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Updating the Trachelocercids (Ciliophora, Karyorelictea). I. A Detailed Description of the Infraciliature of *Trachelolophos gigas* N. G., N. Sp. and *T. filum* (Dragesco & Dragesco-Kernéis, 1986) N. Comb.

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ABSTRACT. *Trachelolophos gigas* n. g., n. sp. and *T. filum* (Dragesco & Dragesco-Kernéis, 1986) n. comb. (basionym: *Tracheloraphis filum*) were discovered in the mesopsammon of the French Atlantic coast at Roscoff. Their morphology and infraciliature were studied in live and protargol impregnated specimens. The new genus, *Trachelolophos,* belongs to the family Trachelocercidae and is unique in having a conspicuous ciliary tuft, which is very likely a highly modified brosse, in the oral cavity. The two species investigated have a very similar infraciliature, differing only in morphometric characteristics and in the nuclear configuration. The entire somatic and oral infraciliature consists of dikinetids which have both basal bodies ciliated or only the anterior or posterior ones, depending on the region of the cell. The right side is densely and uniformly ciliated. Its kineties extend onto the left side to the glabrous stripe, where an anterior and posterior secant system are formed, reducing the number of kineties in the narrowed neck and tail region. The left side bears a narrow glabrous stripe bordered by slightly irregularly arranged dikinetids having rather stiff cilia (bristles), possibly forming an uninterrupted, prolate ellipsoidal (bristle) kinety as indicated by their ciliation. The bristle kinety commences subapically at the right margin of the glabrous stripe, extends posteriorly, then anteriorly at the left, to end up at the right margin again. The dikinetids of the right posterior portion of the bristle kinety have the *posterior* basal bodies ciliated, whereas the *anterior* basal bodies are ciliated in its left and right anterior portion. The ends of the bristle kinety meet distinctly subapically at the right margin of the glabrous stripe, as indicated by the diametrically opposed ciliation of the dikinetids. The anterior region (head) of the cell bears a distinct circumoral kinety composed of very regularly arranged dikinetids, associated with nematodesmata forming an oral basket together with the nematodesmal bundles originating from the oralized somatic dikinetids at the anterior end of the somatic kineties. The systematics of trachelocercid ciliates are briefly reviewed and discussed.

Supplementary key words. Interstitial fauna, Loxodidae, oralized somatic dikinetids, systematics, *Trachelonema, Tracheloraphis.*

KARYORELICTIDS have "primitive," i.e. nondividing diploid macronuclei and are thus a key group for understanding ciliate phylogeny [3, 5, 25, 26, 29]. However, their somatic and oral infraciliature (ciliary pattern) is poorly explored. Only recently were detailed studies performed on *Remanella* [15], *Cryptopharynx* [16] and *Kentrophoros* [14], substantially amending some classic studies on *Loxodes* [27], the sole freshwater karyorelictid. The situation for trachelocercids, the largest group within the Karyorelictea, is still worse. Most of the few reports available on their infraciliature are superficial and contain confusing mistakes concealing their real diversity [2, 7, 8, 11, 33, 36]. There are only few exceptions, viz. the classic transmission electron microscopic investigation by Raikov et al. [32] on the somatic cortical ultrastructure of *Tracheloraphis phoenicopterus* and the protargol studies by Dragesco & Dragesco-Kernéis [9] and Wilbert [35] on some species from Africa and the Red Sea in Israel. These studies showed that trachelocercids have a complex oral infraciliature and a somatic ultrastructure reminiscent of that found in heterotrichs. A close relationship between karyorelictids and heterotrichs, reflected most recently in the proposed classification of ciliates found in Corliss [4], is also supported by their ribosomal gene sequences [1].

The incompleteness of previous studies is not simply caused by superficial work but also by methodological problems. Most trachelocercids are fragile and explode when conventional fixatives are applied. Using a new, very "strong" fixative and Wilbert's [13] protargol technique, we obtained excellent preparations from many species, showing a world of new details on which we shall report in a series of papers [17].

MATERIALS AND METHODS, TERMINOLOGY

Organisms and preparations. *Trachelolophos gigas* and *T. filum* occurred sparsely in the mesopsammon, i.e. in the upper 0–4 cm sand layer of the French Atlantic coast at Roscoff. Samples were collected and treated exactly as described by Fauré-Fremiet [12], i.e. the specimens were detached from the sand grains by adding about 5 ml of a 12% $MgCl_2$ solution to about 20 ml sand and sea water. The mixture was then gently rotated in a petri dish so that the sand collected in the center and the ciliates could be picked up individually with a capillary pipette from the clear supernatant.

Cells were studied in vivo using a high-power oil immersion objective [13]. The infraciliature was revealed by protargol impregnation [13; protocol 2, Wilbert's method], using a new fixative found by trial and error: 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 [14–16], but does not prevent contraction in contractile species. Specimens were fixed for 10–15 min and washed three times in distilled water. Seven excellently prepared specimens each were obtained and evaluated. Some others were of usuable quality and served for completing morphometry. The nuclear apparatus of *T. gigas* was studied also after staining with methyl green-pyronin [13].

Counts and measurements on silvered specimens were performed at a magnification of 1,000×. In vivo measurements were conducted at a magnification of 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.

Terminology (Fig. 1). Standard terms as outlined in [3, 24, 34] are used. However, some explanation of the basic organization and terminology of trachelocercid ciliates appears appropriate to standardize and facilitate forthcoming genus and species descriptions. Our diagrams (Fig. 1) are based on the present and literature data [2, 7, 9, 11, 17, 35] and figured as seen in the light microscope.

The orientation of the trachelocercid cell, based on the site of the "mouth," is somewhat problematic. This is because ontogenetic data are lacking and ingestion possibly occurs along

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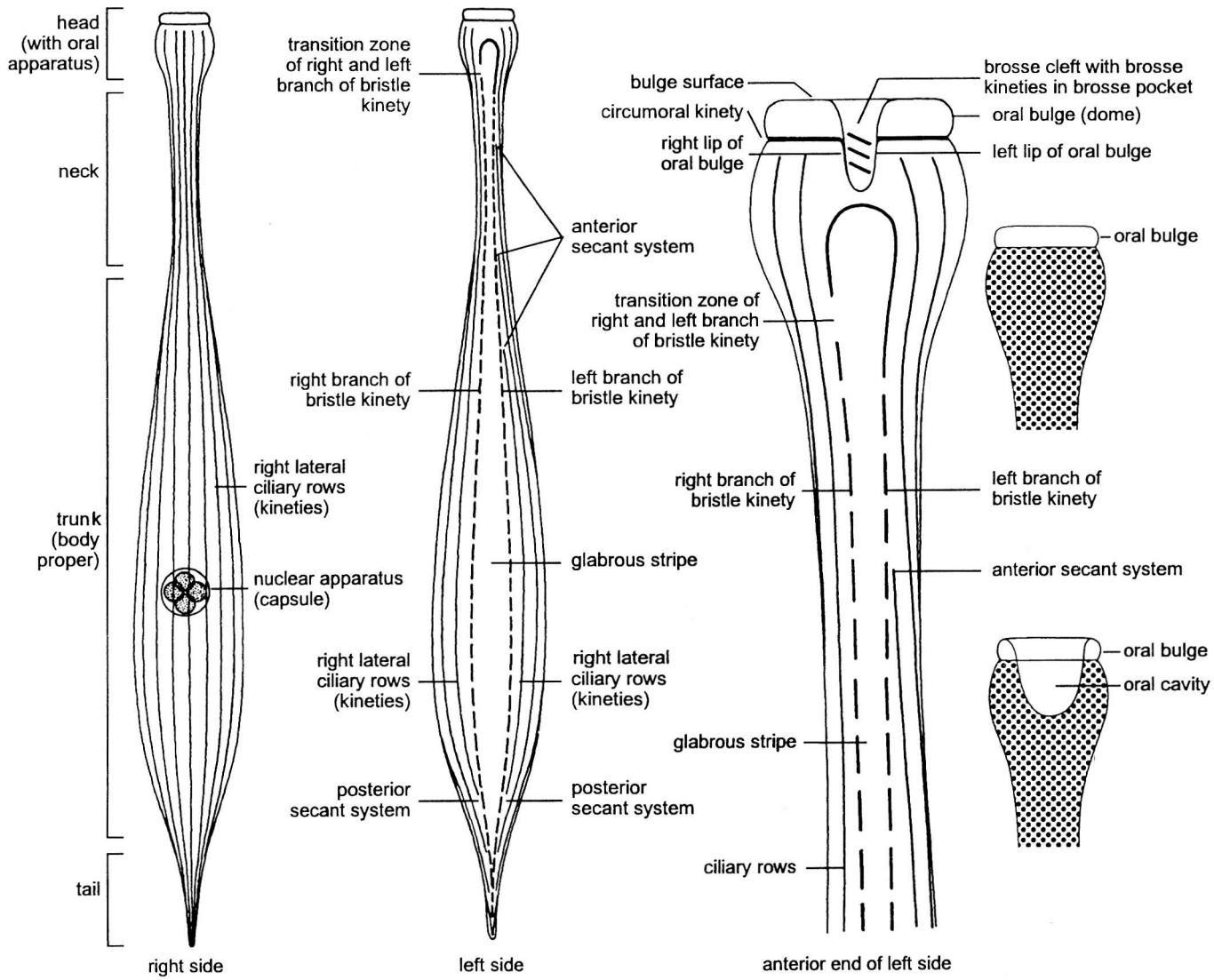


Fig. 1. Descriptive terminology for trachelocercid ciliates. See terminology section for detailed explanation. Brosse kineties are numbered 1, 2, 3 . . . from anterior to posterior, as are adoral membranelles in hymenostome ciliates. Note that a brosse is lacking in *Trachelocerca* (Foissner & Dragesco, unpubl. observ.) and that it is modified to a ciliary tuft in *Trachelolophos* (Fig. 3, 38). The rightmost figures show that an oral cavity may be present (e.g. *Trachelolophos*) or lacking (e.g. *Trachelocerca*; Foissner & Dragesco, unpubl. observ.).

the glabrous stripe [22, 23], but the "head" (Fig. 1) possesses structures (e.g. dikinetids with nematodesmata; Fig. 12–18, 38, 42) that appear homologous to the functional oral apparatus of other, especially gymnostomatid and prostomatid ciliates [18, 19]. However, the bristle kinety (Fig. 1) is likely homologous to the left ciliary row found in loxodids, which have the oral apparatus located subapically on the ventral side [15]. We thus designate, homologically, the surface with the bristle kinety as the left side.

Bristle kinety (abbreviation suggested, BK): A row of modified, often rather irregularly arranged dikinetids with stiff cilia, bordering the margins of the glabrous stripe (Fig. 1, 11, 18, 26, 35, 43, 51). Whether the bristle kinety is a single row (as it often appears to be) or composed of several short rows needs to be clarified by morphogenetic studies.

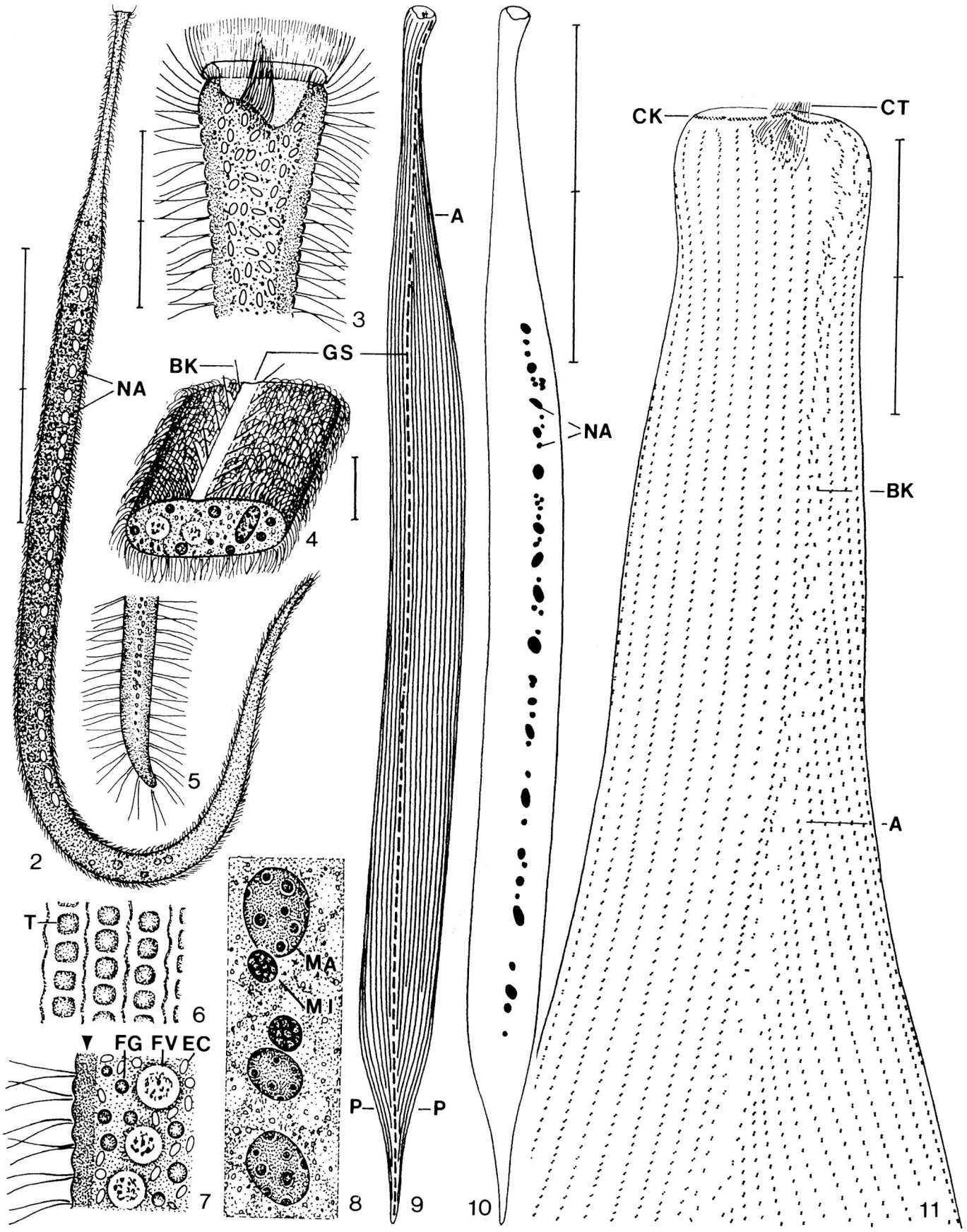
Brosse (B): As defined in [3], i.e. one or several short, oblique kineties near anterior end of cell. The brosse is modified to a ciliary tuft in *Trachelolophos* (Fig. 14, 38, 55) and lacking in *Trachelocerca* (Table 2). It is possibly homologous to the adoral ciliature of typical ciliates.

Brosse cleft (BC): A narrow slit in the left surface of the head where the brosse cilia emerge; produces the right and left lip of the oral bulge. Possibly, the slit is covered by the pellicle of the oral bulge.

Brosse pocket (BP): A more or less deep cavity or groove in the left side of the head containing the brosse kineties.

Circumoral kinety (CK): Surrounds base of oral bulge, composed of a single row (e.g. in *Trachelolophos,* Fig. 38) or of several rows (e.g. *Prototrachelocerca* [17]) of dikinetids, interrupted at brosse cleft. The circumoral kinety(ies) is possibly homologous to the paroral ciliature of typical ciliates.

Cortical granules (G): Small (0.2–3 μm), often refractile granules in the periphery of the cell, sometimes corresponding to extrusomes (mucocysts = protrichocysts, nematocysts. . .). Size, colour, shape and arrangement of the cortical granules are important species characteristics.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Glabrous stripe (GS) or zone: A more or less wide, nonciliated area in the median of the left surface, bordered by the bristle kinety and often rippled in contracted specimens (Fig. 1, 4, 9, 19, 35, 52).

Nuclear capsule (NC): The nuclei of trachelocercids are either individually distributed in the cytoplasm or enclosed by a special membrane (capsule) forming a single, tight aggregate [29].

Oral bulge (OB): A nonciliated, often very hyaline eminence on anterior end of head (Fig. 1, 3, 43). Often called "pericytostomal lip" [2].

Oral cavity (OC): A cylindroid or concave depression in centre of bulge surface; not to be confused with brosse pocket (Fig. 1, 3, 24, 42).

Postciliodesma (PD): As defined in [3], i.e. a conspicuous bundle of microtubules formed by overlapping postciliary microtubule ribbons at the right side of the ciliary rows (Fig. 19, 22, 27, 35).

Secant system (SE): As defined in [3], i.e. lines of convergence of kineties over the surface of the body. In trachelocercids suture lines occur at the left side of the glabrous stripe where some somatic kineties abut to the bristle kinety (Fig. 1, 9, 11, 19, 23, 27, 35, 51).

RESULTS

Trachelolophos n. g.

Diagnosis. Trachelocercidae Kent [21] with conspicuous ciliary tuft in head (oral) cavity and simple, uninterrupted circumoral and bristle kinety, each composed of single row of dikinetids.

Type species. *Trachelolophos gigas* n. sp.

Etymology. Composite of the Greek nouns "trachelos" (neck) and "lophos" (tuft). Maculine gender.

Trachelolophos gigas n. sp.

(Fig. 2–38, Table 1)

Diagnosis. In vivo about 2,000 × 50 μm. Neck cylindroid, distinctly separate from flattened, parallel-sided trunk; tail long but indistinctly separate from trunk. 17–33 ($\bar{x}$ = 25) macronuclei forming strand in trunk. Cortex 3–5 μm thick, gelatinous, without conspicuous granules. 26–30 ($\bar{x}$ = 28) ciliary rows on neck, 52–71 ($\bar{x}$ = 62) on trunk; glabrous stripe narrow, corresponds to area occupied by one kinety and two interkinetal spaces. Oral ciliary tuft composed of 33–50 ($\bar{x}$ = 44) cilia.

Type location. Mesopsammon of French Atlantic coast at Roscoff, W 4°, N 48°50′.

Type specimens. One holotype and one paratype of *T. gigas* as two slides of protargol (Wilbert technique) impregnated specimens have been deposited in the collection of microscope slides of the Oberösterreichische Landesmuseum in Linz (LI), Austria, accession numbers: 9–10/1995. Relevant specimens are marked by a black ink circle on the cover glass.

Etymology. "gigas" (giant) refers to the large size of the organism.

Description (Fig. 2–38, Table 1). Morphometric data shown in Table 1 are repeated in this section only as needed for clarity. All observations are from field material. Thus, it cannot be excluded that different species were mixed, although we excluded specimens which deviated in at least one prominent character (see *T. filum,* described below).

Size in vivo about 2,000 × 50 μm, less distinctly contractile than many other trachelocercids, size and shape thus comparatively well preserved in protargol slides (Table 1, Fig. 9, 32). Shape rather constant, prolate fusiform as shown in Fig. 1, 9; head trumpet-shaped and up to 50 μm wide, neck comparatively short and cylindroid, widens abruptly to long, parallel-sided, distinctly (about 2:1) flattened trunk gradually narrowing to long tail with distal end pointed and slightly curved (Fig. 2, 3–5, 9, 24). Macronuclei globular to distinctly (up to 2:1) ellipsoid, with many small nucleoli; not in capsules but individually arranged in trunk, left of cell median, forming conspicuous strand. Micronuclei globular, near and between macronuclei, stain bluish with methyl green-pyronin, like macronuclear nucleoli, indicating presence of DNA (Fig. 8, 10, 21, 32, 36). No contractile vacuole. Cortex conspicuous, i.e. pellicle underlain by 3–5 μm thick, gelatinous layer distinctly separate from granular cytoplasm, lacks specific granules and/or mucocysts, forms columnar blisters (tubercles) in contracted specimens (Fig. 5–7, 24). Cytoplasm colourless, cells appear greyish at low (40×) magnification, contains numerous 5–10 μm sized food vacuoles with granular content, many 1–3 μm sized fat globules and many about 2 × 1 μm sized crystalline (?) inclusions slightly accumulated in head, which is thus a little darker than the rest of the cell (Fig. 3, 7, 24). Movement like other large trachelocercids, i.e. elegantly gliding and winding between sand grains and organic debris.

Somatic infraciliature (Fig. 2, 9, 11, 19–23, 26, 27, 33–35). The surface of *T. gigas* is densely ciliated, leaving blank only a narrow zone, the glabrous stripe, extending along the whole body length near the median of the left side. The cilia, which are rather stiff and can be spread, are about 12 μm long and arranged in longitudinal rows, which are distinctly separate from the circumoral kinety and extend between flat cortical crests. The ciliary rows are gradually shortened anteriorly in the neck region left of the glabrous stripe and posteriorly, where the body narrows to the tail, at both sides of the stripe. In other words, an anterior secant system is formed on the left surface of the neck, where many kineties abut to the left branch of the bristle kinety. Thus, the head, neck, and tail have only about half the kinety number present on 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; furthermore, the ciliary rows are slightly more widely spaced on the right than on the left surface of the cell.

The entire infraciliature consists of dikinetids which, however, have a highly specialized ciliation and fibrillar system. The dikinetids are rotated about 20°–30° counter-clockwise to the kinety axis and associated with conspicuous, overlapping post-

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Fig. **2–11**. *Trachelolophos gigas* from life (**2–7**), and following methyl green-pyronin staining (**8**), and protargol impregnation (**9–11**). **2**. Right lateral view of typical specimen. **3**. Head with ciliary tuft in oral cavity. **4**. Transverse section in trunk region. Note distinct flattening of cell and stiff cilia of bristle kinety. **5**. Distal end of tail consisting almost entirely of gelatinous ectoplasm (cp. **7**). **6**. Tubercles occur between ciliary rows in contracted specimens. **7**. Optical section in trunk region. Arrowhead marks thick, gelatinous layer underneath pellicle. **8**. Part of nuclear apparatus. **9, 10**. Overview of infraciliature of left side and nuclear apparatus (see following figures for details). **11**. Infraciliature of left side of head and neck. The two branches of the bristle kinety are recognizable due to their rather widely spaced and irregularly arranged dikinetids. A, anterior secant system; BK, bristle kinety; CK, circumoral kinety; CT, ciliary tuft in oral cavity; EC, ellipsoid crystals (inclusions); FG, fat globules; FV, food vacuoles; GS, glabrous stripe; MA, macronucleus; MI, micronucleus; NA, nuclear apparatus; P, posterior secant system; T, tubercles. Bar divisions = 200 μm (**2**, **9**, **10**) and 20 μm (**3**, **4**, **11**), respectively.

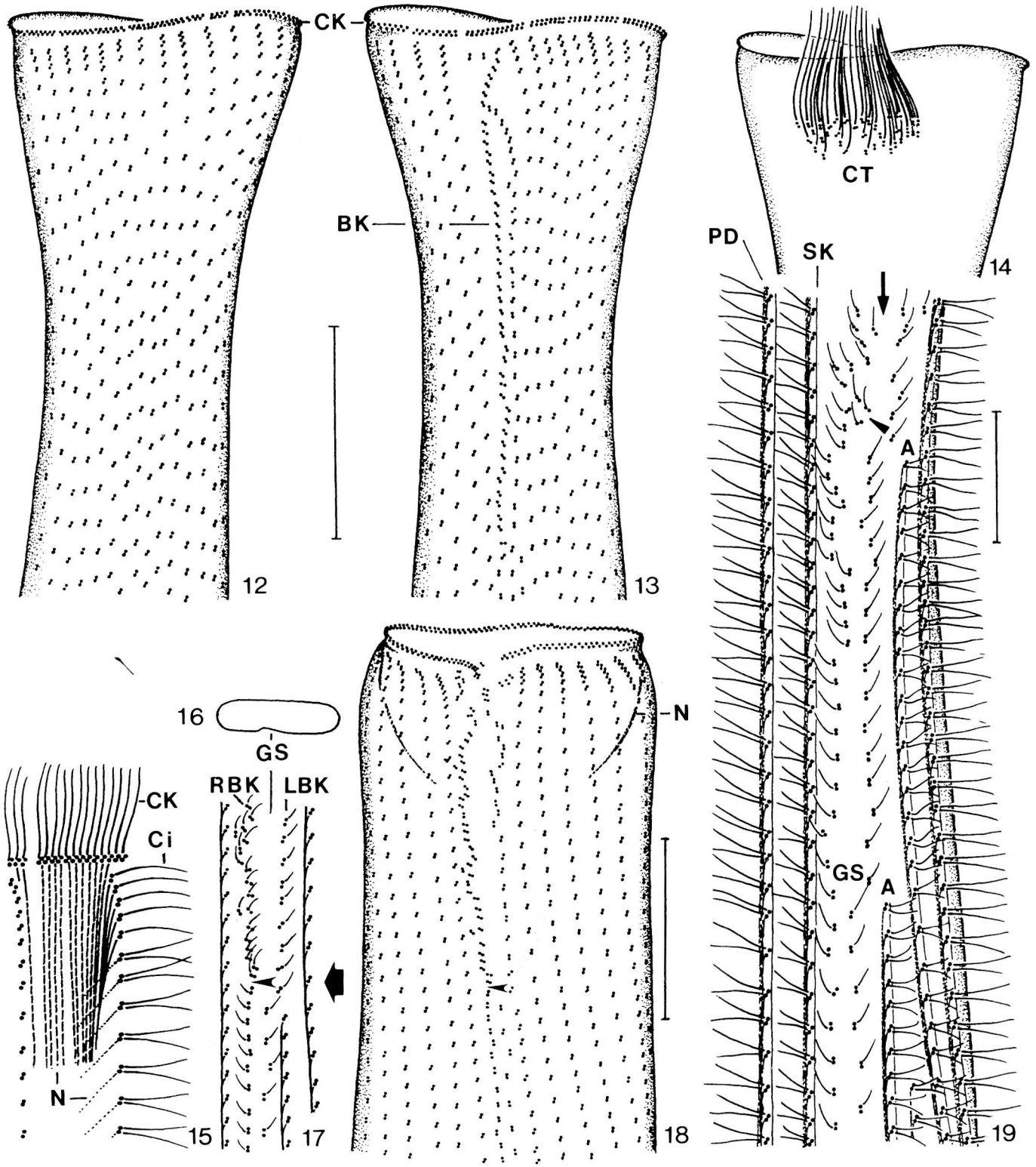

Fig. **12–19**. *Trachelolophos gigas,* somatic and oral infraciliature after protargol impregnation. **12–14**. Right and left side of head, and ciliary tuft inside oral cavity (cp. **3**). **15**. Details of the somatic and oral fibrillar system. **16–19**. Details of the anterior left lateral somatic infraciliature. Figures 16–18 are from same specimen. The bristle kinety borders the glabrous stripe which is slightly depressed (**16**). The ends of the bristle kinety meet subapically at the right margin of the glabrous stripe, as indicated by the opposed ciliation of the dikinetids (arrowheads). Note that in Fig. 19 the anterior arch of the bristle kinety is not shown, i.e. it is about 10 μm above the arrow separating its right and left branch. A, anterior secant system; BK, bristle kinety; Ci, cilia of somatic kinety; CK, cilia of the circumoral kinety; CT, ciliary tuft in oral cavity; GS, glabrous stripe; LBK, left branch of bristle kinety; N, nematodesmata, PD, postciliodesma; RBK, right branch of bristle kinety; SK, subkinetal microtubule ribbon (?). Bars = 20 μm.

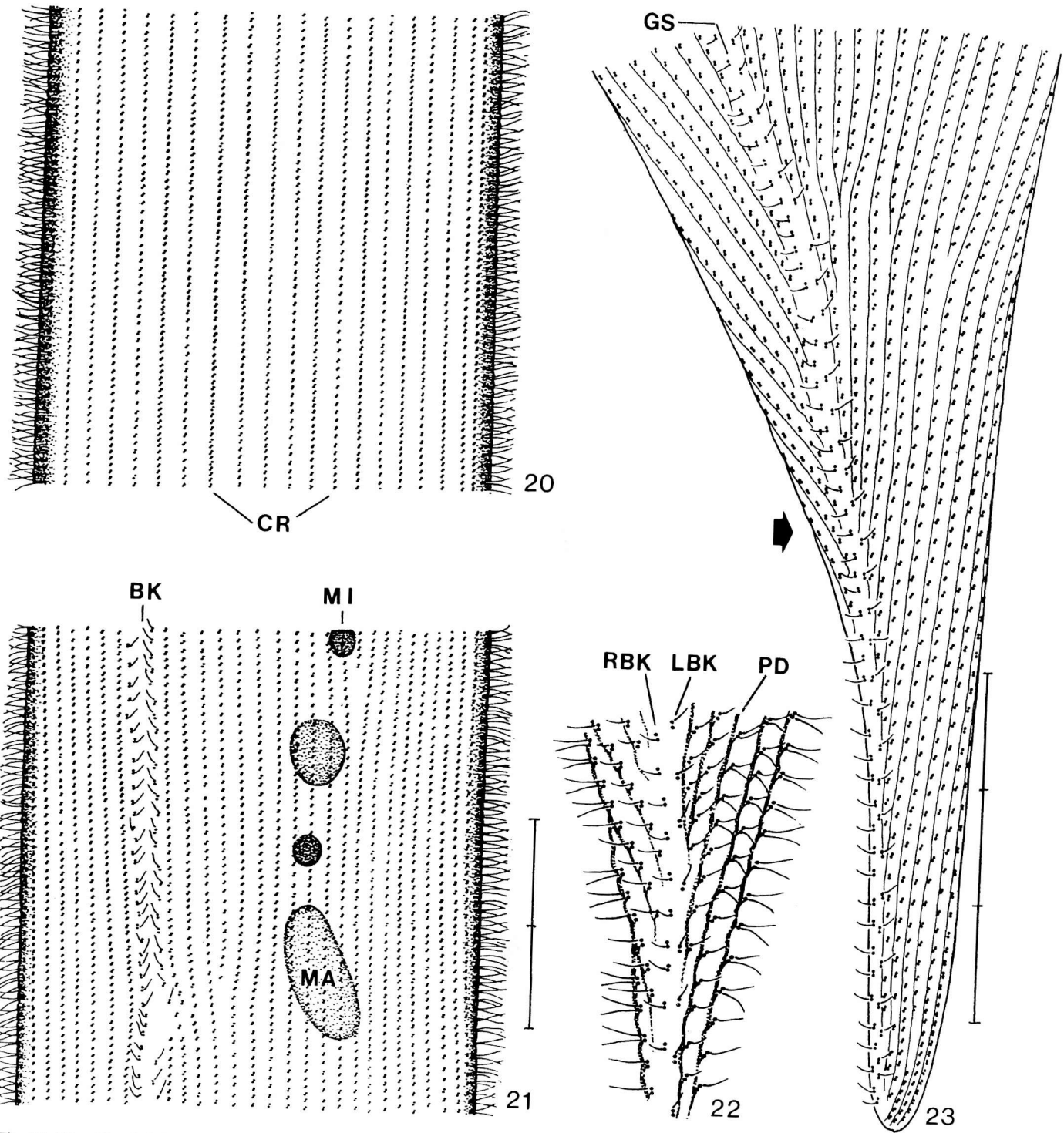

Fig. **20–23**. *Trachelolophos gigas,* somatic infraciliature after protargol impregnation. **20, 21**. Right and left side of trunk. The cell is densely and uniformely ciliated, except for the narrow glabrous stripe bordered by the bristle kinety. **22, 23**. Left side of tail region, where the ciliary rows form the posterior secant system, i.e. they abut to the glabrous stripe. Figure 22 is an enlarged portion from Fig. 23 (arrow), showing that the posterior ends of the somatic kineties at the right margin of the glabrous stripe have the anterior basal bodies ciliated, whereas the posterior basal bodies are ciliated in the neighbouring (right) branch of the bristle kinety. Thus, the bristle kinety is very likely not composed of posterior fragments from the somatic ciliary rows. BK, bristle kinety; CR, somatic ciliary rows; GS, glabrous stripe; MA, macronucleus; MI, micronucleus; LBK, left branch of bristle kinety; PD, postciliodesma; RBK, right branch of bristle kinety. Bar division = 20 μm.

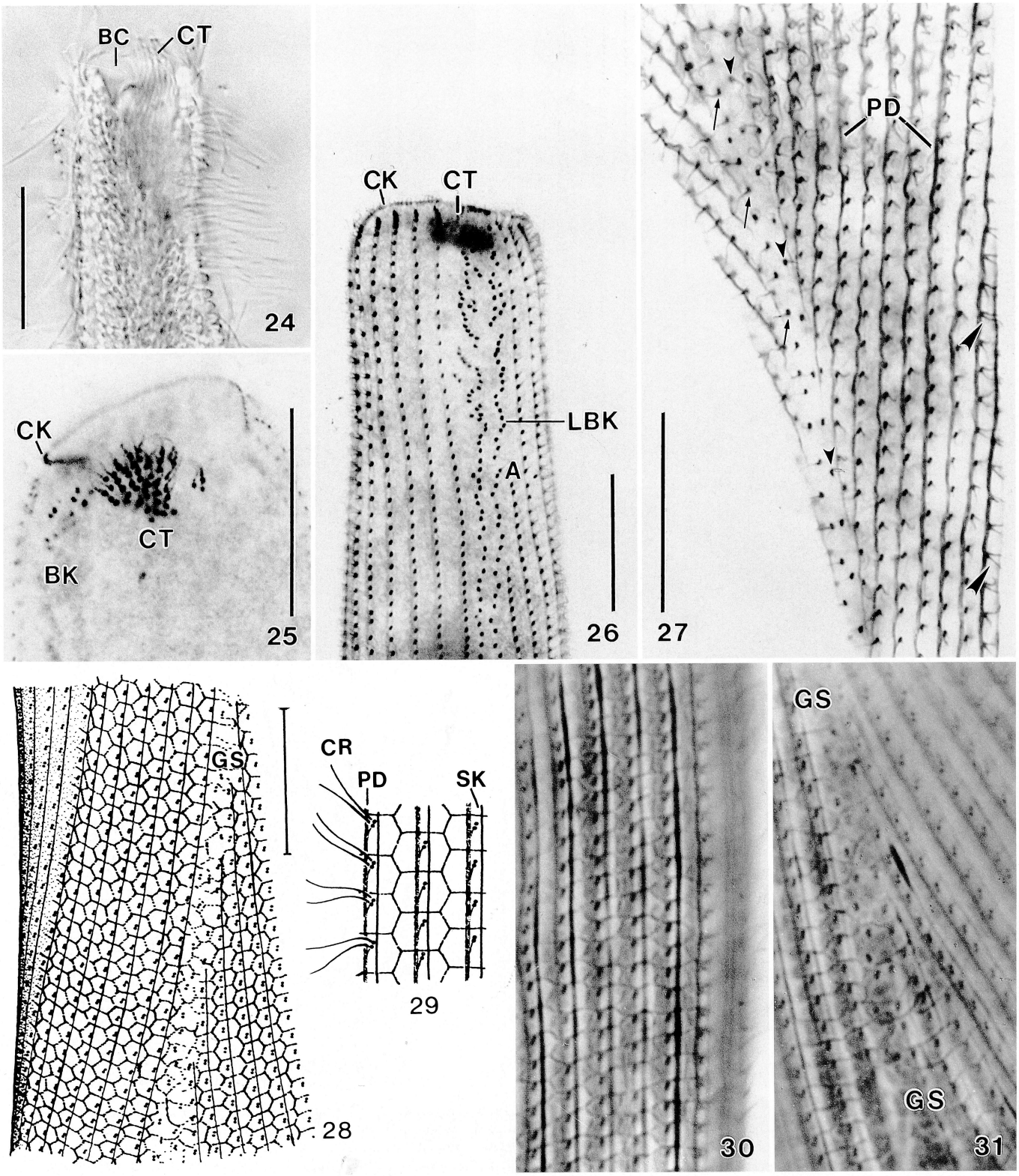

Fig. **24–31**. *Trachelolophos gigas* from life (**24**) and after protargol impregnation (**25–31**). **24, 25**. Contracted head showing buccal cavity containing distinct ciliary tuft. **26**. Infraciliature of left side of head and neck. **27**. Infraciliature of left side of tail, where the ciliary rows form the posterior secant system (cp. **22**, **23**), i.e. they abut to the bristle kinety whose right, respectively, left branch has the posterior (arrows), respectively, anterior (small arrowheads) basal bodies of the dikinetids ciliated. Large arrowheads mark normal somatic dikinetids having both basal bodies ciliated. **28–31**. Honeycombed structure in the cortex of a regenerating specimen. A, anterior secant system; BC, buccal cavity; BK, bristle kinety; CK, circumoral kinety; CR, ciliary row; CT, ciliary tuft; GS, glabrous stripe; LBK, left branch of bristle kinety; PD, postciliodesmata; SK, subkinetal microtubule ribbon (?). Bars = 20 μm.

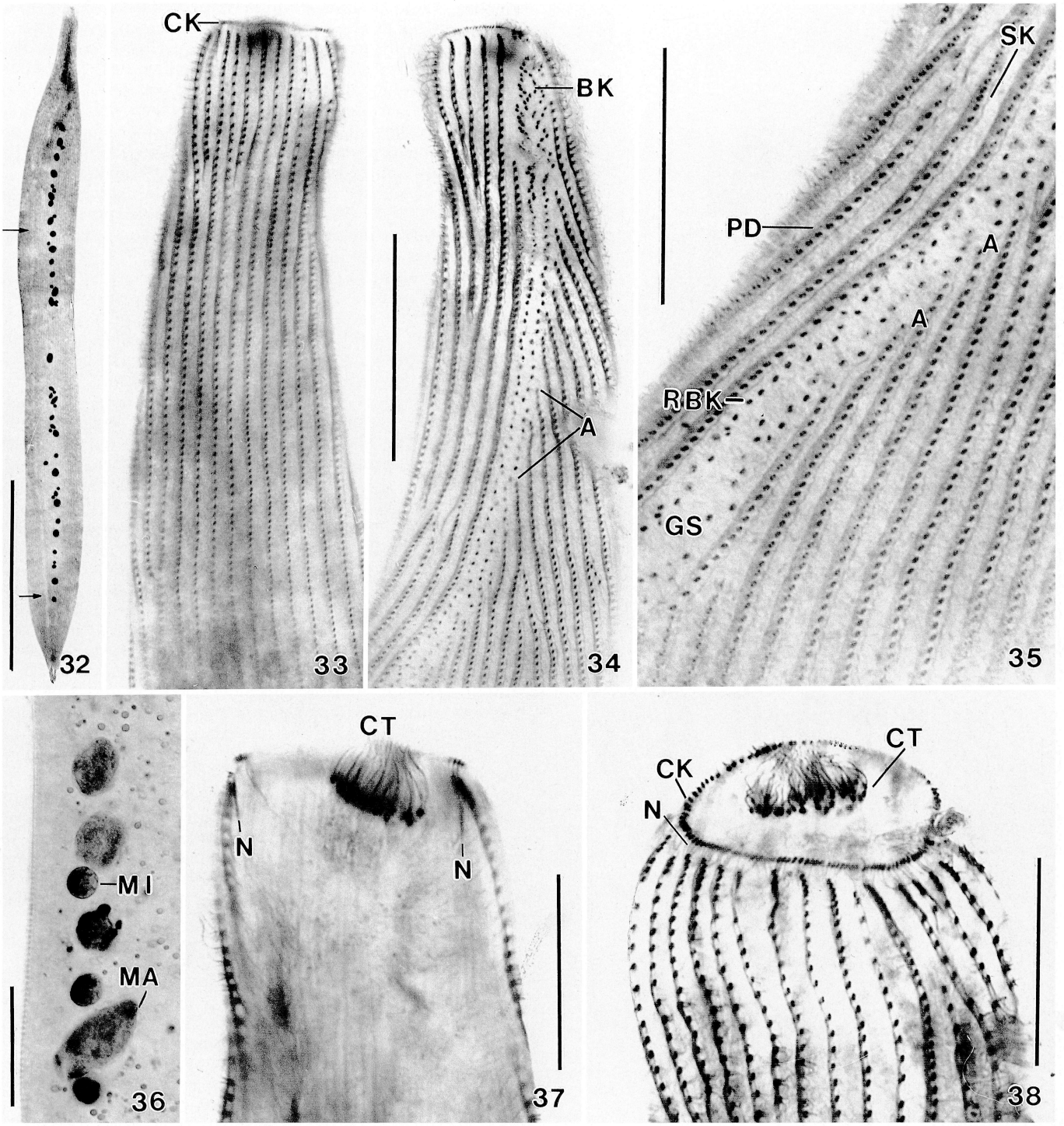

Fig. **32–38**. *Trachelolophos gigas,* somatic and oral infraciliature and nuclear apparatus after protargol impregnation. **32**. Overview showing nuclear strand and glabrous stripe (arrows). **33, 34**. Ciliary pattern on right and left side of head and neck. **35**. Left side of neck region at higher magnification, showing details of the somatic infraciliature and fibrillar system. **36**. Part of nuclear apparatus. **37, 38**. Head with ciliary tuft in optical section and oblique polar view. A, anterior secant system; BK, bristle kinety; CK, circumoral kinety; CT, ciliary tuft in oral cavity; GS, glabrous stripe; MA, macronucleus; MI, micronucleus; N, nematodesmata; PD, postciliodesma; RBK, right branch of bristle kinety; SK, subkinetal microtubule ribbon (?). Bars = 400 μm (**32**), 40 μm (**33**, **34**) and 20 μm (**35–38**), respectively.

ciliary microtubule ribbons which originate from the posterior basal bodies of the dikinetids and form a thick, faintly impregnated postciliodesma right of each ciliary row. A thin, sharply impregnated fibre, possibly a myoneme or subkinetal microtubule ribbon [31, 32], extends close to the left of each ciliary row (Fig. 19, 27). Both basal bodies of the dikinetids are ciliated in the main portion of the cell (Fig. 20, 21). The posterior cilium is lacking in about five dikinetids at the anterior end of the head

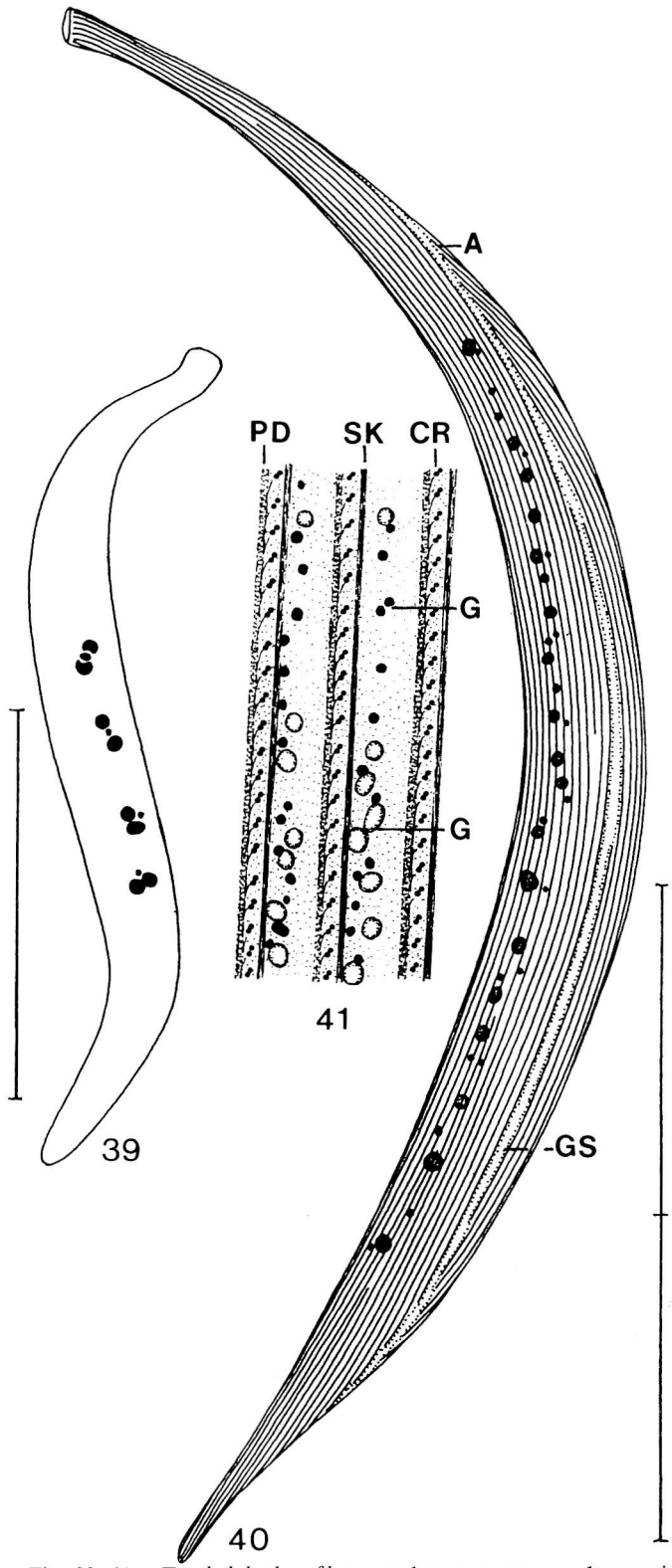

Fig. **39–41**. *Trachelolophos filum,* nuclear apparatus and somatic infraciliature after protargol impregnation. **39**. Nuclear apparatus of smallest (length 420 μm) specimen found. **40**. Nuclear apparatus and infraciliature of left side of largest (1,100 μm) specimen found. **41**. Cortical fine structure of specimen shown in Fig. 40. Two types of cortical granules can be distinguished. A, anterior secant system; CR, ciliary row; G, cortical granules; GS, glabrous stripe; PD, postciliodesma; SK, subkinetal microtubule ribbon (?). Bar division = 200 μm.

kineties. These kinetids are more narrowly spaced than those on the trunk, and associated with distinct nematodesmal fibres originating from the posterior, nonciliated basal bodies. The nematodesmata from the condensed kinetids unite to form small bundles extending almost parallel to the cell surface. Similar fibres originate from the neck dikinetids which, however, have both basal bodies ciliated. These fibres do not form bundles and extend obliquely posteriad to the neck midline (Fig. 15, 37, 38). The nematodesmata-bearing kinetids of the head and neck region are thus oralized somatic dikinetids as defined by Foissner & Foissner [18]. The posterior cilium is also lacking in three to ten dikinetids at the posterior end of the kineties, i.e. around the secant system of the tail region (Fig. 22, 27).

The glabrous stripe extends along the whole length of the body and is very narrow, i.e. corresponds to an area occupied by about one kinety and two interkinetal spaces (Fig. 9, 11, 13, 19, 21, 23, 26, 27, 34, 35). It is slightly depressed, especially in the head region (Fig. 4, 16), and bordered by the bristle kinety which consists, like the ordinary ciliary rows, of dikinetids. However, the bristle kinety is easily distinguished from the ordinary somatic kineties 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 (Fig. 11, 19, 22, 23, 27, 35). Furthermore, the bristle kinetids have a unique ciliation, most parsimoniously explained with the assumption that they belong to a single kinety extending along the glabrous stripe margins, quite similar to the left lateral kinety of the loxodids [16]. The bristle kinety commences subapically at the right margin of the glabrous stripe, extends posteriorly, then anteriorly at the left, to end up at the right margin again. The dikinetids of the right posterior portion of the bristle kinety have the *posterior* basal bodies ciliated, whereas the *anterior* basal bodies are ciliated in its left and right anterior portion. Both ends of the bristle kinety are very close together subapically at the right margin of the glabrous stripe. Thus, there is a point where the ciliation of the dikinetids is diametrically, i.e. by 180° opposed (Fig. 17, 19, 43, 46). Frequently, the dikinetids of the anterior portion are more irregularly and more obliquely arranged than those farther behind; furthermore, isolated dikinetids and/or minute dikinetidal fragments occur between the arch of the bristle kinety and the circumoral kinety (Fig. 11, 13, 17–19, 21–23, 26, 27, 34, 35). There is thus a slight but distinct variability in the anterior region of the bristle kinety and, in fact, none of the specimens studied agreed completely in this respect.

A honeycombed structure impregnated very clearly in the cortex of a regenerating specimen which had lost the posterior body half. The pattern was less distinct in the glabrous stripe (Fig. 28–31).

Oral infraciliature. The head, which bears the oral apparatus, is trumpet-shaped when fully extended (Fig. 3, 12) and cylindroid when contracted (Fig. 18, 24, 26). Its anterior end bears an inconspicuous, i.e. about 3 μm thick, hyaline oral bulge at the base of which the circumoral kinety extends (Fig. 3, 18, 38). The centre of the bulge and head is hollowed to an about 13 μm deep oral cavity (Fig. 3, 24). On the bottom of the cavity, slightly off centre (possibly approaching the bristle kinety), is a small eminence covered with a roundish patch of about 44 disordered dikinetids each having only one basal body ciliated. The cilia of this patch are about 15 μm long, mobile, and form a conspicuous tuft extending slightly beyond the oral bulge and recognizable also in live specimens (Fig. 3, 11, 14, 24–26, 37, 38).

The circumoral kinety consists of dikinetids having only one basal body ciliated, possibly the posterior. The kinety appears to be composed of about 10 segments separated by inconspic-

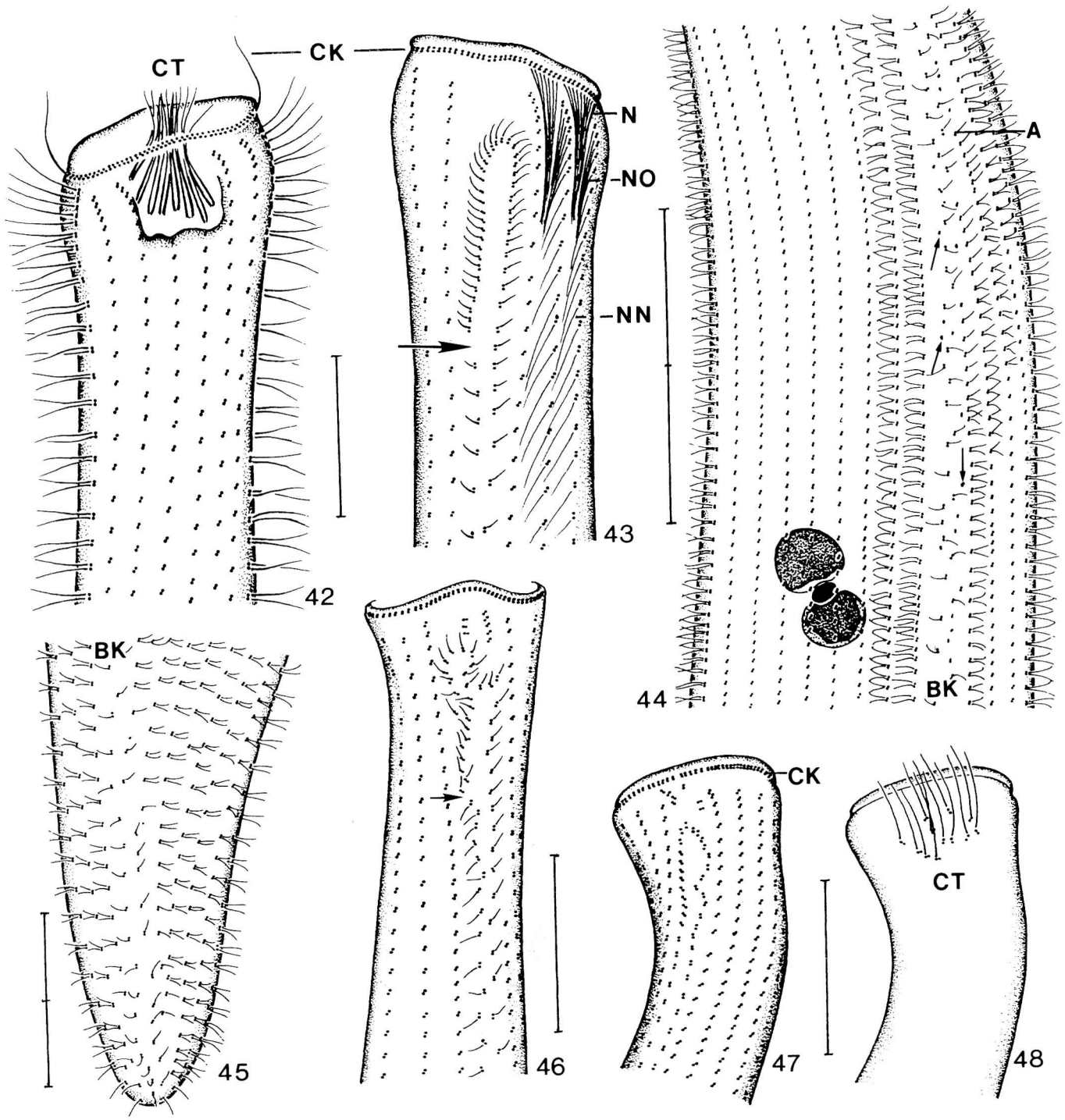

Fig. **42–48**. *Trachelolophos filum,* oral and somatic infraciliature after protargol impregnation. **42, 43**. Right and left side of head and anterior neck region. This specimen very clearly shows the ends (arrow) of the bristle kinety, where the ciliation of the dikinetids is diametrically (180°) opposed, indicating that the branches of the bristle kinety belong to a single ciliary row extending along the margins of the glabrous stripe. **44**. Left side of anterior trunk region. Note that the anterior dikinetids of the kineties forming the secant system have only the anterior basal bodies ciliated. Arrows mark small granules without cilia. **45**. Left side of posterior end. The posterior cilium is lacking in the distalmost somatic dikinetids. **46–48**. Variability of bristle kinety. Arrow marks point where the ends of the bristle kinety meet, i.e. the ciliation of the dikinetids is in 180° opposition. Figures 47 and 48 are from same specimen. A, anterior secant system; BK, bristle kinety; CK, circumoral kinety; CT, ciliary tuft in buccal cavity; N, nematodesmata originating from circumoral kinety; NN, nematodesmata originating from neck dikinetids; NO, nematodesmata originating from anterior (oralized) dikinetids of somatic ciliary rows; Bar division = 20 μm.

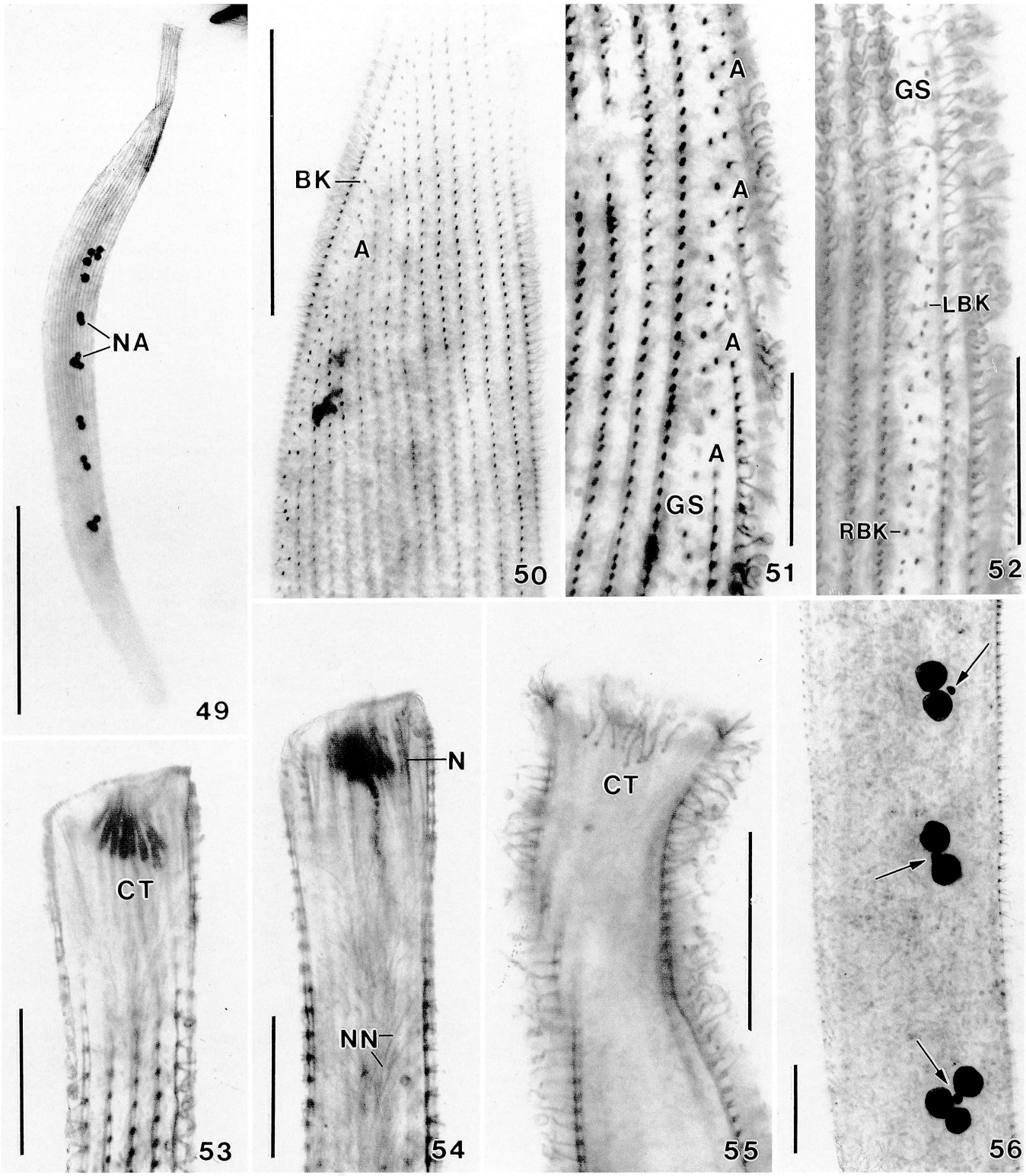

Fig. **49–56**. *Trachelolophos filum,* infraciliature and nuclear apparatus after protargol impregnation. **49**. Typical specimen. **50, 51**. Anterior secant system. **52**. Glabrous stripe in mid-body. **53, 54**. Head and neck of specimen shown in Fig. 42, 43. **55**. The ciliary tuft in the oral cavity consists of dikinetids having only one basal body ciliated. **56**. Higher magnification of nuclear apparatus of specimen shown in Fig. 49. Arrows mark micronuclei between macronuclei. A, anterior secant system; BK, bristle kinety; CT, ciliary tuft; GS, glabrous stripe; LBK, left branch of bristle kinety; N, nematodesmata originating from circumoral kinety; NA, nuclear apparatus; NN, nematodesmata originating from neck dikinetids; RBK, right branch of bristle kinety. Bars = 200 μm (**49**), 50 μm (**50**) and 20 μm (**51–56**), respectively.

Table 1. Morphometric data from *Trachelolophos gigas* (upper line) and *T. filum* (lower line).[a]

Character	$\bar{x}$	SD	CV	Min.	Max.	n
Body, length[b]	1,343.3	369.6	27.5	800	2,100	9
	654.3	226.0	34.5	420	1,100	7
Body, width at head	32.6	5.5	17.0	24	41	9
	18.9	2.6	13.8	14	22	7
Body, (maximum) width at trunk[b]	100.3	23.4	23.3	65	136	9
	54.0	13.1	24.3	40	80	7
Glabrous stripe, width in mid-body[c]	6.9	1.9	27.3	4	10	8
	5.9	1.1	18.6	5	8	7
Nuclear strand, length	725.6	233.2	32.1	250	1,050	9
	298.6	168.6	56.5	135	600	7
Macronucleus, length[d]	16.7	4.7	28.1	10	22	9
	8.9	1.6	17.7	7	11	7
Macronucleus, width[d]	10.3	3.0	28.7	6	15	9
	8.3	1.4	16.6	6	10	7
Micronucleus, length	6.4	1.5	23.6	3	8	9
	3.4	0.8	24.6	2	4	7
Micronucleus, width	5.6	1.3	23.8	3	8	9
	2.9	0.7	23.8	2	4	7
Somatic kineties, number on head	28.1	1.4	4.9	26	30	9
	14.7	1.6	10.9	12	17	7
Somatic kineties, (maximum) number on trunk	61.7	7.2	11.6	52	71	7
	30.1	3.3	11.1	26	35	7
Dikinetids, number in 10 μm in neck region	5.4	1.0	18.8	4	7	9
	4.7	1.0	20.2	3	6	7
Dikinetids, number in 10 μm in trunk region	7.1	0.8	11.0	6	8	9
	5.6	0.8	14.0	4	6	7
Tuft dikinetids, number	43.8	6.8	15.4	33	50	9
	12.0	1.2	10.2	10	13	5
Nuclear groups, number	—	—	—	—	—	—
	6.8	4.7	68.6	4	16	6
Macronuclei, total number[e]	24.9	6.2	25.1	17	33	8
	14.9	9.2	62.0	6	30	7
Micronuclei, total number	14.8	4.6	31.2	7	21	8
	8.3	6.1	73.2	3	20	7

[a] All data are based on the investigation of protargol impregnated and mounted morphostatic specimens. Measurements in μm. CV, coefficient of variation in %; Max, maximum; Min, minimum; n, number of specimens investigated; SD, standard deviation; $\bar{x}$, arithmetic mean.

[b] Values rather different from those of live specimens because cells contract when fixed for preparation.

[c] Measured between bordering somatic kineties.

[d] Fully developed macronuclei.

[e] Including developing ones.

uous spaces one to two dikinetids wide (Fig. 12, 13, 25, 26, 33, 38). The basal bodies of the dikinetids are arranged in zigzag and associated with nematodesmata forming an oral basket together with the nematodesmal bundles originating from the oralized somatic dikinetids at the anterior end of the somatic kineties (Fig. 15, 18, 37, 38).

Comparison with related species. No other species with a tuft of cilia in the oral cavity has been described. However, this attribute is not easily recognized and most trachelocercids have been only superficially studied. If we disregard this special feature, three species remain which resemble *T. gigas*. *Tracheloraphis discolor* Raikov, 1962 [30] is similar to *T. gigas* in size, shape, glabrous stripe and kinety number, but possesses 6–17 nuclear capsules each with four macronuclei and two micronuclei, which is highly dissimilar to the simple nuclear configuration of *T. gigas*. *Tracheloraphis dogieli* Raikov, 1957 [28] is similar in size, shape, nuclear apparatus and kinety number, but has a broad, conspicuous glabrous stripe. *Trachelocerca multinucleata* Dragesco, 1960 [7] is similar to *T. gigas* in shape, nuclear apparatus and glabrous stripe, but is smaller (1,000–1,300 μm), unflattened, has more than 100 ciliary rows, and fine trichocysts in the centre of the oral bulge. Possibly, cilia were mistaken for trichocysts (see *T. filum*); if so this species would belong to *Trachelolophos*. Likewise, *T. discolor* and *T. dogieli* could belong to the new genus because they have a distinct oral cavity.

Trachelolophos filum (Dragesco & Dragesco-Kernéis, 1986) n. comb.

(Fig. 39–56, Table 1)

History and identification. Dragesco & Dragesco-Kernéis [9] briefly described a new trachelocercid, *Tracheloraphis filum*, from a saline, temporary pool in Benin, Africa. It is distinguished from the congeners by a trichocyst bundle in the oral cavity, a very narrow glabrous stripe, and a nuclear apparatus usually consisting of several pairs of macronuclei, each with an interposed micronucleus. Dragesco & Dragesco-Kernéis [9] found eight specimens, but the type slide contains only four cells, whose reinvestigation showed that they match the original description, which is, however, rather incomplete due to the poor quality of the impregnation. For instance, only the anterior portion of the bristle kinety was recognized and the ciliary tuft in the oral cavity was misinterpreted as trichocyst bundle.

The population found at Roscoff matched the type specimens in all respects, except for a higher number of somatic kineties, viz. 26–35 ($\bar{x}$ = 30) vs. 20–24 ($\bar{x}$ = 22). This difference is considered as insufficient for separating the two populations at spe-

Table 2. Genus distinction in trachelocercid karyorelictids.

Character	*Trachelocerca* Ehrenberg [10]	*Tracheloraphis*[a] Dragesco [7]	*Trachelonema*[a] Dragesco [7]	*Prototrachelocerca* Foissner [17]	*Trachelolophos* n. gen.
Brosse	Absent	Present	Present	Present	Absent[e]
Ciliary tuft in oral cavity	Absent	Absent	Absent	Absent	Present
Circumoral kinety[b]	Simple and uninterrupted	Simple and interrupted	Simple and interrupted	Complex and interrupted	Simple and uninterrupted
Bristle kinety[c]	Simple	Complex	Complex	Mixed	Simple
Glabrous stripe	Narrow to wide	Wide	Very wide[d]	Wide	Narrow

[a] *Trachelonema* has almost the same characteristics as *Tracheloraphis* and should thus be synonymized with this genus.

[b] Simple, single row of dikinetids; complex, two or more rows of dikinetids. See [17] for details.

[c] Simple, single row of dikinetids; complex, many minute kineties composed of 2–5 dikinetids (Foissner & Dragesco, unpubl. data); mixed, basically like "simple" type, but with some minute kineties interposed, similar to "complex" type.

[d] Extending along whole width of body.

[e] Very likely, the ciliary tuft within the oral cavity is homologous to the brosse.

cies or subspecies level because very little is known about variability in trachelocercids.

Type material. We have deposited Dragesco & Dragesco-Kernéis' type slide of *T. filum* in the Oberösterreichische Landesmuseum in Linz (LI), Austria, accession number: 11/1995. Two voucher slides of the population described in this paper have been deposited at the same locality, accession numbers: 12–13/1995. Relevant specimens are marked by a black ink circle on the cover glass.

Redescription. (Fig. 39–56, Table 1). Like Dragesco & Dragesco-Kernéis [9], we found only few specimens and did not observe live cells. One of the seven specimens studied is distinctly larger (1,100 μm) and has more nuclei (30 macronuclei and 20 micronuclei) than the other cells (Fig. 40). However, variation in the nuclear apparatus is great (6–24 macronuclei) also in the other specimens (Fig. 39, 49) and thus the large individual very likely belongs to the same species as the other cells.

Trachelolophos filum and *T. gigas* differ only in morphometric characteristics (size, number of kineties and dikinetids in ciliary tuft, etc.). The structure of the infraciliature is identical. Thus, we desist from a complete description, which would be a repetition of that given for *T. gigas,* and refer to the detailed figures and figure explanations. In the large specimen mentioned above and in one other specimen the cilia of the oral ciliary tuft form distinct rods, reminiscent of the "trichocysts" described by Dragesco & Dragesco-Kernéis [9]. A detailed analysis of these and the type specimens showed that the rods are actually formed by two closely spaced cilia, which, when intensely stained, appear as thick rods (Fig. 42, 53). Faintly impregnated cells show the tuft to be composed of closely spaced dikinetids having only one basal body ciliated, as in *T. gigas* (Fig. 48, 55). Thus, *Trachelloraphis filum* Dragesco & Dragesco-Kernéis [9] is transferred to the genus *Trachelolophos*: *T. filum* (Dragesco & Dragesco-Kernéis, 1986) n. comb.

DISCUSSION

***Trachelolophos* as a new genus.** Following a note from Kahl [20], Delphy [6] hastily split trachelocercid karyorelictids 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; invalid because no type species was fixed). Later, Dragesco [7] split the trachelocercids again using, however, the absence (*Trachelocerca*)/presence (*Tracheloraphis, Trachelonema*) of a glabrous stripe and its relative width as sole characters. Unfortunately, the features used by Delphy [6] and Dragesco [7] are highly questionable because, e.g., all trachelocercids have a glabrous stripe, although it is inconspicuous in some species and thus difficult to recognize without silver impregnation. Likewise, a contractile vacuole is lacking in all true trachelocercids, and whether or not the distal end of the tail is slightly curved often remains ambiguous and is at best a species character.

Later investigators did not improve this situation, but simply followed Dragesco's view and moved species from one genus to the other. The characters we apply to distinguish trachelocercid genera are based on the somatic and oral infraciliature and are summarized in Table 2. This compilation uses results from the present and former [9, 17] investigations as well as unpublished material. *Trachelolophos* is apparently near *Trachelocerca,* differing in the peculiar tuft of cilia within the oral cavity. However, if the tuft is considered as a highly modified brosse, *Trachelolophos* would be more closely related to *Tracheloraphis* than to *Trachelocerca.* This needs to be clarified by ontogenetic studies.

The two species of *Trachelolophos* described in this paper are not unique. Meanwhile, we found at least two other distinct species (with few nuclei near mid-body), which will be described later.

Bristle kinety. The ciliation and arrangement of the bristle kinety suggest that it is a single ciliary row surrounding the glabrous stripe (Fig. 9, 11, 17–19, 21–23, 26, 27, 34, 35, 43, 46). This would certainly be an unusual pattern for a somatic ciliary row! However, our interpretation is supported by a detailed investigation of *Cryptopharynx* and *Apocryptopharynx,* loxodid karyorelicteans with a left lateral (bristle) kinety extending along the entire cell margin [16]. This kinety, whose course can be easily followed due to the broadly rounded ends of the organisms, has the same ciliation pattern as the bristle kinety of *T. gigas.* Other interpretations cannot, however, be completely ruled out in the absence of ontogenetic evidence, viz. that the bristle kinety is composed of two kineties, i.e. a right and left branch, with opposed kinetids, or of many small kineties originating from the anterior and/or posterior end of those somatic kineties which abut to the glabrous stripe. The last mentioned possibility is unlikely because the kineties in the right posterior region of the organism have the anterior basal bodies ciliated, whereas the posterior basal bodies are ciliated in the neighbouring portion of the bristle kinety (Fig. 22).

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