

Updating the Trachelocercids (Ciliophora, Karyorelictea). IV. Transfer of *Trachelocerca entzi* Kahl, 1927 to the Gymnostomatea as a New Genus, *Trachelotractus* gen. n. (Helicoprорodontidae)

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Summary. The morphology and infraciliature of *Trachelocerca entzi* Kahl, 1927, a highly contractile mesopsammal ciliate found on the French Atlantic coast at Roscoff, were studied in live and protargol impregnated specimens. The somatic infraciliature consists of ciliated monokinetids, except for two specialized kineties which have ciliated dikinetids forming a brush near the anterior end and spiral around the cytopharyngeal opening. The head and neck kinetids bear distinct nematodesmata, i.e. are oralized somatic kinetids. The head has a crown-like peribuccal ridge containing long extrusomes (toxicysts). The oral apparatus is simple, i.e. composed of a conical cytopharyngeal basket whose anterior end is surrounded by a few dikinetids possibly belonging to the anterior end of the spiral (brush)kineties. These characters largely match those known from *Helicoprорodon*. A glabrous stripe framed by a specialized bristle kinety, as found in trachelocercid and loxodid karyorelictids, is lacking. Thus, *T. entzi* is transferred from the karyorelictids to the gymnostomatids, viz. the family Helicoprорodontidae as a new genus, *Trachelotractus* gen. n., differing from *Helicoprорodon* by the possession of a typical gymnostomatous brush and the arrangement of the head extrusomes, which form a single circumpharyngeal bundle in *Trachelotractus* and a distinct spiral in *Helicoprорodon*.

Key words: infraciliature, *Helicoprорodon*, mesopsammal, Trachelocercidae, *Trachelotractus entzi* (Kahl, 1927) gen. n., comb. n.

INTRODUCTION

Little substantial alpha-taxonomic work has been done on karyorelictid ciliates since the pioneering study by Dragesco (1960), probably because they are rather fragile and thus difficult to preserve and stain. Notable exceptions are the papers by Raikov (1962), Dragesco and Dragesco-Kernéis (1986) and Wilbert (1986). Only recently, Foissner (1995, 1996a-c) and Foissner and Dragesco (1996a, b) updated the matter and provided detailed descriptions of the infraciliature of some time-

honoured and some new genera. During these studies, we found also *Trachelocerca entzi* Kahl, 1927, a conspicuous, highly contractile species, which has never been investigated in detail since the original description. Only Dragesco (1960) provided a brief redescription confirming Kahl's observations.

The present paper describes in detail the morphology and infraciliature of *T. entzi* and shows that it does not belong to the karyorelictid trachelocercids but to an entirely different group, the gymnostomatid helicoprорodontids. The same previously happened to *Trachelocerca fusca* Kahl, 1928, which became type of the (gymnostomatid or trichostomatid) genus *Paraspathidium* Noland, 1937, and *Trachelocerca trepida* Kahl, 1928, which became type of another gymnostomatid genus, *Pseudotrachelocerca*

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Song, 1990. Very likely, several other trachelocercids are also misplaced, e.g. *Trachelocerca conifera* Kahl, 1930 and *T. minor* Gruber, 1888.

MATERIALS, METHODS AND TERMINOLOGY

Trachelotractus entzi and *Helicoprordodon* sp. were found on 14. 9. 1994 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'), France. 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% MgCl₂ 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 (Foissner 1991). The infraciliature was revealed by protargol impregnation [Foissner 1991; protocol B (Wilbert's method)], using the fixative described by Foissner and Dragesco (1996a): 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 most mesopsammal ciliates 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 were also studied in transient preparations stained with methyl green-pyronine (Foissner 1991).

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, those of impregnated cells were made with a camera lucida. All figures are oriented with the anterior end of the organism directed to the top of the page. Terminology is according to Corliss (1979) and Foissner and Foissner (1988).

RESULTS

Trachelotractus gen. n.

Diagnosis: Helicoprordontidae with few (two) parallel brush kineties spiralling around cytopharyngeal opening in single turn. Brush subapical, composed of ciliated dikinetids. Head extrusomes in single circumpharyngeal bundle attached to peribuccal ridge.

Type species: *Trachelocerca entzi* Kahl, 1927.

Etymology: Composite of the Greek noun *trachelos* (neck) and the Latin noun *tractus* (extension), referring

to the similarity with *Trachelocerca* in general appearance and contractility. Masculine gender.

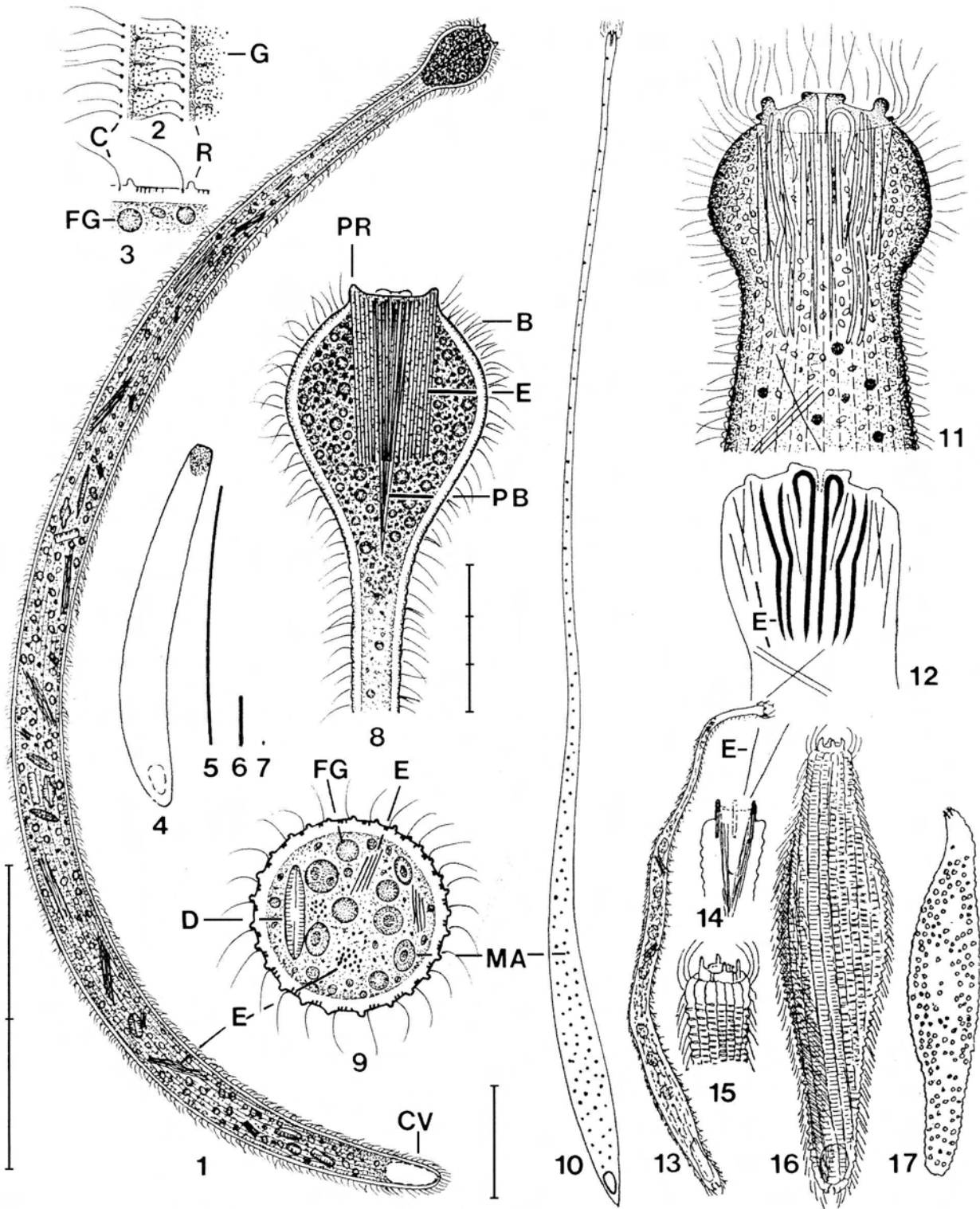
Redescription of *Trachelotractus entzi* (Kahl, 1927) comb. n. (Figs. 1-9, 18-27, 29-41, Table 1)

Improved diagnosis: Extended about 1000 x 35 µm, contracted about 300 x 50 µm. Vermiform, head globular with crown-like peribuccal ridge, distinctly set off from cylindroid neck which gradually widens to trunk. About 150 - 600 macronuclei. One contractile vacuole in posterior end. Three types of rod-shaped extrusomes, i.e. long (35 µm) and short (7 µm) toxicysts in head and trunk, and minute (< 1 µm) mucocysts in cortex. An average of 28 ciliary rows on trunk and 20 on head. Brush consisting of two rows indistinctly separate from respective somatic kineties.

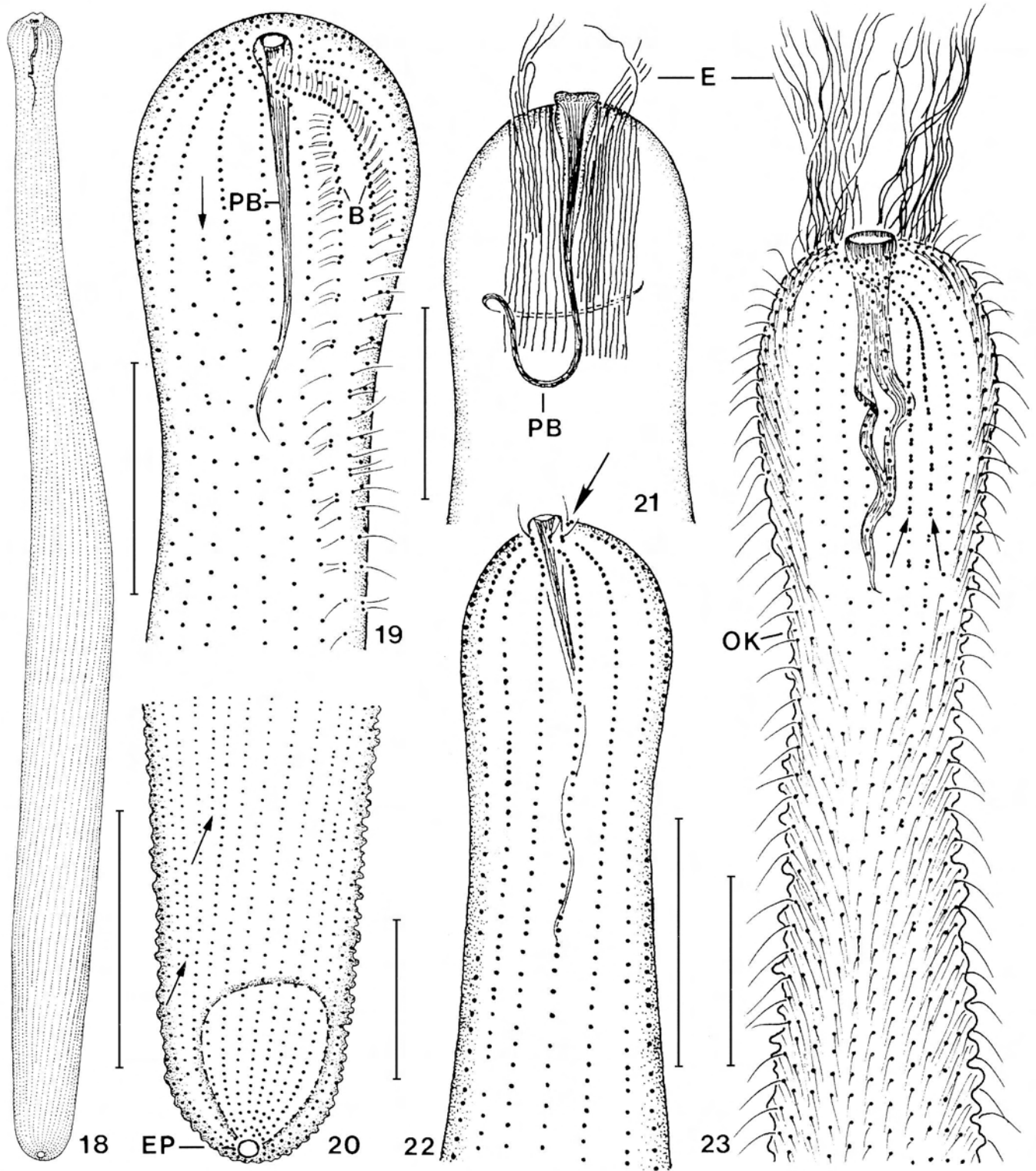
Specimens investigated and type material: The redescription is based on 15 well-impregnated specimens; some others were of useable quality and served for completing morphometry. No type material from *T. entzi* has been mentioned in the literature. Thus, I have deposited two neotype slides with specimens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

Redescription: Morphometric data shown in Table 1 are repeated in this section only as needed for clarity. One specimen was excluded from the analysis because it had about 55 kineties and thus possibly belonged to another species.

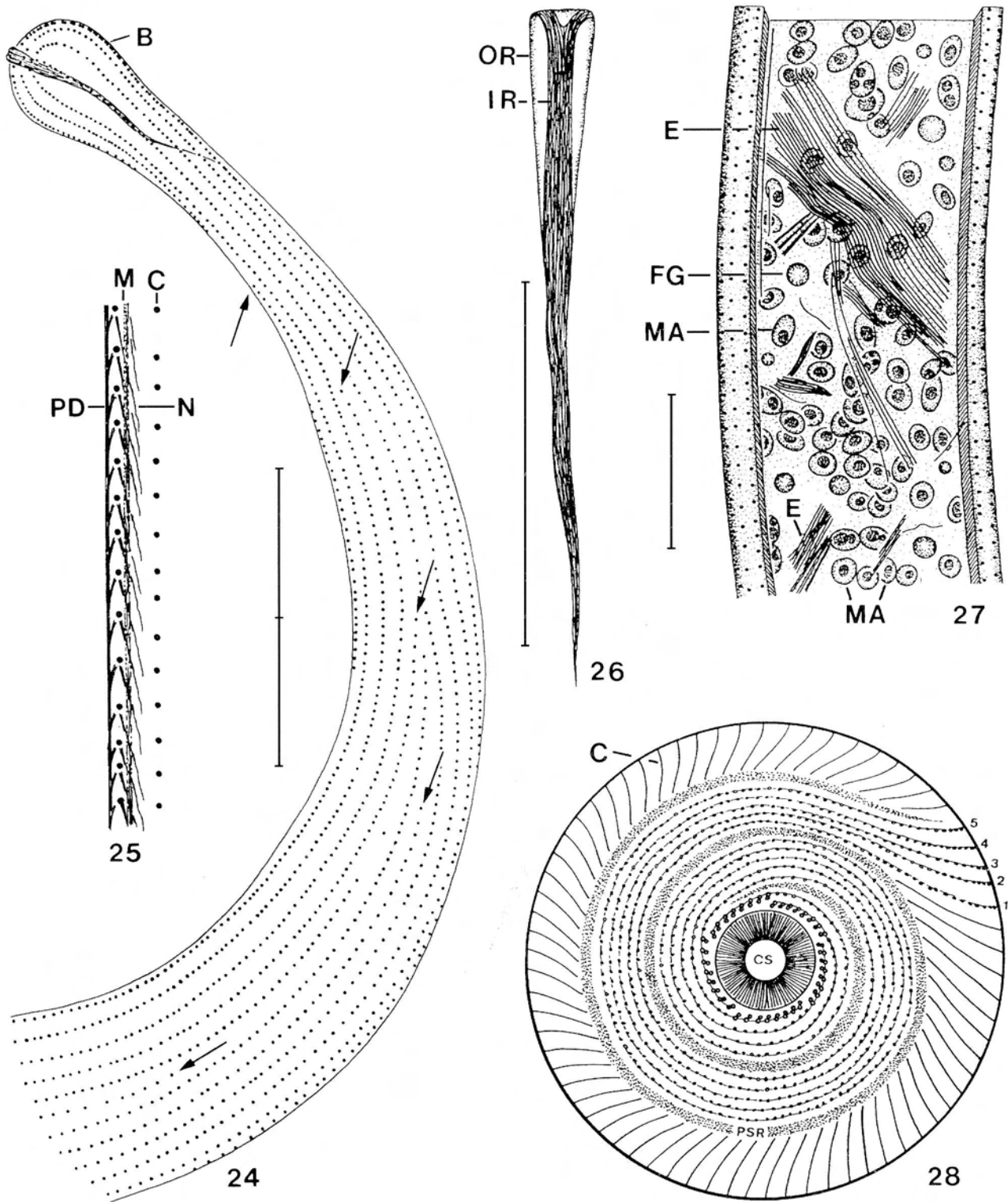
Largest, possibly fully extended specimens up to 1300 µm long and about 35 µm wide. Vermiform with conspicuous, globular dark head distinctly set off from narrowed, greyish neck; trunk cylindroid, brownish in dissecting microscope, gradually narrowed posteriorly but not tail-like (Figs. 1, 9, 18, 29). Head globular to pyriform, about as wide as trunk, black at low magnification because packed with highly refractile, 1-3 µm sized fat globules and 1-2 µm sized irregularly shaped granules different from the ellipsoidal inclusions found in many trachelocercids (Foissner and Dragesco 1996a,b); peribuccal ridge circular, rather flat and with some minute processes, contains tightly packed extrusomes forming conspicuous core around cytopharyngeal basket, respectively, in central portion of head (Figs. 8, 11, 15, 21, 31). Very flexible and contractile, fully contracted specimens cylindroid and about 300 µm long (Fig. 4); contraction very likely due to fibre (myoneme), rarely impregnated with protargol (Fig. 25), located in small ridge left of each ciliary row (Figs. 2, 3, 9), rather slow, length and



Figs. 1 - 17. *Trachelotractus entzi* from life (1 - 11, 13 - 16) and after hematoxylin staining (12, 17). Figures 1 - 9 originals, 10 - 12 from Dragesco (1960), 13 - 17 from Kahl (1927). 1, 10, 13 - extended specimens; 2, 3 - surface view and optical section of cortex; 4, 16 - contracted specimens, length about 300 μm ; 5, 6, 7 - long (35 μm) and short (7 μm) toxicyst and cortical granule (mucocyst? 0.3 μm), drawn to scale; 8, 11, 12, 14, 15 - fine structure of head. Note curved thick "fibres" in Figs. 11, 12, very likely bundles of exploding toxicysts; 17 - nuclear apparatus. B - (dorsal)brush, C - ciliary rows, CV - contractile vacuole, D - diatom, E - extrusomes, FG - fat globules, G - cortical granules (mucocysts?), MA - macronuclei, PB - pharyngeal basket, PR - peribuccal ridge, R - cortical ridge containing myoneme. Scale bar division 100 μm (Figs. 1, 10) and 10 μm (Fig. 8)



Figs. 18 - 23. *Trachelotractus entzi*, oral and somatic ciliary pattern (infraciliature) after protargol impregnation. 18 - total view of typical specimen; 19, 20 - anterior and posterior body portion at higher magnification. Arrows mark shortened kineties; 21 - head with circumpharyngeal extrusome bundle partially extruded (cp. Fig. 31); 22 - oral infraciliature. Arrow marks dikinetids around pharyngeal opening; 23 - head and neck infraciliature. Note brush kineties (arrows) spiralling around pharyngeal opening and nematodesmata of oralized somatic kinetids (OK). B - (dorsal)brush, E - extrusomes, EP - excretory pore of contractile vacuole, OK - oralized somatic kinetids, PB - pharyngeal basket. Scale bars 100µm (Fig. 18) and 20µm (Figs. 19 - 23)



Figs. 24 - 28. *Trachelotractus entzi* (24 - 27) and *Helicoprorodon gigas* (28; from Raikov and Kovaleva 1980), infraciliature after protargol impregnation (24 - 27) and transmission electron microscopy (28). 24 - reduction of ciliary rows (arrows) in head and neck region; 25 - somatic fibrillar system in head and neck region, where kinetids have an associated nematodesma; 26 - pharyngeal basket; 27 - cytoplasmic inclusions in trunk region; 28 - schematic apical view showing five (numbered 1 - 5) somatic kineties spiralling around cytostome (CS). Spiral kineties have dikinetids at anterior end and are separated by the peribuccal ridge (PSR) which contains long extrusomes (cp. Figs. 42 - 44). B - brush, C - ciliary rows, E - extrusomes, FG - fat globules, IR - inner region of oral basket, M - myoneme, MA - macronuclei, N - nematodesma, OR - outer region of oral basket, PD - postciliodesma. Scale bar division 20µm

Table 1. Morphometric data from *Trachelotractus entzi* *

Character	\bar{X}	M	SD	SD $_{\bar{x}}$	CV	Min	Max	n
Body, length	753.3	775.0	220.3	51.9	29.2	350	1150	18
Body, maximum width	38.6	37.5	8.4	2.0	21.7	26	54	18
Body, width at head	22.8	24.0	3.6	0.8	15.6	16	29	18
Macronucleus, length	4.1	4.0	0.9	0.2	20.9	3	6	18
Macronucleus, width	3.6	3.5	0.7	0.2	18.6	3	5	18
Oral basket, length	34.0	35.0	6.7	1.6	19.6	18	44	18
Oral basket, width	4.0	4.0	0.9	0.2	22.9	3	6	18
Distance anterior end to end of right brosse kinety	17.4	16.5	5.0	1.2	28.9	10	30	18
Distance anterior end to end of left brosse kinety	21.8	20.0	6.8	1.5	31.3	15	40	18
Somatic kineties, maximum number on trunk	29.4	28.0	4.5	1.1	15.2	25	40	18
Somatic kineties, number on head	19.1	20.0	3.0	0.7	15.6	13	24	18
Cilia, number in a row	400.3	420.0	108.6	25.6	27.1	220	650	18
Brosse kineties, number	2.0	2	0.0	0.0	0.0	2	2	18

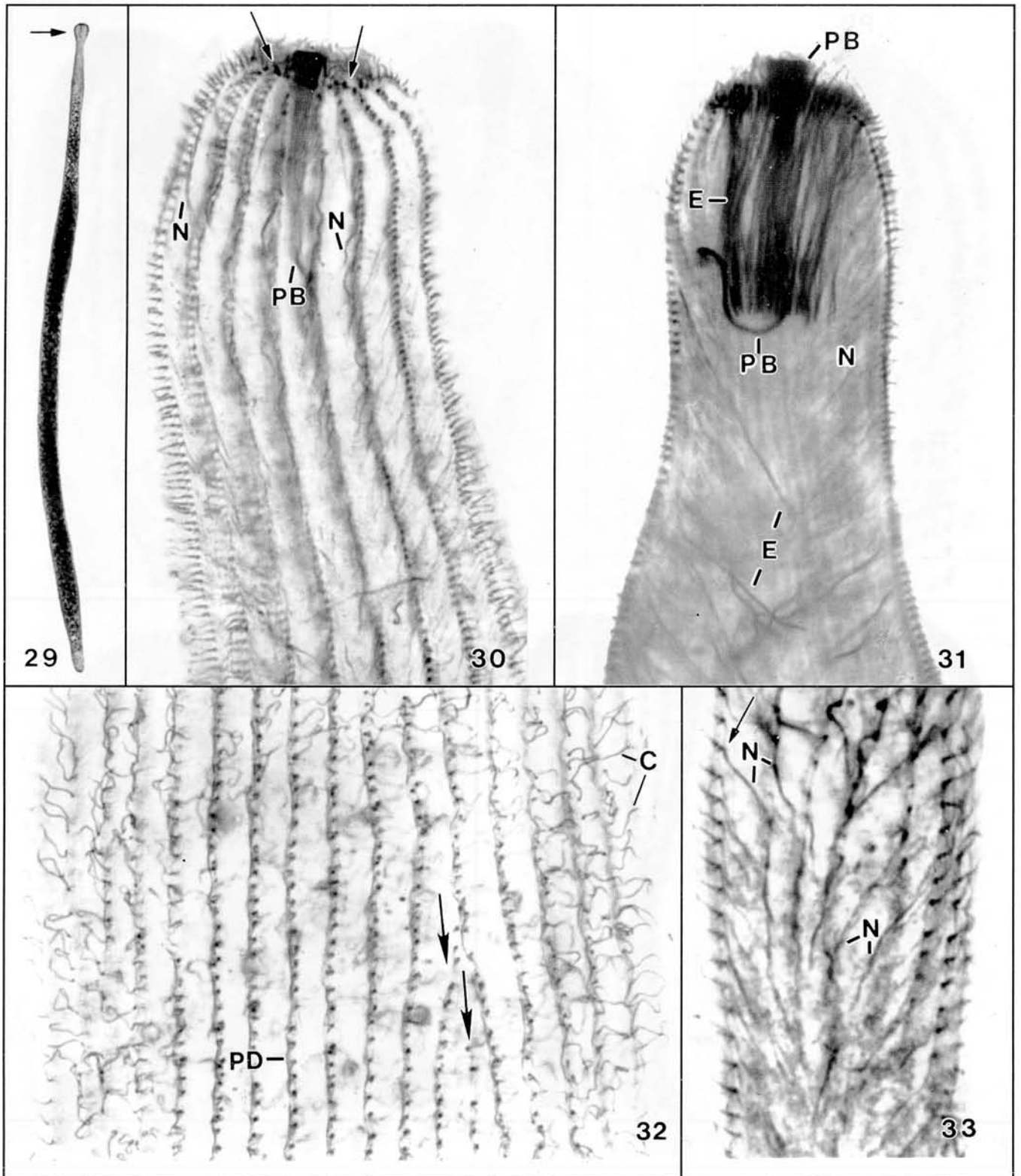
* Data based on protargol-impregnated and mounted specimens from field. Measurements in μm . Abbreviations: CV - coefficient of variation in %, M - median, Max - maximum, Min - minimum, n - number of individuals investigated, SD - standard deviation, SD $_{\bar{x}}$ - standard deviation of mean, \bar{X} - arithmetic mean

shape of cell thus comparatively well preserved in protargol slides (Table 1).

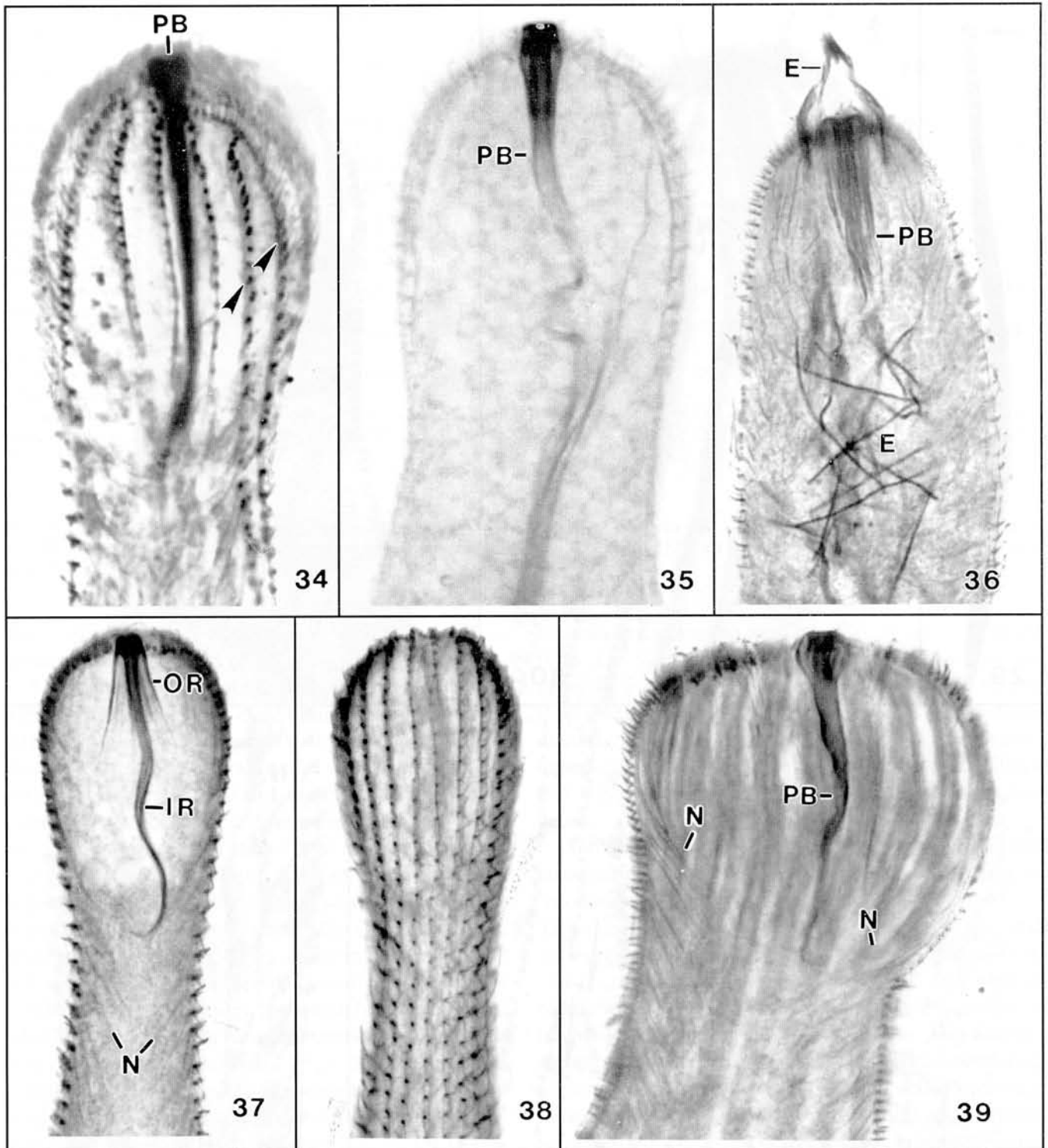
Macronuclei small, globular to slightly ellipsoidal, distributed throughout body, exact number and micronuclei difficult to ascertain because of many similar sized cytoplasmic inclusions, 300 - 600 nuclei seem to be common, with possibly up to 1000 in largest cells (Figs. 9, 27). Contractile vacuole distinct, in rear end with single excretory pore in centre of posterior pole (Figs. 1, 20). Two size-types, 25 μm and 7 μm long, of thin, rod-shaped extrusomes in peribuccal ridge and scattered throughout cytoplasm singly and in large bundles (Figs. 1, 27, 36), never attached to somatic cortex, unlike in *Helicoprorodon* (Figs. 42, 44). Long extrusomes usually curved and/or wrinkled in protargol slides, those attached to peribuccal ridge often completely or partially extruded providing cells with conspicuous apical beard (Figs. 21, 23, 31, 36); if completely extruded, head centre appears more pale than head margin and neck, where the nematodesmata of the oralized somatic kinetids extend (Figs. 23, 37, 38). Cortex conspicuous because ornamented and forming about 2 μm thick, vitreous layer sharply separated from granular cytoplasm, contains many minute (about 0.3 x 0.15 μm) granules (mucocysts ?) irregularly arranged in broad stripe left of ciliary rows (Figs. 2, 3, 7); ornamented by small ridges extending left of each ciliary row and laterally between ciliary rows, lateral ridges especially pronounced

in contracted specimens whose cortex is distinctly wrinkled (Figs. 2, 3, 9, 16, 20, 23). Cytoplasm colourless, contains many 1 - 5 μm sized fat globules, innumerable 3 x 2 μm sized ellipsoid inclusions, and many small (7 - 20 μm long) diatoms; whether diatoms were actively ingested or contained in prey organisms has been not observed. Glides and winds elegantly between sand grains and organic debris.

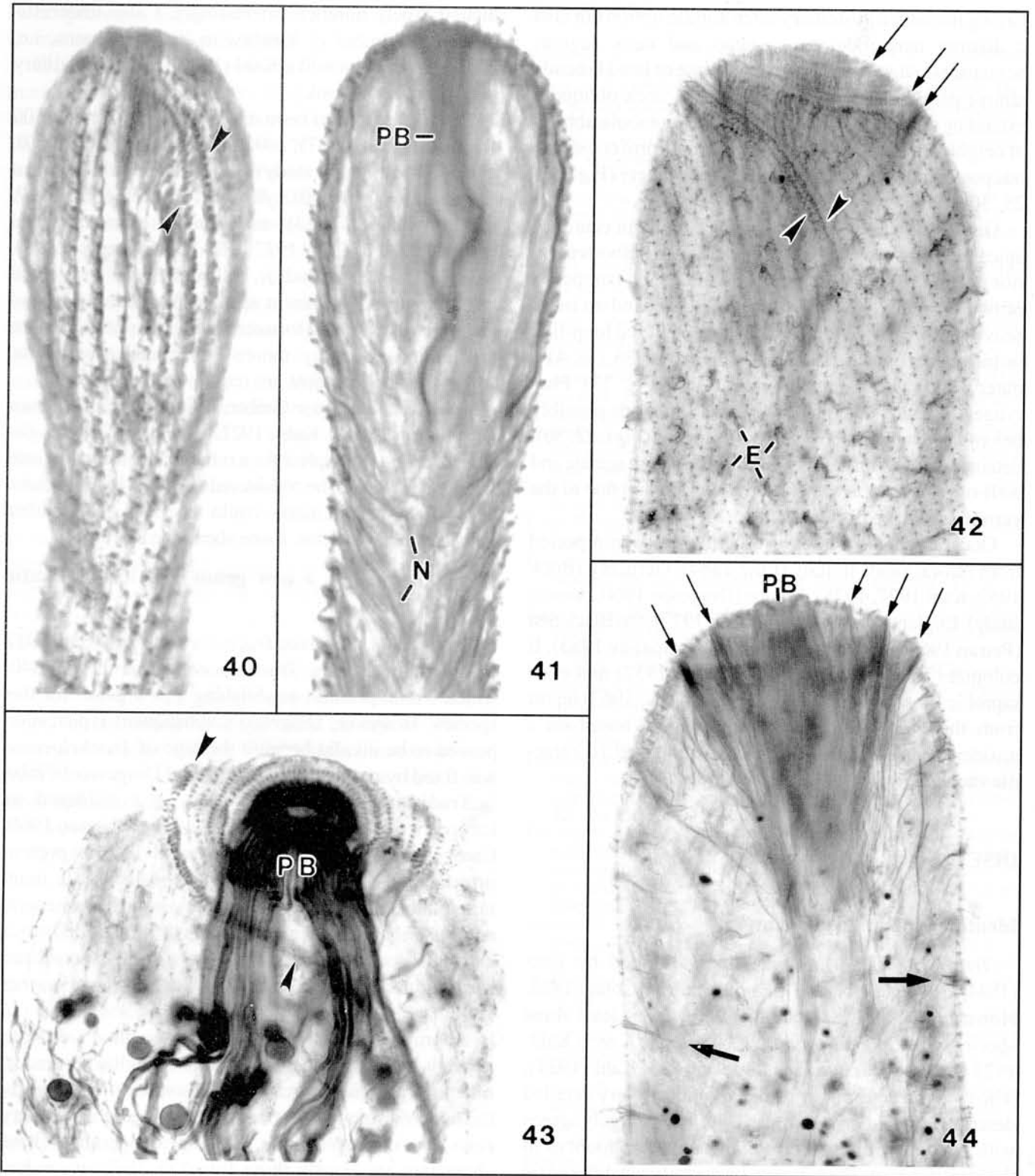
Surface very densely ciliated, cilia about 8 μm long and arranged in longitudinal rows (kineties) becoming more or less distinctly spiral in contracted cells (Figs. 1, 18, 30, 32; Table 1); about one third of kineties shortened in head and neck region and subterminally in posterior body portion, abridgement occurs over whole perimeter and without regularity, thus no secant system is formed, unlike in trachelocercids (Figs. 19, 20, 24; Table 1). Two kineties subapically specialized to distinct (dorsal) brush consisting of paired basal bodies (dikinetics) having about 4 μm long, rather stiff cilia; brush kineties posteriorly not distinctly separated from their respective somatic kineties because of rather large zone where brush dikinetics irregularly alternate with somatic monokinetics; at least one brush kinety continues apically and curves around cytopharyngeal opening, thus most ciliary rows abut to brush kineties (Figs. 8, 19, 23, 34, 40). Two kinds of somatic monokinetics, viz. normal ones having a distinct postciliary microtubule ribbon in trunk, and oralized somatic kineties



Figs. 29 - 33. *Trachelotractus entzi*, infraciliature after protargol impregnation. 29 - total view of typical specimen with globular head (arrow); 30 - head and anterior neck region. Arrows mark dikinetids surrounding pharyngeal opening; 31 - head and anterior neck region of specimen with intact circumpharyngeal extrusome bundle (cp. Fig. 21); 32 - surface view of posterior neck region showing shortened kineties (arrows); 33 - neck region showing oralized somatic kineties which have a distinct nematodesma associated with the basal body (arrow). C - cilia, E - extrusomes, N - nematodesmata, PB - pharyngeal basket, PD - postciliodesma



Figs. 34-39. *Trachelotractus entzi*, infraciliature of head and anterior neck region after protargol impregnation. 34 - arrows mark brush kineties composed of dikinetids (cp. Fig. 19); 35 - overbleached specimen with wrinkled pharyngeal basket; 36 - specimen just extruding circumpharyngeal extrusome bundle; 37, 38 - same specimen focused to centre and surface. The head appears pale because the circumpharyngeal extrusome bundle has been extruded (cp. Fig. 31); 39 - the head and neck kinetids have associated nematodesmata obliquely extending to neck midline. E - extrusomes, IR - inner region of oral basket, N - nematodesmata, OR - outer region of oral basket, spread fan-like in this specimen, PB - pharyngeal basket



Figs. 40 - 44. *Trachelotractus entzi* (40, 41) and *Helicoprion* sp. (42 - 44), oral and somatic infraciliature after protargol impregnation. 40, 41 - same specimen focused to surface and centre. Arrows mark brush kineties spiralling around pharyngeal opening; 42, 43, 44 - like *Trachelotractus*, *Helicoprion* has two specialized kineties (arrowheads) spiralling around pharyngeal opening; however, the kineties are not composed of dikinetids but associated with distinct nematodesmata. The peribuccal ridge contains long extrusomes which, together with the nematodesmata of the neighbouring spiral kineties, form a conspicuous, spiral core (thin arrows; cp. Fig. 28). Thick arrows mark extrusome bundles attached to somatic cortex. E - extrusomes, N - nematodesmata of oralized somatic kinetids, PB - pharyngeal basket

having not only a postciliary microtubule ribbon but also a distinct nematodesma in head and neck region; nematodesmata about 30 µm long, those of head kinetids almost parallel to cell surface, those of neck obliquely extending to neck midline; postciliary microtubule ribbons of neighbouring kinetids overlap and thus form conspicuous postciliodesma close to right of each kinety (Figs. 23, 25, 30-33, 36-39, 41).

Oral apparatus and infraciliature simple, in centre of apical end. Pharyngeal basket conical with bulbous anterior portion, about as long as head (Table 1), composed of two distinct zones, viz. an outer lightly and an inner heavily impregnated region, sometimes curved loop-like or bifurcate (Figs. 8, 19, 21-24, 26, 31, 34-36, 39, 41); outer region very rarely spread fan-like (Fig. 37). Pharyngeal opening surrounded by few dikinetids possibly belonging to anterior ends of brush kineties (Figs. 22, 30); details, however, difficult to recognize because minute and well-oriented apical views were not obtained due to the vermiform shape of the organism.

Occurrence and ecology: *T. entzi* has been reported from littoral sands in Italy (Entz 1884), Germany (Bock 1952, Kahl 1927, 1928), France (Dragesco 1960, present study), England (Hartwig and Parker 1977), the Black Sea (Petran 1967) and the Caspian Sea (Agamaliev 1983). It colonizes fine and coarse sands (Bock 1952) and even saprobic sites (Dragesco 1960). Biernacka's (1963) report from the Polish sea coast is very likely based on a misidentification because the specimens lacked a contractile vacuole.

DISCUSSION

Identification and synonymy

Trachelotractus entzi was first described by Entz (1884) as *Trachelocerca phoenicopterus* Cohn, 1866. However, Entz (1884) obviously mixed at least three species, viz. *T. phoenicopterus* Cohn, 1866, *T. entzi* Kahl, 1927 and *Lagynus sulcatus* Gruber, 1888. Kahl (1927), who recognized Entz's mistake, provided a very detailed description of *T. entzi* (Figs. 13 - 17), which largely agrees with my observations. Thus, there can be no doubt as to the identification. There is only one significant difference, viz. the number of kineties, about 20 according to Kahl (1927) and 25-40 (29, Table 1) in my specimens, which matches the value ("about 30") observed by Dragesco (1960). Thus, it is reasonable to assume that Kahl (1927), not having the advantage of silver impregnation, underes-

timated kinety number. Interestingly, I also underestimated the number of kineties in live specimens, i.e. recorded, very much like Kahl (1927), "about 20 ciliary rows" in my notebook.

Great variation has been reported in body length [300 - 1000 µm (Kahl 1927), 200 - 900 µm (Dragesco 1960), up to 1300 µm (this study)], body shape [club-shaped (Dragesco 1960; Fig. 10), cylindroid-fusiform (Kahl 1927, this study; Figs. 1, 13)] and number of macronuclei [several hundreds (Kahl 1927), 150-200 (Dragesco (1960), about 300 - 600 (this study)], indicating that *T. entzi* could be a complex of different species. However, size and shape are very difficult to ascertain in this species because of its high contractility; more systematic measurements, using video microscopy, are required.

Trachelocerca minor Gruber, 1888 is possibly a senior synonym of *T. entzi* Kahl, 1927. However, Gruber's description is too incomplete for a reliable identification, and thus *T. minor* should be considered as species indeterminata. Alternatively, this name could be used for another *Trachelotractus* species, if one should be discovered.

Trachelotractus as a new genus and its systematic position

Dragesco (1960) fixed *Trachelocerca entzi* Kahl, 1927 as type of the genus *Trachelocerca* Ehrenberg, 1840, which would prohibit establishing a new genus for this species. However, Dragesco's subsequent typification proved to be invalid because the type of *Trachelocerca* was fixed by monotypy (Foissner and Dragesco 1996b).

Traditionally, *T. entzi* has been considered as karyorelictid trachelocercid (Kahl 1930, Dragesco 1960, Carey 1992). This is not supported by the present investigations. *Trachelotractus entzi* lacks all main infraciliary characteristics of the karyorelictids in general and the trachelocercids in particular, viz. somatic dikinetids and a glabrous stripe surrounded by a highly specialized bristle kinety (Dragesco and Foissner 1996b, Foissner 1996c).

A proper classification of *T. entzi* must take into account its four main characteristics, viz. the peribuccal ridge with its typical extrusomes, the somatic monokinetids, the oralized somatic kinetids, and the specialized ciliary rows curving around the pharyngeal opening. These characters are exactly those found in *Helicoprodon*, which has a gymnostomatid (haptorid) ultrastructure (Dragesco 1960, Lipscomb and Riordan 1991, Raikov and Kovaleva 1980, Puytorac and Kattar 1969; Figs. 28, 42 - 44). Thus, *Trachelotractus* is assigned to the family Helicoprodonidae Small and Lynn, 1985, suborder

Helicoprordontina Foissner and Foissner, 1988, class Gymnostomatea Bütschli, 1889.

Trachelotractus entzi possesses, like most gymnostomatids, a typical brush consisting of two rows of paired basal bodies with shortened cilia (Figs. 19, 23, 34, 40). This is markedly different from *Helicoprordontina*, which very likely lacks a brush (Puytorac and Kattar 1969, Raikov and Kovaleva 1980, Lipscomb and Riordan 1991), although two of the somatic kineties which spiral around the anterior end, are specialized, i.e. associated with distinct nematodesmata making the subapical kinetids more distinct than the neighbouring normal somatic ones (Fig. 42). Thus, these kineties might be homologous to the brush kineties of *Trachelotractus* and other gymnostomatids. Another main difference concerns the spiral kineties, which perform about 1 turn in *Trachelotractus* (Figs. 19, 23, 34, 40) and 4 - 6 turns in *Helicoprordontina* (Dragesco 1960, Puytorac and Kattar 1969, Raikov and Kovaleva 1980, Lipscomb and Riordan 1991; Figs. 28, 43). This is associated with a marked difference in the arrangement of the extrusomes, which form a simple, circumpharyngeal bundle in *Trachelotractus* and a distinct spiral, which parallels the apical spiral kineties, in *Helicoprordontina* (Raikov and Kovaleva 1980; Figs. 28, 43,44).

In sum, the differences between *T. entzi* and *Helicoprordontina* spp. do not appear to be excessively large, but are nevertheless distinct enough to warrant generic separation. In fact, *T. entzi* looks like a simplified *Helicoprordontina*, indicating that it might be close to the stem species from which both *Trachelotractus* and *Helicoprordontina* evolved.

Spiroprordontina (a junior synonym of *Gymnozoum*; Petz et al. 1995a) is another genus resembling *Trachelotractus* and *Helicoprordontina*, especially in having some kineties curving around the cytopharyngeal apparatus. However, *Gymnozoum* is very likely closely related to the cyrtophorids, as indicated by morphological and nuclear characteristics (Petz et al. 1995a) as well as morphogenetic (Petz et al. 1995b) and ultrastructural (Sniezek and Small 1993) evidence. *Gymnozoum* is broadly ellipsoidal, acontractile, and lacks extrusomes and is thus easily distinguished from *Trachelotractus* and *Helicoprordontina*.

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