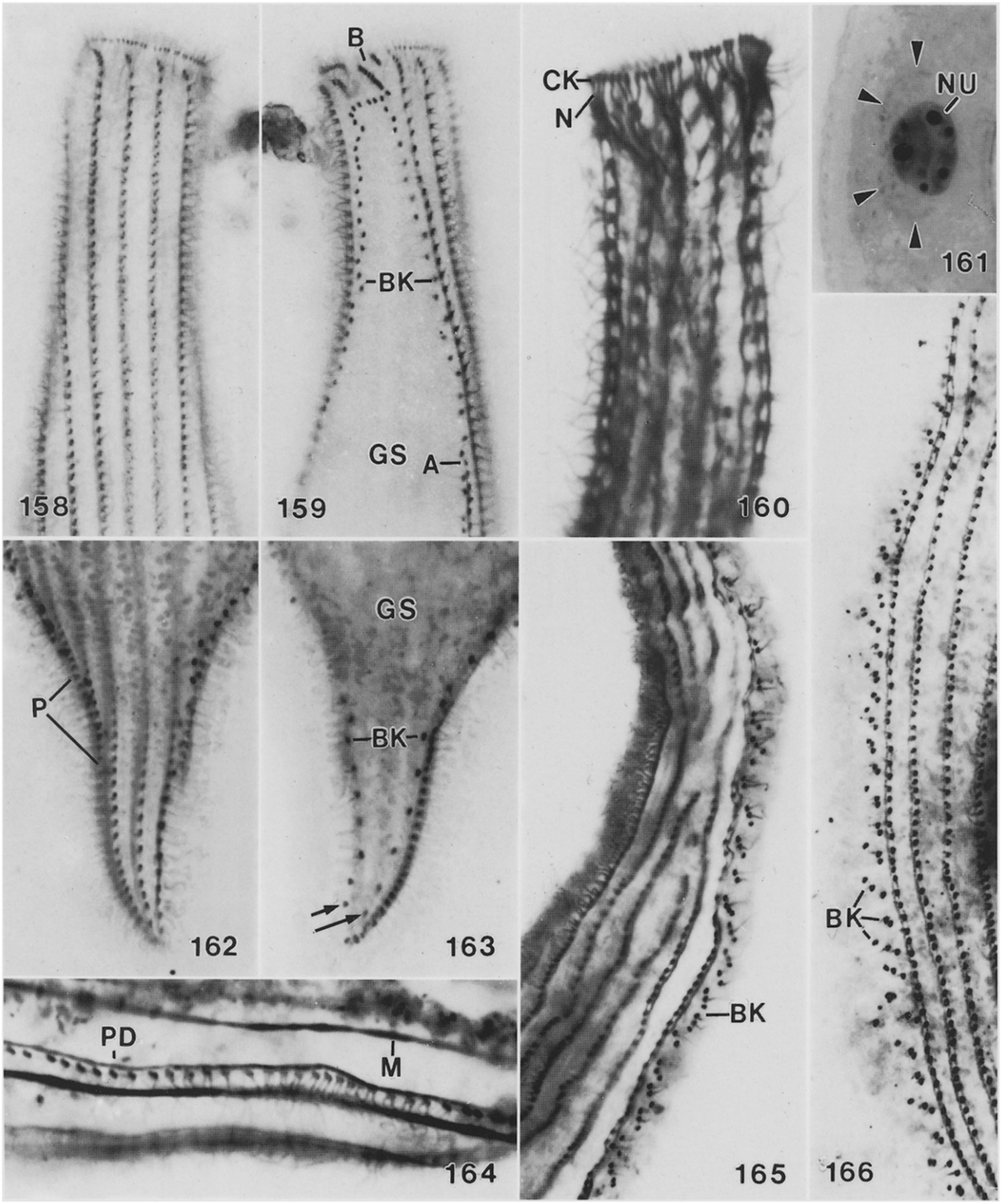
Redescription of *Tracheloraphis longicollis* (Dragesco, 1960) nov. comb., type of the genus *Trachelonema* Dragesco, 1960 (Figs. 148–172, Table 4)

Identification and taxonomy: Our data agree with the original description. Thus, there are no doubts as to the identification, all the more so as we collected the material at the locus classicus. Live specimens are easily confused with *Trachelocerca sagitta*, which is very similar in size, shape, nuclear apparatus and kinety number, but less distinctly flattened and ciliated on both sides. Furthermore, it lacks a brosse, which is, however, difficult to recognize without silver impregnation in *T. longicollis*. See genus *Tracheloraphis* for discussion of genus synonymy.

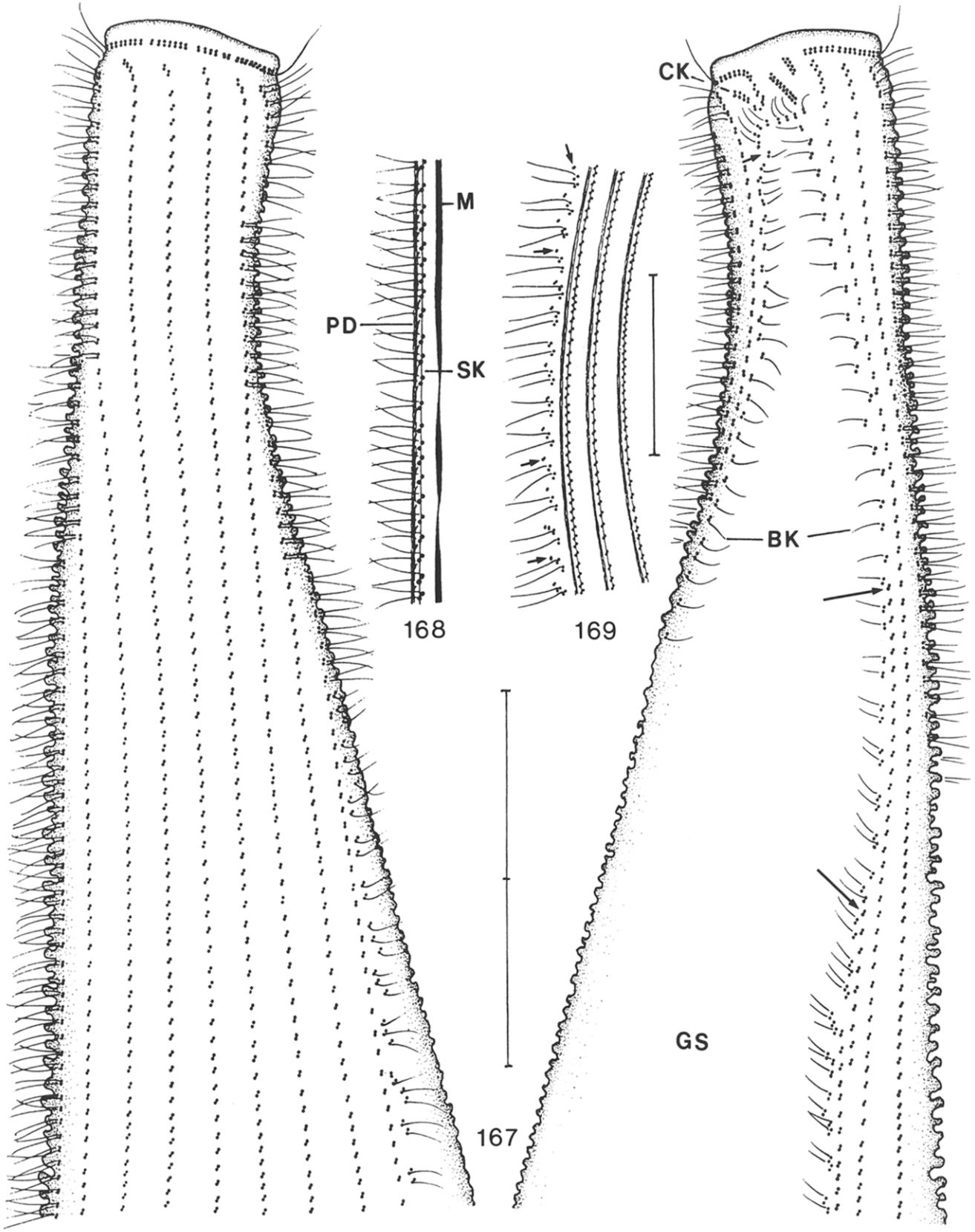
Specimens investigated and type material: The redescription is based on 10 well-impregnated specimens; some others were of usuable quality and served for completing morphometry. No type material of *T. longicollis* has been mentioned in the literature. Thus, we declare the population collected at the locus classicus and described below as neotype and deposit two slides with neotype specimens, prepared as described, in the Oberösterreichisches Landesmuseum in Linz (LI). Relevant specimens are marked by a black ink circle on the cover glass.



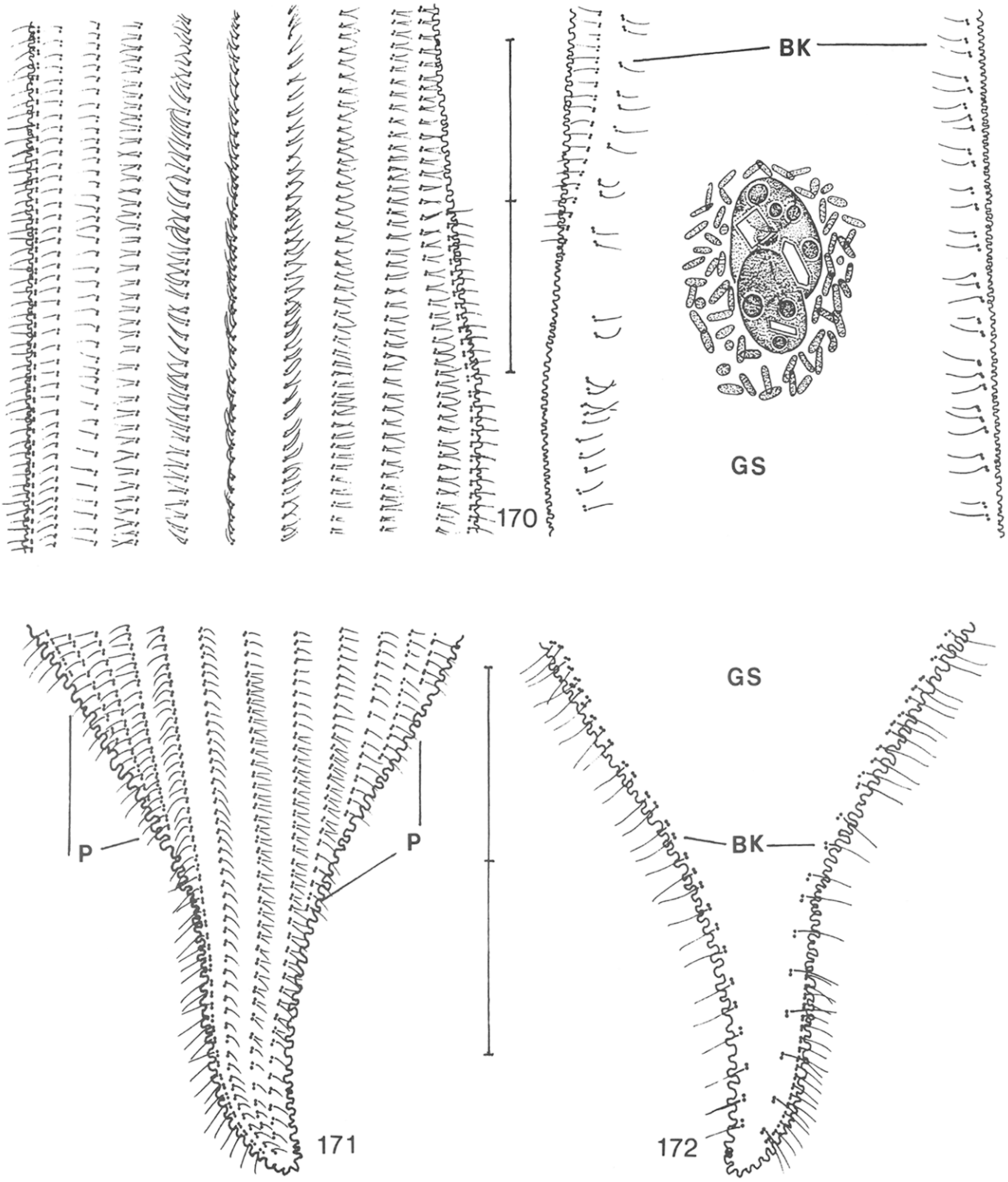
Figs. 148–157. *Trachelotaphis longicollis* from life (Figs. 148–151, 156; from DRAGESCO 1960) and after protargol impregnation (Figs. 153–155, 157). **148, 149.** Gliding and swimming specimens. **150.** Fully contracted specimen. **151.** Transverse section in trunk region. **152.** Nuclear apparatus, methylgreen stain. **153.** Infraciliature of left and right side. **154, 155, 157.** Infraciliature and ciliation of right and left side of head and neck. Figures 155 and 157 show same specimen as Fig. 153. Arrow marks site where right end and anterior arch of bristle kinety abut and ciliation of bristle dikinetids is opposed by 90–180°. **156.** Optical section of cortex showing widely spaced cortical granules. A = anterior secant system, B = brosse, BK = bristle kinety, CK = circumoral kinety, G = cortical granules, GS = glabrous stripe, N = nematodesmata, NA = nuclear apparatus. Scale bar division 20 μm (Figs. 154, 155, 157) and 100 μm (Figs. 148, 153).



Figs. 158–166. *Tracheloraphis longicollis*, infraciliature and nuclear apparatus after protargol impregnation. **158, 159.** Right and left side view of head and neck infraciliature. **160.** The nematodesmata originating from the circumoral dikinetids form a distinct basket. **161.** The nuclei form a tight cluster and are surrounded by a layer of cylindroid structures (arrowheads and Fig. 170). **162, 163.** Right and left side view of tail infraciliature. Arrows mark posteriormost dikinetids of bristle kinety (cp. Figs. 171, 172). **164.** Somatic fibrillar system. **165, 166.** In the trunk region, the bristle kinety is composed of many short, oblique rows (cp. Fig. 159). A = anterior secant system, B = brosse, BK = bristle kinety, CK = circumoral kinety, GS = glabrous stripe, M = myoneme, N = nematodesmata, NU = nucleoli, P = posterior secant system, PD = postciliodesma.



Figs. 167–169. *Tracheloraphis longicollis*, somatic and oral infraciliature after protargol impregnation. **167.** Right and left side view of head and neck region. Note loop-like curved right end of circumoral kinety. Large arrows mark anterior secant system. Small arrow marks site where right end and anterior arch of bristle kinety abut and ciliation of bristle dikinetids is opposed by 180°. **168.** Somatic fibrillar system. **169.** In the trunk region, the bristle kinety is composed of many small, oblique rows. Arrows



Figs. 170–172. *Tracheloraphis longicollis*, right and left side views of somatic infraciliature and ciliation in trunk and tail after protargol impregnation. Note cylindroid structures covering nuclear apparatus and highly differentiated, but variable ciliation. The specimen shown in Fig. 170 has both basal bodies of the dikinetids ciliated, except of the three rightmost kineties and the leftmost kinety, while that shown in Fig. 171 has ciliated dikinetids only subterminally at the tail base and subapically in the neck region. BK = bristle kinety, GS = glabrous stripe, P = posterior secant system. Scale bar division 20 μm.

mark unciliated granules (dikinetids? extrusomes?). BK = bristle kinety, CK = circumoral kinety, GS = glabrous stripe, M = myoneme, PD = postciliodesma, SK = subkinetal microtubule ribbon. Scale bar division 20 μm.

Table 4. Morphometric characteristics from *Tracheloraphis longicollis* (upper line) and *T. oligostriata* (lower line).

Character[1])	$\bar{x}$	M	$SD_{\bar{x}}$	SD	CV	Min	Max	n
Body, length[2])	289.5	280.0	72.6	18.7	25.1	172	410	15
	293.5	280.0	91.2	21.0	31.1	142	450	20
Body, width at head	17.2	16.0	3.6	0.9	21.1	12	25	15
	12.0	12.0	1.5	0.4	12.8	9	15	17
Body, (maximum) width at trunk[3])	53.7	55.0	8.6	2.3	16.5	33	66	15
	33.3	30.5	6.8	1.6	20.5	23	45	20
Glabrous stripe, width in mid-body[3])	about same as maximum body width							
	about same as maximum body width							
Anterior end to (first) nuclear capsule, distance	161,5	150.0	49.9	12.9	30.9	87	270	15
	59.4	64.5	12.3	3.4	20.7	38	72	10
Nuclear group, length	15.7	15.0	3.2	0.8	20.1	11	22	15
	9.4	9.0	1.5	0.4	15.9	7	13	18
Nuclear group, width	10.5	11.0	1.2	0.3	11.9	8	12	15
	4.6	5.0	0.8	0.2	16.7	3	6	21
Macronuclei, length	not measured because too tightly spaced							
	4.7	5.0	0.9	0.2	20.0	3	6	24
Macronuclei, width	not measured because too tightly spaced							
	3.5	3.5	0.9	0.2	25.7	2	5	24
Micronuclei, diameter	seen in two specimens only							
	1.2	1.3	0.1	0.1	3.4	1	1.5	16
Brosse kinety 1, length	2.1	2.0	0.5	0.1	25.8	1	3	15
	4.3	4.0	0.5	0.2	12.2	4	5.5	10
Brosse kinety 2, length	3.9	4.0	0.5	0.1	11.7	3	4.5	15
	lacking							
Somatic kineties, number on head	8.7	9.0	1.2	0.3	14.1	7	10	15
	5.9	6.0	–	–	–	5	6	18
Somatic kineties, (maximum) number on trunk	12.2	12.0	0.8	0.2	6.3	11	13	15
	5.9	6.0	–	–	–	5	6	18
Dikinetids, number in 10 µm in neck region	5.7	6.0	2.3	0.6	41.1	3	11	15
	8.1	8.0	1.1	0.4	13.6	6	10	10
Dikinetids, number in 10 µm in trunk region	9.4	8.0	3.3	0.8	34.8	6	17	15
	9.9	10.0	1.1	0.4	11.1	9	11	10
Bristle kinety, (maximal) number of kinetids in oblique row[4])	2.9	3.0	0.8	0.2	27.5	2	4	15
	3.7	4.0	0.6	0.2	17.0	3	5	13
Brosse kineties, number	2.0	2.0	0.0	0.0	0.0	2	2	15
	1.0	1.0	0.0	0.0	0.0	1	1	11
Dikinetids in brosse kinety 1, number	3.7	4.0	1.0	0.3	26.4	2	5	15
	8.2	8.0	0.9	0.3	10.7	7	9	11
Dikinetids in brosse kinety 2, number	6.9	6.0	1.2	0.3	17.2	5	9	15
	lacking							
Nuclear groups, number	1.0	1.0	0.0	0.0	0.0	1	1	15
	9.0	9.5	2.3	0.6	25.3	5	13	16
Macronuclei, total number	very likely invariably 4							
	18.4	18.0	4.1	0.9	22.1	12	28	20
Micronuclei, total number	very likely invariably 2							
	9.7	10.0	2.4	0.6	24.4	7	18	20

[1]) Data based on protargol impregnated and mounted morphostatic specimens from field. 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 which strongly contract when fixed for preparation.

[3]) Data of very limited value because species are highly contractile and trunk often becomes inflated due to preparation procedures.

[4]) Including granule(s) at proximal end which possibly is not a kinetid but some sort of extrusome.

Improved diagnosis: Fully extended cells in vivo 600–900 µm long. Filiform and flattened ribbon-like, neck and tail indistinctly separate from trunk, head claviform and dark, distal end of tail curved. 4 macronuclei and 2 micronuclei forming tight cluster in centre of trunk. 11–13 somatic ciliary rows; glabrous stripe as wide as body, left side thus barren. Bristle kinety at margins of left side, of usual structure in anterior and posterior third of cell, composed of many minute kineties each comprising 2–4 dikinetids in trunk region. 2 oblique brosse kineties. Cortical granules inconspicuous, about 1 µm across, colourless, loosely spaced.

Redescription: Our live observations are not very detailed and match the original description by DRAGESCO (1960) to which the reader is referred (Figs. 148–152, 156). Thus, we describe only the infraciliature, which basically agrees with that of *T. phoenicopterus*, differing mainly in morphometric characteristics. The macronuclei usually contain a protein crystal. They form a tight cluster surrounded by a voluminous layer of pale, cylindroid structures faintly stained with protargol (Figs. 161, 170). One specimen contained a voluminous (60 × 35 µm) food vacuole, possibly an ingested ciliate.

Somatic infraciliature (Figs. 153–172). *Tracheloraphis longicollis* has only the right surface ciliated, the left is barren, i.e. occupied by the glabrous stripe, at the margins of which, the bristle kinety extends. The cilia are arranged in longitudinal rows which are distinctly separate from the circumoral kinety and extend between flat cortical crests. The anterior end of the ciliary rows has condensed, i.e. more narrowly spaced dikinetids and is slightly curved to the right. Usually, the condensation is inconspicuous or even lacking in some kineties. One to four ciliary rows are gradually shortened in the neck region left of the glabrous stripe and posteriorly, where the body narrows to the tail, on both sides of the stripe (Figs. 153, 157, 159, 162, 167, 171). In other words, an anterior and posterior secant system are formed at the margins of the cell where some kineties abut to the bristle kinety. Thus, the head, neck and tail have about one quarter fewer kineties than the trunk (Table 4). The ciliary rows neighbouring the right branch of the bristle kinety are unshortened anteriorly and thus run alongside 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. 167, 170).

The entire infraciliature consists of dikinetids whose ciliation and fibrillar system highly resemble those of *T. phoenicopterus*, with, however, some differences (Figs. 155, 157–160, 164, 166, 168, 169). First, oralized somatic dikinetids are very likely lacking, at least were not recognizable despite the high quality of the preparations. Second, the ciliation of *T. longicollis* is extremely variable. In some specimens most dikinetids have both basal bodies ciliated, while in others only the anterior basal bodies bear a cilium. Usually, the condensed dikinetids at the anterior end of the ciliary rows and the kineties neighbouring the glabrous stripe have barren posterior basal bodies. See Figures 155, 157, 167, 170 and 171 for some of the variations observed.

The contractile apparatus of *T. longicollis* consists of a myoneme close to the left of each kinety (Figs. 164, 168). As in the other species investigated, the distinctiveness of the myonemes varies highly, depending on preparation conditions. The myonemes are flattened ribbon-like and extend the whole length of the kinety, but are wider (thicker, i.e. about 0.6 µm) in the trunk than in the head and tail region (< 0.2 µm). No myonemes impregnated in the glabrous stripe.

The glabrous stripe extends along the whole body length and width, except on the neck and head, where it gradually narrows, occupying only about one third of the head's width (Figs. 153, 154, 157, 159, 167). The glabrous stripe is bordered by the bristle kinety which is very similar to that of *T. phoenicopterus*, especially in having small, oblique kineties in the trunk region (Figs. 153, 154, 157, 159, 165–167, 170, 172). *Tracheloraphis longicollis* possibly lacks the nematodesmata-like fibres associated with the dikinetids forming the anterior arch of the bristle kinety in *T. phoenicopterus*.

Oral infraciliature (Figs. 153–155, 157–160, 167). The oral infraciliature of *T. longicollis* consists of a circumoral kinety and a small brosse difficult to recognize in living specimens. The circumoral kinety extends in the flat furrow separating the oral bulge from the head and is composed of a single row of vertically oriented dikinetids having only the posterior basal body ciliated. Each circumoral dikinetid is associated with a distinct nematodesma obliquely extending into the head. The nematodesmata of neighbouring dikinetids unite to conspicuous bundles, forming a cone-shaped oral basket (Figs. 154, 155, 160). As in the other species investigated, the circumoral kinety of *T. longicollis* is very likely composed of several fragments, as indicated by small gaps, 1–2 dikinetids wide, and the bundled arrangement of the nematodesmata (Fig. 155). The circumoral kinety is interrupted where the brosse kineties are inserted. Its left end simply abuts to the margin of the brosse cleft, i.e. to the left lip of the oral bulge. The right end is more complicated. It extends along the oblique margin of the brosse cleft and curves back at the cleft vertex in such a steep angle that a loop-like structure, or a small oblique segment, is formed paralleling the descending portion of the circumoral kinety and the anterior end of the neighbouring somatic kinety (Figs. 154, 157, 159, 167).

The brosse is located in a flat cavity, the brosse pocket, just above the arch of the bristle kinety, and intersects the circumoral kinety (Figs. 154, 157, 159, 167). The brosse invariably consists of 2 oblique kineties, arranged in parallel and one behind the other, composed of closely spaced dikinetids having only the posterior basal body ciliated. Brosse kinety 1 is invariably smaller than kinety 2.

Redescription of *Tracheloraphis oligostriata* (RAIKOV, 1962) nov. comb. (Figs. 173–194, Tables 4, 5)

Identification and taxonomy: Our observations match the original description and several more or less detailed redescriptions, all based, however, entirely on live observations and/or classical histological techniques (Table 5). Thus, there is no doubt about the identification. Obviously, two of the main characters, viz. the number of ciliary rows and macronuclei, vary considerably within and/or between populations.

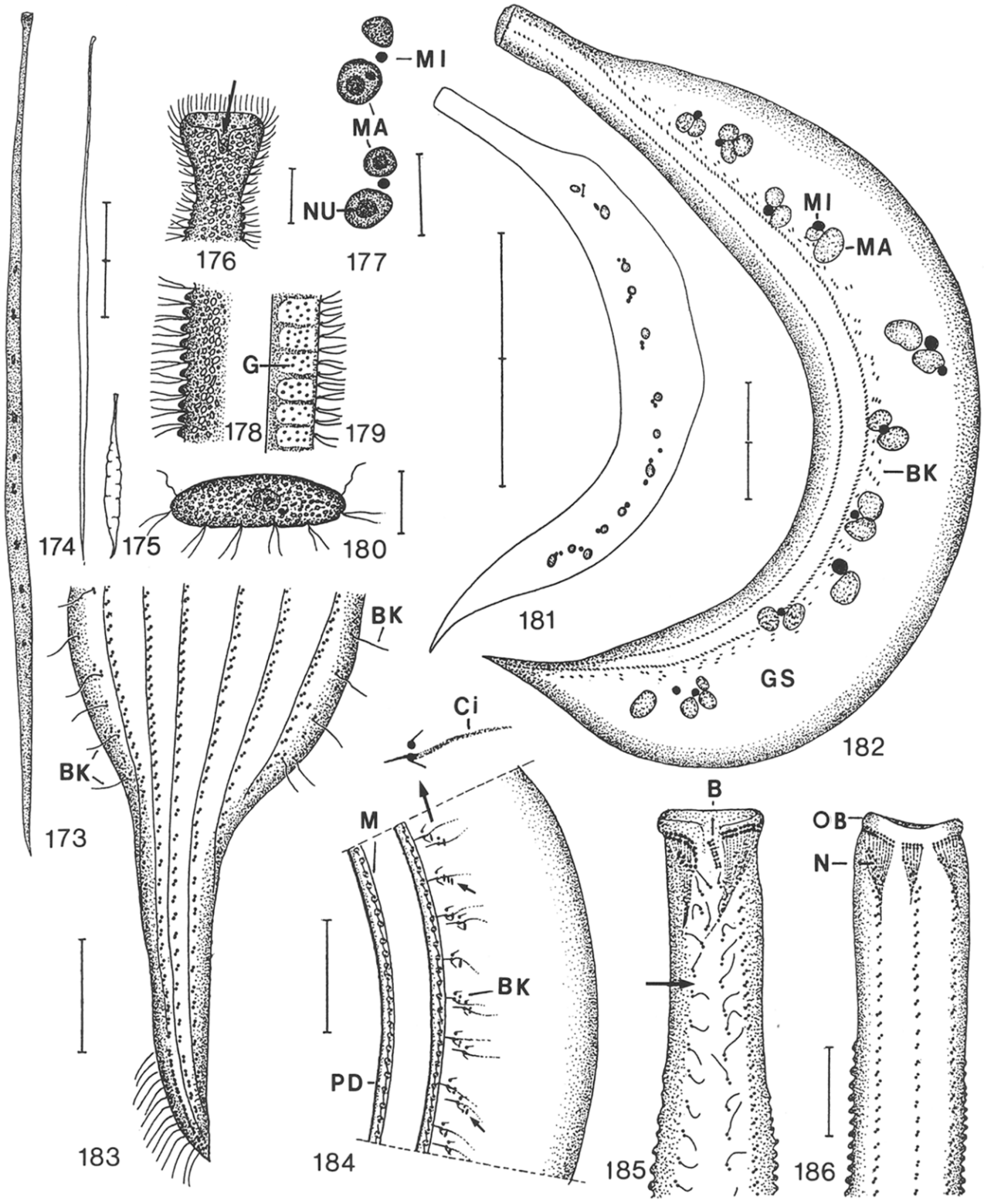
Improved diagnosis (based on our observations and literature data mentioned in Table 5): Fully extended cells 300–800 µm, usually about 400–600 µm long. Filiform and flattened ribbon-like, neck and tail indistinctly separate from trunk, head calciform and usually rather transparent, distal end of tail curved. 4–28, usually 8–18 macronuclei in single strand, frequently arranged in groups each consisting of two macronuclei with single micronucleus in between. 5–8, usually 6–8, somatic ciliary rows; glabrous stripe as wide as body, left side thus barren. Bristle kinety at margins of left side, of usual structure in anterior and posterior third of cell, composed of many minute kineties each comprising 2–5 dikinetids in trunk region. 1 slightly oblique brosse kinety. Cortical granules inconspicuous, about 1 µm across, colourless.

Description of Sète population (Figs. 173–194, Table 4): Extended specimens in vivo about 300–500 µm long, highly flexible and contractile, size and shape thus poorly preserved in protargol slides (Figs. 173, 181, 182, 187, 190, Table 4); trunk distinctly, that is about 3:1 flattened, cells thus ribbon-like (Fig. 180). Greyish and rather transparent in dissecting and bright-field microscope. Fully extended specimens filiform with anterior and posterior region gradually tapering, neck and tail thus indistinctly set off from trunk (Figs. 173, 174). Glabrous stripe about as wide as body in trunk region, slightly convex, without groove in midline (Fig. 180). Head calciform and thus distinctly set off from neck, bright because studded with ellipsoid inclusions; oral bulge indistinctly set off from head, surface flat, contains 1.5 × 1 µm sized granules, possibly extrusomes; brosse cleft distinct (Figs. 176, 185). Distal end of tail pointed and curved (Figs. 173, 174). Fully contracted specimens about 150–300 µm long, banana-shaped with many transverse and oblique folds, left side distinctly protruding and tuberculate (Figs. 175, 181, 182). Nuclei form distinct strand in trunk, number and arrangement highly variable, frequently 2–3 macronuclei with 1–2 micronuclei in between unite to a small cluster (Figs. 173, 177, 181, 182, 193); macronuclei and micronuclei globular to slightly ellipsoid, macronuclei with one, rarely two large nucleoli and some inconspicuous chromatin condensations (Figs. 177, 193). No

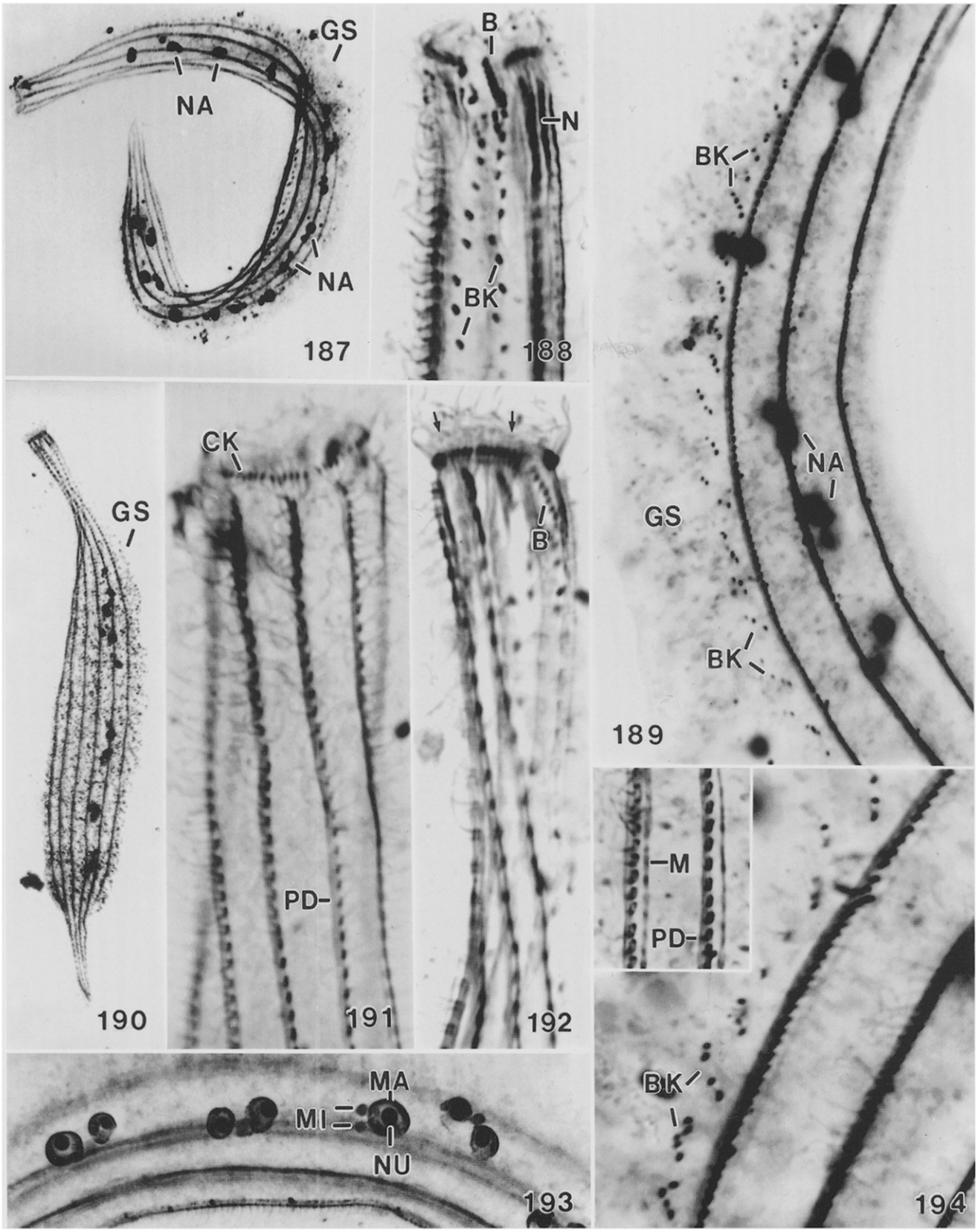
Table 5. Comparison of *Tracheloraphis oligostriata* populations.

Authors	Characters[1])				
	Length in vivo (µm)	Kineties, number	Macronuclei, number	Brosse kineties, number	Glabrous stripe, width
RAIKOV (1962)	500–800	6	8–18	?	~as body
DRAGESCO (1963)	?	8	6–8	?	~as body
KATTAR (1970)	700[2])	6–7	12	?	~as body
BORROR (1972)	390–620	7	12–24	1	~as body
CZAPIK & JORDAN (1976)	400[2])	8	8–18	?	~as body
WRIGHT (1983)	200–600[2])	6	4–16	?	?
Present data, Roscoff[3])	?	6	8–16	1	~as body
Present data, Sète[4])	300–550	5–6	12–28	1	~as body

[1]) All data inexact, except those extracted from Table 4, i.e. number of specimens investigated and variation unknown.
[2]) Possibly in vivo, but not definitely stated so.
[3]) Four specimens investigated.
[4]) See Table 4.



Figs. 173–186. *Tracheloraphis oligostriata* from life (Figs. 173–176, 178–180) and after protargol impregnation (Figs. 177, 181–186). **173–175.** Slightly contracted, fully extended, and completely contracted specimen. **176.** Head with brosse cleft (arrow). **177, 181.** Nuclear apparatus. **178, 179.** Optical section and surface view of cortex. **180.** Transverse section in trunk region. **182.** General lateral view of infraciliature and nuclear apparatus. **183.** Infraciliature of right side of tail. Note condensed dikinetids at right tail end. **184.** Fine structure of bristle kinety and somatic infraciliature. Arrows mark unciliated granules (dikinetids? extrusomes?). **185, 186.** Infraciliature of left and right side of head and neck. Arrow marks site where right end and anterior arch of bristle kinety abut and ciliation of bristle dikinetids is opposed by 180°. B = brosse, BK = bristle kinety, Ci = cilium, G = cortical granules, GS = glabrous stripe, M = myoneme, MA = macronuclei, MI = micronuclei, N = nematodesmata, NU = nucleolus, OB = oral bulge, PD = postciliodesma. Scale bar division 10 μm (Figs. 176, 177, 180, 182, 183 - 186) and 50 μm (Figs. 174, 181).



Figs. 187–194. *Tracheloraphis oligostriata*, infraciliature and nuclear apparatus after protargol impregnation. **187, 190.** General right lateral views showing typical nuclear configuration and kinety number (6). **188, 191, 192.** Left and right lateral views of head and neck infraciliature. Arrows mark oral bulge. **189, 194.** Bristle kinety in trunk region; inset shows somatic fibrillar system. **193.** Nuclear apparatus. B = brosse, BK = bristle kinety, CK = circumoral kinety, GS = glabrous stripe, M = myoneme, MA = macronuclei, MI = micronuclei, N = nematodesmata, NA = nuclear apparatus, NU = nucleolus, PD = postciliodesma.

contractile vacuole. Cortex very flexible, in contracted specimens conspicuously tuberculate, indistinctly set off from granular endoplasm, contains numerous small, colourless granules (Figs. 178, 179). Cytoplasm with some food vacuoles containing unidentifiable debris and many 2–4 µm sized ellipsoid (crystalline?) inclusions, which become inflated and reddish, respectively, blue after prolonged supravital action of methylgreen-pyronin and cresyl blue.

Infraciliature (Figs. 183–194): The somatic and oral infraciliature of *T. oligostriata* is very similar to that of *T. longicollis*. Most important differences concern morphometric characteristics, compiled in Table 4. Thus, we refrain from a complete description of the infraciliature and refer to the description of *T. longicollis*, the detailed figures and figure explanations. Nevertheless, a few features are different or were seen clearly only in this species, and are thus described in some detail.

The somatic ciliation of *T. oligostriata* is as variable as that of *T. longicollis*, i.e. some specimens have both basal bodies of the dikinetids ciliated in the main portion of the cell, while others mainly have only the anterior basal bodies ciliated. The two rightmost kineties have condensed, i.e. more narrowly spaced dikinetids at the tail end, highly reminiscent of the condensation found in loxodids (FOISSNER 1996b); however, the condensed dikinetids of *T. oligostriata* are not associated with special fibres, as in loxodids, and could thus simply be caused by a strong or special mode of contraction of the tail during fixation. The bristle kinety, first seen by BORROR (1972), is structured as described in *T. longicollis*, i.e. consists of short, oblique kineties in the trunk region, each composed of ciliated and unciliated argyrophilic granules; usually ciliated and unciliated granules alternate within a row, the latter being slightly smaller and often unpaired, but sometimes they are distinctly paired or triplicate (Figs. 184, 189, 194). Furthermore, a special fibrillar system, highly reminiscent of that described in *Trachelocerca ditis* (Fig. 62a), was recognizable in a few excellently prepared specimens (Fig. 184). It consists of a comparatively thick fibre extending from the ciliated basal body to the somatic kineties and of a very fine fibre extending from each basal body of a pair into the glabrous stripe. The unpaired granules or paired granules without a cilium lack these fibrillar associates, indicating that they are not kinetids but a special type of cortical granule, possibly extrusomes.

The brosse of *T. oligostriata* invariably consists of a single kinety slightly obliquely implanted at the right wall of the brosse pocket (Figs. 176, 185, 188, 192). Interestingly, BORROR (1972) already described the brosse in detail, using solely live observation; even the number of cilia (about 8) match our data exactly (Table 4).

Nomenclatural emendations

As already mentioned, the correct genders of *Tracheloraphis* (feminine) and *Trachelonema* (neuter) were not recognized by several authors. Thus, quite a lot of species names must be emended according to article 31b of the ICZN (1985). Only the original spelling will be corrected, i.e. subsequent generic combinations are not considered. Furthermore, incorrect second spellings frequently found, for instance, in CAREY (1992), are not emended.

Tracheloraphis africana nom. corr. (*T. africanus* DRAGESCO, 1965), *T. angustivittata* nom. corr. (*T. angustivittatus* BORROR, 1963), *T. caudata* nom. corr. (*T. caudatus* DRAGESCO & RAIKOV, 1966), *T. crassa* nom. corr. (*T. crassus* RAIKOV, 1963), *T. enigmatica* nom. corr. (*T. enigmaticus* DRAGESCO, 1960), *T. flexuosa* nom. corr. (*T. flexuosus* RAIKOV & KOVALEVA, 1968), *T. hamata* nom. corr. (*T. hamatus* WRIGHT, 1982), *T. indistincta* nom. corr. (*T. indistinctus* WRIGHT, 1982), *T. lactea* nom. corr. (*T. lacteus* RAIKOV & KOVALEVA, 1968), *T. nivea* nom. corr. (*T. niveus* WRIGHT, 1982), *T. sarmatica* nom. corr. (*T. sarmaticus* AGAMALIEV & KOVALEVA, 1966 in AGAMALIEV 1966b), *T. serrata* nom. corr. (*T. serratus* RAIKOV & KOVALEVA, 1968), *T. striata* nom. corr. (*T. striatus* RAIKOV, 1962).

Trachelonema binucleatum nom. corr. (*T. binucleata* AGAMALIEV, 1966b), *T. lanceolatum* nom. corr. (*T. lanceolata* RAIKOV, 1962), *T. longicolle* nom. corr. (*T. longicollis* DRAGESCO, 1960), *T. minimum* nom. corr. (*T. minima* DRAGESCO, 1960), *T. oligostriatum* nom. corr. (*T. oligostriata* RAIKOV, 1962), *T. sulcatum* nom. corr. (*T. sulcata* KOVALEVA, 1966).

Discussion

Generic classification of trachelocercid karyorelictids

As reviewed in the introduction and by FOISSNER & DRAGESCO (1996), the generic classification of trachelocercids is controversial and bewildering, obviously because inappropriate characters have been used. We thus suggest that the classification should be based entirely on infraciliary features, particularly the oral structures. Using this standard, four genera can be distinguished (Table 6): *Prototrachelocerca* (with brosse interrupting compound circumoral ciliature), *Tracheloraphis* (with brosse interrupting simple circumoral kinety), *Trachelolophos* (with brosse near centre of oral bulge and uninterrupted simple circumoral kinety), and *Trachelocerca* (without brosse and uninterrupted simple circumoral kinety). The somatic infraciliature of the

Table 6. Genus distinction in trachelocercid karyorelictids.

Character	*Trachelocerca*[1])	*Tracheloraphis*[1])	*Trachelolophos*[2])	*Prototrachelocerca*[3])
Brosse	absent	present	absent[4])	present
Ciliary tuft in oral cavity[4])	absent	absent	present[4])	absent
Circumoral kinety[5])	simple & uninterrupted	simple & interrupted	simple & uninterrupted	complex & interrupted
Bristle kinety[6])	simple	simple or complex	simple	mixed
Glabrous stripe	usually ≤ 1/3 of body width	usually ≥ 1/3 of body width	≤ 1/3 of body width	about 1/3 of body width

[1]) This paper.
[2]) From FOISSNER & DRAGESCO (1996).
[3]) From FOISSNER (1996a).
[4]) Very likely, the ciliary tuft within the oral cavity is a highly modified brosse.
[5]) Simple = single row of dikinetids; complex = two or more rows of dikinetids. See FOISSNER (1996a) for details.
[6]) Simple = single row of dikinetids; complex = many minute kineties composed of 2–5 dikinetids in trunk region; mixed = basically like "simple" type, but with some minute kineties interposed, similar to "complex" type. See FOISSNER (1996a) for details.

trachelocercids shows a great homogeneity, although some details vary, for instance, the ciliation of the dikinetids and the fine structure of the bristle kinety (Table 6).

The classification suggested is based on much more material than shown in this paper and our previous studies (FOISSNER, 1996a; FOISSNER & DRAGESCO 1996), viz. on about 40 well impregnated species. All fit one of the genera listed above. Thus, these genera possibly comprise most of the trachelocercid diversity.

Species taxonomy

Of the 67 trachelocercids compiled in CAREY's (1992) book, many were superficially described and all data are entirely based on live observations and/or classical histological techniques, which do not reveal the infraciliature. Thus, species identification is often difficult and sometimes a matter of choice. Obviously, all species need redescription because even the generic characters can be reliably recognized in protargol stains only. A suitable technique is now available. The descriptions and redescriptions we provided in this and our previous papers (FOISSNER 1996a; FOISSNER & DRAGESCO 1996) may serve as representative examples of how the work ought to be done. Any future description should at least contain a detailed morphology and morphometry based on protargol impregnated specimens. Furthermore, live observation is still indispensable because several important characters, e.g. the shape, size and colour of the cells and cortical granules, can be recognized in life specimens only.

Bristle kinety and brosse: key characters for revealing evolution in karyorelictids

Very recently, HIRT et al. (1995) published molecular-biological evidence for a close relationship of loxodid and trachelocercid karyorelictids, confirming the pioneering studies of RAIKOV (1958) and CORLISS (1974). Our data from the infraciliature, analysed with HENNIG's (1982) cladistic method, provide further support for this hypothesis and reveal some infraordinal relationships (Fig. 197, Table 7). Loxodids (FOISSNER 1996b,c) and trachelocercids have a unique synapomorphy, viz. the bristle kinety framing a more or less wide non-ciliated area, the glabrous stripe. Unfortunately, the ontogenesis of the bristle kinety is unknown, but certainly it is a highly specialized part of the trachelocercid and loxodid infraciliature, distinctly set off from the somatic kineties (Fig. 62a, 196). This is supported by transmission electron microscope investigations showing that the bristle kinetids lack postciliary microtubules and have a stengthened transverse microtubule ribbon directed to the glabrous stripe (RAIKOV & KOVALEVA 1995 and Figs. 184, 196). Furthermore, they have a short fibre directed to the somatic ciliary rows (Figs. 62a, 184, 196) and an argyrophilic granule, possibly a parasomal sac (Figs. 27, 55, 59, 196). See Figure 195 for some hypotheses on the patterning of the bristle kinety.

The trachelocercid clade is defined by two unique characters (synapomorphies), viz. the apicalization of the oral apparatus and the brosse (Fig. 197, Table 7). Admittedly, the first character is rather speculative and partially based in EISLER's (1992) hypothesis that

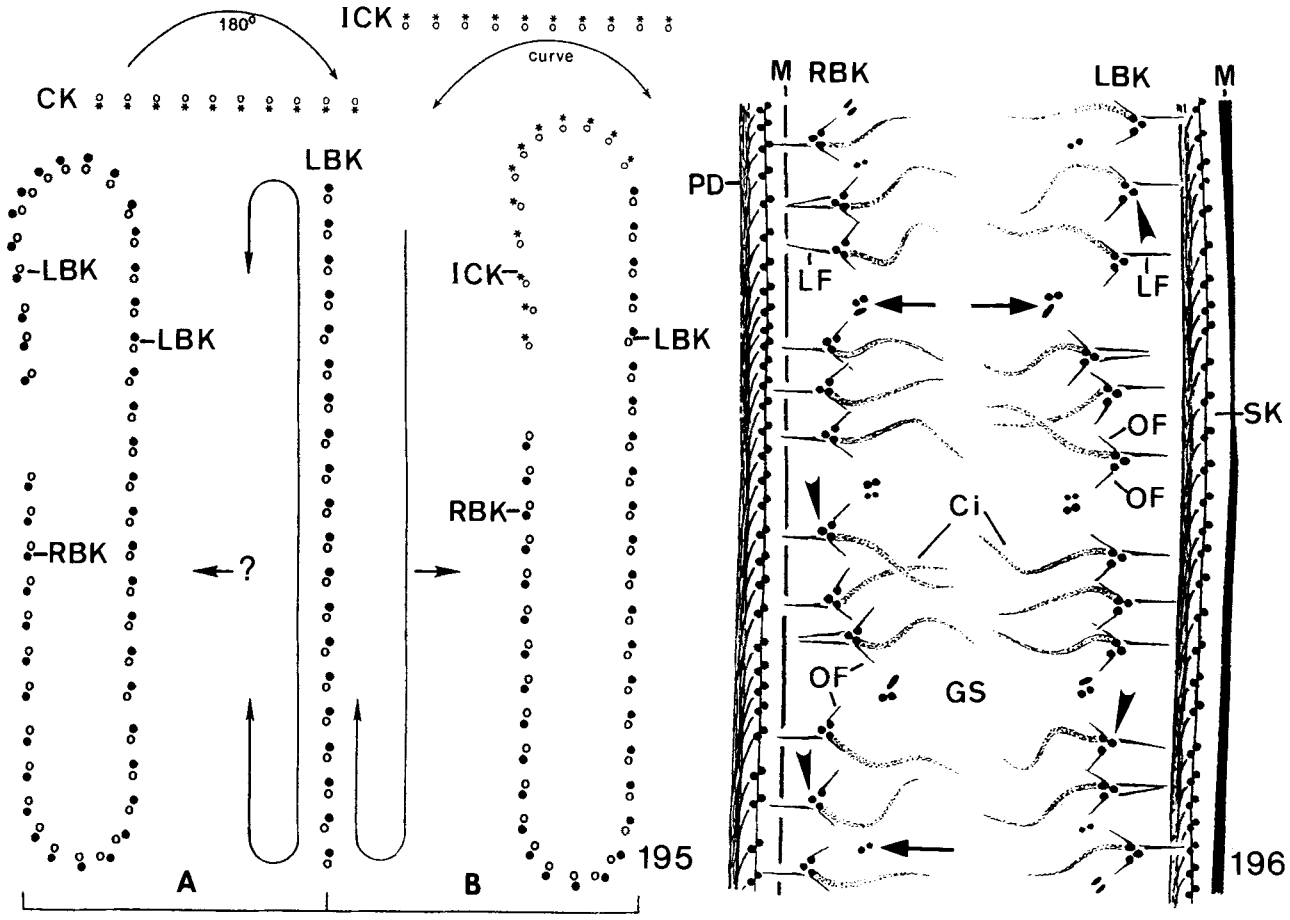


Fig. 195. Two hypotheses on patterning of the trachelocercid (and very likely also loxodid) bristle kinety. Both suggestions assume that the left branch of the bristle kinety curves around the posterior end of the cell and extends upward along the right margin of the glabrous stripe. This has been well documented in some trachelocercids (Figs. 22, 23, 54, 62) and loxodids (FOISSNER 1996c). The assumption that it is the left and not the right branch of the bristle kinety which curves upward is based on the observation that the right branch is the only part of the trachelocercid somatic infraciliature having the posterior basal body of the dikinetids ciliated, indicating that it is composed of inverted kinetids. The U-like shape of the bristle kinety causes the dikinetids to be opposed by 180° in its right and left branch, respectively, as shown by their ciliation and fibrillar system (Fig. 196). Hypothesis A, favoured in our previous papers (FOISSNER 1996a,b,c, FOISSNER & DRAGESCO 1996), considers the bristle kinety as a single ciliary row extending around the glabrous stripe. This suggestion hardly explains why the ciliation of the dikinetids is opposed by 90–180° where the ends of the kinety meet (Figs. 90, 118, 157, 167, 185). Hypothesis B, based on the more complete material of the present paper, assumes that the open anterior end of the bristle kinety is covered by an inverted, more or less distinctly curved fragment of the circumoral ciliature. This not only explains the opposed ciliation of the dikinetids in the region where the ends of the bristle kinety seemingly meet, but also that the anterior arch of the bristle kinety is frequently rather distinctly set off (Figs. 90, 91, 98, 142, 159) and has attached distinct fibres (Figs. 92, 94, 120, 142, 143), highly reminiscent of the nematodesmata associated with the circumoral dikinetids. The anterior arch of the bristle kinety is very likely lacking or inconspicuous in *Trachelocerca* (Figs. 14, 17, 58, 66) as well as in cryptopharyngid (FOISSNER 1996c) and kentrophorid (FOISSNER 1995) loxodids. CK = circumoral kinety fragment, ICK = inverted circumoral kinety fragment, LBK = left branch of bristle kinety, RBK = right branch of bristle kinety, ● ciliated basal body of dikinetids composing bristle kinety, ○ unciliated basal body of dikinetids composing bristle kinety and circumoral kinety fragment, * ciliated basal body of circumoral kinety fragment.

Fig. 196. Fine structure of the somatic and bristle infraciliature of trachelocercid ciliates as revealed by protargol impregnation. The figure does not refer to a particular species but summarizes observations from species of various genera. As concerns the somatic infraciliature (dikinetids), all species investigated so far have the same pattern. It is uncertain whether this applies also to the bristle kinety (kinetids) because the distinctiveness of the details shown highly depends on preparation conditions. Arrows mark paired and unpaired barren granules, possibly extrusomes. Arrowheads denote unciliated granules close to the bristle dikinetids, possibly parasomal sacs. Note that ciliation and fibrillar associates of the bristle dikinetids are opposed by 180° in the left and right branch of the bristle kinety, respectively. Ci = cilia, GS = glabrous stripe, LF = lateral fibre directed to somatic kineties, LBK = left branch of bristle kinety, M = myoneme, OF = oblique fibres directed to glabrous stripe, PD = postciliodesma formed by overlapping postciliary microtubule ribbons originating from posterior body of somatic dikinetids, RBK = right branch of bristle kinety, SK = subkinetal microtubule ribbon.

Table 7. Characters and character states used in Figure 197.

Apomorph ■	Plesiomorph □
1 bristle kinety framing glabrous stripe	without
2 simple circumoral kinety[1])	compound circumoral kinety[1])
3 apical oral apparatus	ventrolateral oral apparatus
4 dorsolateral kinety[2])	without
5 epipellicular scales or mucilage[2])	without
6 brosse	without
7 loss of brosse	with brosse
8 brosse modified to ciliary tuft	brosse consisting of short, oblique kineties

[1]) For definition see footnote 5 in Table 6.
[2]) See FOISSNER (1996c).

ancestral ciliates had ventrolaterally located oral structures as, for instance, found in *Loxodes*. However, there is also direct support for an apicalization of the trachelocercid oral apparatus, viz. the location of the site where the ends or components (Fig. 195) of the bristle kinety meet. In trachelocercids, this site is close underneath the circumoral kinety because the anterior arch of the bristle kinety is short or, as in *Trachelocerca*, even lacking (Figs. 14, 66, 90, 157). In the sister group, the loxodids, the right anterior branch of the bristle kinety is much longer in some genera and extends along the entire oral apparatus and thus meets the other end only at the level of the posterior buccal vertex (FOISSNER 1996b, c). It is easy to imagine that a trachelocercid pattern arises if, for instance, the oral apparatus of *Remanella* is shifted anteriorly, i.e. apicalized.

The brosse, very likely secondarily reduced in *Trachelocerca*, is an outstanding feature. It appears, at least light microscopically, very similar to that of gymnostomatid and, especially, prostomatid ciliates (FOISSNER et al. 1994, 1995). Our data suggest that it is part of the (circum)oral ciliature or of the bristle kinety the anterior arch of which is, like the brosse kineties and the circumoral dikinetids, associated with distinct nematodesmata (Figs. 92, 95, 96, 120, 142, 143, 195). Possibly, the brosse is homologous to the intrabuccal kinety or the left part of the paroral ciliature of the loxodids. Unfortunately, these suggestions are purely speculative because we did not find a single divisional stage among more than 1,000 well impregnated specimens.

Evolution within trachelocercids is difficult to follow because of the great homogeneity of the somatic infraciliature, as explained above, and the undirected variation of the nuclear apparatus; all genera, except possibly *Trachelocerca*, contain species with a strand of isolated nuclei or with a single nuclear cluster (capsule). Thus, only few apomorphies, all related to the oral structures, remain for reconstructing evolution, and only one synapomorphy has been identified, viz. the simple circumoral kinety, uniting the genera *Tracheloraphis*, *Trachelolophos*, and *Trachelocerca* (Fig. 197, Table 7). Certainly, *Trachelocerca* is difficult to place. We consider the lack of the brosse a derived character because the majority of the trachelocercids have a brosse and complex paroral structures, as found in *Prototrachelocerca*, occur in the loxodid sister group (FOISSNER 1996a, c). Possibly, ontogenetic data will provide deeper insights.

Improved characterization of the order Trachelocercida and the family Trachelocercidae

Order Trachelocercida JANKOWSKI, 1978: Large (> 300 µm) to very large (> 2,000 µm), slender (< 100 µm) Karyorelictea CORLISS, 1974 with apical oral apparatus composed of simple or compound circumoral (paroral ?) ciliature and a conspicuous brosse (adoral ?), both with distinct nematodesmata. Brosse comprising one or more short, ciliated kineties interrupting circumoral ciliature or unstructured ciliary tuft near centre of oral cavity; secondarily reduced in genus *Trachelocerca*. Body usually highly contractile and laterally compressed, right side completely ciliated, left with more or less wide glabrous stripe bordered by highly specialized bristle kinety. Somatic and oral ciliature composed of dikinetids throughout, specialized and condensed in anterior region of cell. All marine and psammophilic. Type family (by original designation): Trachelocercidae KENT, 1881.

Remarks: See FOISSNER (1996a) for nomenclature and authorship of order. JANKOWSKI (1978, 1980) gave vague and partially incorrect diagnoses because he included the trachelocercids in the pleurostomatids (1978: oligomerization of somatic kineties, with diploid nucleus and apical oral apparatus; 1980: worm or band-like ciliates with apical mouth lacking nematodesmata; head (mouth) with slit; macronuclei diploid, sometimes

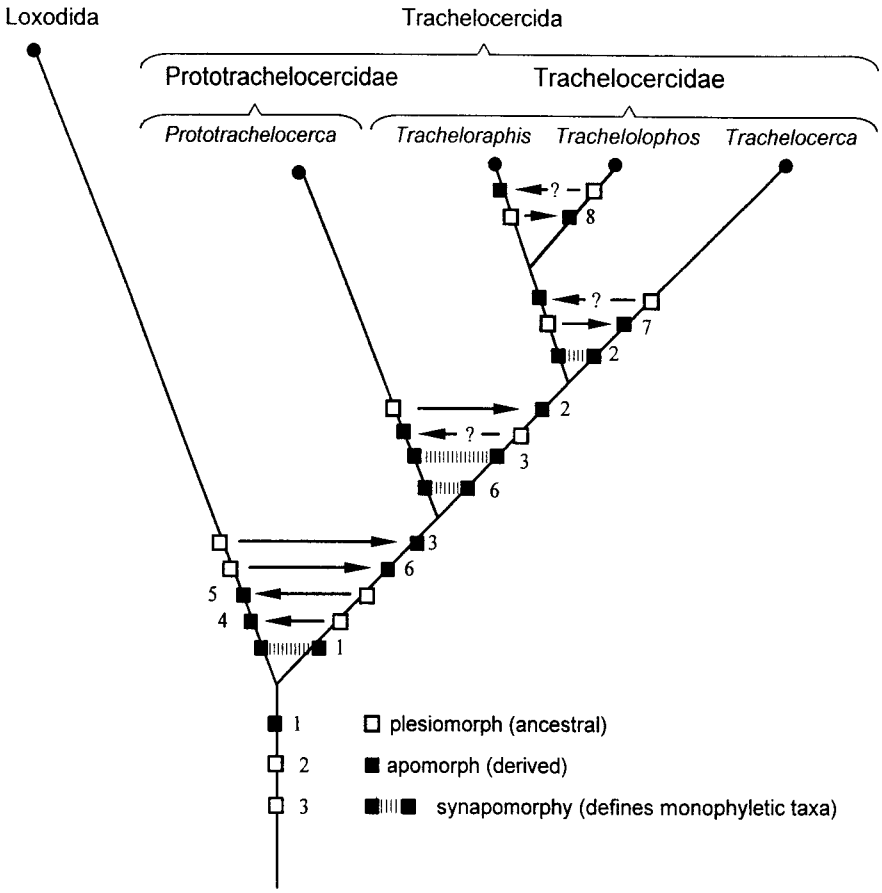


Fig. 197. Cladistic (phylogenetic) relationships of trachelocercid karyorelictids. See Table 7 for characters and character states used.

in complex group including micronuclei; with tendency to reduce kineties on left surface; inhabiting marine psammon). However, he recognized one of the main characters, viz. the apical location of the oral apparatus, which distinguishes the trachelocercids from all other karyorelictids. The bristle kinety surrounding the glabrous stripe is a synapomorphy uniting trachelocercids and loxodids (see above).

Family Trachelocercidae KENT, 1881: Trachelocercida JANKOWSKI, 1978 with simple circumoral ciliature comprising a single row of dikinetids. Type genus: *Trachelocerca* EHRENBERG, 1840 (new designation).

Remarks: KENT (1881) assigned the genera *Trachelocerca*, *Lacrymaria*, *Phialina*, *Lagynus*, and *Chaenea* to the Trachelocercidae. He did not fix a type genus. We selected *Trachelocerca* as type because KENT (1881) named the family after this genus and most of the other genera are now considered to belong to families (Lacrymariidae, Enchelyidae) of the gymnostomatid haptorids.

The Trachelocercidae differ from the Prototrachelocercidae FOISSNER, 1996 by the circumoral ciliature which is composed of more than one row of dikinetids in the latter.

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