AGTA Protozoologica

Updating the Trachelocercids (Ciliophora, Karyorelictea). V. Redescription of *Kovalevaia sulcata* (Kovaleva, 1966) gen. n., comb. n. and *Trachelocerca incaudata* Kahl, 1933

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Summary. The morphology and infraciliature of *Trachelonema sulcata* Kovaleva, 1966 and *Trachelocerca incaudata* Kahl, 1933, two trachelocercid karyorelictids from the French Atlantic coast at Roscoff, were studied in live and protargol-impregnated specimens, as well as with the scanning electron microscope. Voucher, respectively, neotype slides with protargol-impregnated specimens of each species have been deposited at the museum of natural history in Linz (LI), Austria. The somatic and oral infraciliature of *T. sulcata* and *T. incaudata* is very similar to that of other trachelocercids. However, the circumoral kinety of *T. sulcata* extends not only around the oral bulge but also along the brosse cleft, thereby assuming a unique, key-hole-like shape. This character is used to define a new genus, *Kovalevaia* gen. n., to which two species are transferred, viz. *K. sulcata* (Kovaleva, 1966) comb. n. (basionym: *Trachelonema sulcata* Kovaleva, 1966) and *K. teissieri* (Dragesco, 1960) comb. n. (basionym: *Trachelonema poljanskyi* Raikov, 1963 is transferred to *Tracheloraphis: T. poljanskyi* (Raikov, 1963) comb. n. A tabulated key to the trachelocercid genera (*Trachelocerca, Trachelolphos, Kovalevaia, Tracheloraphis, Prototrachelocerca*) is provided.

Key words: Ciliophora, infraciliature, Karyorelictea, Kovalevaia sulcata (Kovaleva, 1966) gen. n., comb. n., mesopsammon, Trachelocerca incaudata, Trachelocercidae.

INTRODUCTION

Trachelocercid karyorelictids are a highly specific component of the marine sand microbenthos (Dragesco 1960, Foissner 1997b). About 70 species have been described (Carey 1992), but detailed data on the infraciliature, i.e. the somatic and oral ciliary pattern, of representative taxa only became available recently (Foissner 1996, 1997a; Foissner and Dragesco 1996a, b). Using silver (protargol) impregnation and scanning electron microscopy, Foissner and Dragesco (1996a, b) redefined the classical genera *Trachelocerca* and *Tracheloraphis*. established the new genus *Trachelolophos*, and synony-mized *Trachelonema* with *Tracheloraphis*.

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The present study, the last in the series, redescribes *Trachelonema sulcata* Kovaleva, 1966 and *Trachelocerca incaudata* Kahl, 1933, highlighting details of their somatic and oral infraciliature, which suggest that *T. sulcata* should be referred to a new genus, *Kovalevaia*. Verylikely, *Trachelocerca, Tracheloraphis, Trachelolophos, Kovalevaia*, and *Prototrachelocerca* comprise most of the generic diversification of the trachelocercids, at least at the morphological level.

Only about 15 out of the 70 species assigned to the trachelocercids can be considered to be properly described (Foissner 1996, 1997a; Foissner and Dragesco 1996a, b; species redescribed in this paper). Thus, a great deal of work remains to be done. An appropriate technique is now available. We not yet know the taxonomic value of most characters used for species distinction in trachelocercids. Thus, each species must be described/redescribed in great detail, including painstaking line drawings and plentiful documentation by micrographs. "Simple" descriptions, as common in the past, should be abandoned because they only increase the prevailing disorder.

MATERIAL, METHODS AND TERMINOLOGY

Kovalevaia sulcata and Trachelocerca incaudata were found in September 1994 in the mesopsammon, i.e. in the upper 0-4 cm sand layer of the 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 allowed to settle for at least 24 h. 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 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 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 all karyorelicitids very well, but does not prevent contraction in contractile species. Specimens were fixed for 10-15 min and washed three times in distilled water. 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 and interpretation of the trachelocercid infraciliature are according to Corliss (1979) and Foissner and Dragesco (1996a,b).

RESULTS

Morphometric data shown in Table 1 are repeated in this section only as needed for clarity. Most characters are highly variably (coefficient of variation > 20 %), as is usual in trachelocercids (Foissner and Dragesco 1996b).

Kovalevaia gen. n.

Diagnosis: Trachelocercidae Kent, 1881 with circumoral kinety not or only slightly interrupted at proximal vertex of brosse cleft and thus distinctly key-holeshaped. Bristle kinety composed of a single row of dikinetids. One or more oblique or straight brosse kineties.

Type species: *Trachelonema sulcata* Kovaleva, 1966. Dedication: genus dedicated to Dr. Valentina G. Kovaleva (Russian Academy of Science, St. Petersburg), who described the type species and performed many important studies on karyorelictid ciliates. Feminine gender.

Redescription of *Kovalevaia sulcata* (Kovaleva, 1966) comb. n. (Figs. 1-54, 89-99, Table 1)

Improved diagnosis (includes descriptions by Kovaleva 1966, Raikov and Kovaleva 1968, and Kovaleva and Golemansky 1979): extended cells in vivo about 600-1200 x 50 µm, slender and flattened ribbonlike (up to 4:1), contract slowly. Neck indistinctly, tail sharply set off from trunk; head, when fully extended, trumpet-shaped and distinctly set off from neck, bright and conspicuous because of large oral cavity lined by brown extrusomes. 9-60, usually about 30 macronuclei forming strand in middle third of body; 3-20, usually about 10 micronuclei. 10-24, usually 14-20 ciliary rows on right side of cell; left side unciliated, except for bristle kinety, glabrous stripe thus about as wide as trunk and with bright, longitudinal groove lacking large extrusomes. Brosse slit distinct, contains single brosse kinety composed of 3-7, on average 4 dikinetids. Cells dark and punctate due to two types of brown cortical



Figs. 1-10. *Kovalevaia sulcata* from life (1, 3, 4, 7, 10) and after protargol impregnation (2, 5, 6, 8, 9). 1 - typical, extended specimen. Note punctate appearance due to large, brown cortical granules (extrusomes), and bright, longitudinal groove, where the large extrusomes are lacking; 2 - enlarged detail from Fig. 6. The oral cavity and the oral bulge are lined by extrusomes; 3 - anterior body portion of fully extended specimen. Note lack of large granules (extrusomes) in cortex of head, except of oral bulge; 4 - right side view of posterior body portion. *Kovalevaia sulcata* has a distinct tail because the body is abruptly narrowed; 5, 6 - shape and nuclear apparatus of prepared specimes; 7 - optical section of cortex; 8 - surface view showing arrangement of cortical granules (extrusomes) in transition zone of right and left body side; 9 - transverse and longitudinal views of large extrusomes; 10 - transverse section of trunk; note strong flattening of cell. BK - bristle kinety, CR - ciliary row, EC - ellipsoid (crystalline ?) inclusions, FG - fat globule, GS - glabrous stripe, LE - large extrusomes (cortical granules), LG - longitudinal groove in centre of glabrous stripe, MA - macronuclei, MI - micronucleus, NA - nuclear apparatus, OB - oral bulge, OC - oral cavity, SE - small extrusomes (cortical granules). Scale bar division 100 µm (Figs. 1, 5, 6) and 10 µm (Figs. 2, 8)



Figs. 11-14. *Kovalevaia sulcata*, somatic infraciliature after protargol impregnation. 11, 12 - lateral views of posterior body portion. Arrowheads mark shortened kineties forming posterior secant system. Note that only the anterior basal bodies are ciliated in the posterior half of the tail. The bristle kinety curves around the posterior body end; thus, the dikinetids in the right branch have the posterior basal bodies ciliated; 13, 14 - lateral views of anterior body portion. Arrowheads mark anterior secant system. BK - bristle kinety, GS - glabrous stripe. Scale bars 40 µm



Figs. 15-26. *Kovalevaia sulcata*, fine structure of somatic and oral infraciliature in anterior body portion after protargol impregnation. 15, 16, 17, 18 - anterior portion of a somatic kinety showing fibrillar associates of dikinetids; 19, 20, 21, 24, 25, 26 - right and left side views. Arrows mark site where right end and anterior arch of bristle kinety abut and ciliation of bristle kinetids is opposed by about 180°. Arrowheads mark fuzzy structure between brosse cleft and bristle kinety; 22 - left side view of specimen whose circumoral kinety is open posteriorly; 23 - the anterior, unciliated basal bodies of the circumoral kinety are slightly smaller. B - brosse, BC - brosse cleft, BK - bristle kinety, C - cilium, CK - circumoral kinety, LBK- left branch of bristle kinety, M - myoneme, N - nematodesmata, OC - oral cavity, PD - postciliodesma, RBK-right branch of bristle kinety, SK - subkinetal microtubule ribbon. Scale bars 10 µm



Figs. 27-37. *Kovalevaia sulcata* from life (27-31) and after protargol impregnation (32-37). For sizes, see text and Table 1. 27, 28, 29, 30, 37extended, gliding specimens. The head (arrow) is trumpet-shaped when fully extended. Note black, punctate appearance of cell due to large, brown cortical granules (extrusomes) lacking in the longitudinal groove, which thus appears as bright line. Arrowheads mark deep oral cavity (cp. Fig. 37); 31 - anterior end showing entrance to oral cavity and cilia of circumoral kinety (arrowhead); 32, 33, 34, 35, 36 - somatic and oral infraciliature. Arrows mark circumoral kinety, which is either discontinuous (Fig. 34) or continuous (Fig. 36) at the posterior vertex of the brosse cleft. B - brosse, BC- brosse cleft, C - cilia, CR - ciliary row, LG - longitudinal groove in centre of glabrous stripe, LE - large extrusomes (cortical granules), M - myoneme, NE - neck, OB - oral bulge, OC - oral cavity, PD - postciliodesma, RBK - right branch of bristle kinety, SE- small extrusomes (cortical granules)

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Figs. 38-45. *Kovalevaia sulcata* in the scanning electron microscope. For sizes, see text and Table 1. 38, 39 - extended and contracted specimens showing general organization, especially the glabrous stripe, which occupies the left side of the cell. Arrowhead marks bristle kinety extending in deep furrow at margin of glabrous stripe. Note that the longitudinal groove on the glabrous stripe (cp. Figs, 1, 10, 29, 42) has flattened due to the preparation procedures. 40 - head showing circumoral kinety; 41, 45 - lateral views showing bristle kinety, which consists of widely spaced cilia. The pellicle appears knobby due to the cortical granules (extrusomes); 42 - left side view of posterior end. The left side is unciliated, except for the bristle kinety (arrowheads), which curves around the cell. Arrows mark flattened longitudinal groove; 43, 44 - head in lateral and frontal view. Arrows mark brosse cleft. Asterisk denotes deep oral cavity. BK - bristle kinety, CK - circumoral kinety, CRS - ciliated right side of cell, GS - glabrous stripe, OB - oral bulge



Figs. 46-54. *Kovalevaia sulcata*, extrusomes (cortical granules) and cytoplasmic inclusions from life (46-48), after protargol impregnation (49, 50,52, 53), and in the scanning electron microscope (51, 54). For sizes, see text. 46, 47, 50 - right and left side views of cortex, which contains innumerable small (about 0.4 μ m) and many large (about 2 x 1 μ m), brown extrusomes. The large extrusomes are lacking in the longitudinal groove extending on the glabrous stripe; 48 - anterior portion showing cytoplasm packed with ellipsoidal inclusions (about 2 x 1 μ m), which were artificially spread into the head during flattening of the cell; 49 - lateral view of strongly contracted cell, showing arrangement of small and large extrusomes and tuberculate glabrous stripe; 51 - part of glabrous stripe showing globular and rod-shaped (arrowheads) extrusomes leaving cell. Arrows denote holes remaining from extruded extrusomes; 52, 53 - large extrusomes in longitudinal (arrows) and transverse view (cp. Figs. 7 - 9); 54 - extruded large extrusomes. CR - ciliary rows, EC - ellipsoidal (crystalline ?) inclusions, GS- glabrous stripe, LE - large extrusomes, LG - longitudinal groove, SE- small extrusomes

Character ¹	$\overline{\mathbf{X}}$	М	SD	SE	CV	Min	Max	n	
Body, $length^2$	756.2	725.0	168.8	42.2	22.3	530	1100	16	
bouy, iongin	495.3	465.0	157.1	39.3	31.7	270	900	16	
Body, width at head	25.0	26.0	5.0	1.3	20.2	15	32	16	
	22.7	22.0	5.0	1.2	21.9	13	31	16	
Body, (maximum) width at trunk ²	64.1	64.0	7.2	1.8	11.2	55	85	16	
v in k	85.9	87.5	22.7	5.7	26.4	50	120	16	
Glabrous stripe, width in mid-body ²			about s	same as trur	nk width				
1	10.1	10.0	2.8	0.7	27.3	6	15	16	
Oral cavity, depth	22.4	21.0	5.1	1.3	22.6	17	35	16	
	oral cavity lacking								
Anterior end to nuclear capsule				no	capsule				
	260.0	245.0	86.7	21.7	33.4	125	470	16	
Macronuclei, respectively,	8.1	8.0	1.4	0.3	16.8	6	10	16	
nuclear capsule, length	21.3	21.0	3.9	1.0	18.4	15	30	16	
Macronuclei, respectively,	7.4	7.0	1.4	0.4	19.0	5	10	16	
nuclear capsule, width	19.1	19.0	2.5	0.6	12.9	15	23	16	
Micronuclei, length	5.6	5.5	1.8	0.5	32.6	3	8	16	
	not investigated								
Micronuclei, width	4.5	4.0	1.5	0.4	32.5	3	8	16	
,				not investigated					
Somatic kineties, number on head	12.9	13.0	1.6	0.4	12.6	10	15	16	
	15.5	16.0	1.7	0.4	11.0	13	18	16	
Somatic kineties, (maximum)	14.1	14.0	1.8	0.5	13.1	11	18,	16	
number on trunk	32.1	32.5	4.1	1.0	12.6	25	40	16	
Circumoral dikinetids, number	not investigated								
	68.1	67.5	16.7	4.2	24.5	40	95	16	
Brosse kineties, number	1.0	1.0	0.0	0.0	0.0	1	1	9	
				n	o brosse				
Dikinetids in brosse kinety, number	4.6	4.0	1.1	0.4	24.6	3	7	9	
	no brosse								
Macronuclei, number	31.5	31.5	8.0	2.3	25.3	22	50	12	
	7.8	8.0	1.0	0.3	12.8	6	10	16	
Micronuclei, number	9.2	8.5	4.4	1.3	47.5	5	20	12	
	2.0	2.0	-	-	-	2	2	4	

Table 1. Morphometric data from Kovalevaia sulcata (upper line) and Trachelocerca incaudata (lower line)

¹ Data based on protargol-impregnated and mounted specimens from field. Measurements in μ m. Abbreviations: CV - coefficient of variation in %, M - median, Max - maximum, Min - minimum, n - number of individuals investigated, SD - standard deviation, SE - standard error of mean, \overline{X} - arithmetic mean

² Data of very limited value because specimens contract more or less distinctly when fixed and/or become inflated due to the preparation procedures

granules (extrusomes): large extrusomes about 2 x 1 μ m, in single row between each two kineties and on glabrous stripe, contain nail-shaped structure; small extrusomes about 0.4 μ m across, form narrowly spaced rows in whole cortex.

Specimens investigated and voucher slides: *Kovalevaia* sulcata is very difficult to study, mainly due to the extrusomes, which impregnate heavily and conceal the infraciliature. Thus, the description of the infraciliature is based only on five mediocrely impregnated specimens; some others were of useable quality and served

for completing morphometry. Voucher slides with specimens from Roscoff, prepared as described, have been deposited in the Oberösterreichische Landesmuseum in Linz (LI), Austria. Relevant specimens are marked by a black ink circle on the cover glass.

Description of Roscoff population: fully extended specimens *in vivo* about 800-1200 x 50 μ m, length:width ratio 15-20:1, trunk flattened ribbon-like (3-4:1; Figs. 1, 10, 27-30, 38). Very flexible and thus usually more or less distinctly curved, occasionally even coiled like a snail-shell. Contracts slowly and not very extensively,

prepared cells thus conspicuously long (Table 1); fully contracted specimens banana-shaped, convex side with glabrous stripe distinctly protruding but only occasionally tuberculate (Figs. 39, 41, 49). Greybrown and opaque in dissecting microscope, dark and punctate under transmitted light of bright-field microscope at low magnification ($\leq x \ 100$) due to large, brown cortical granules = extrusomes (Figs. 1, 10, 27-30); left side (glabrous stripe) with narrow, longitudinal groove lacking large, brown extrusomes and thus appearing as bright line at low magnification (Figs. 1, 10, 27, 29, 47); groove usually flattened in SEM preparations (Figs. 38, 39, 42). Extended specimens slender with anterior third gradually tapering, neck thus indistinctly set off from trunk; neck very agile, looks like a groping elephant proboscis, especially when head is fully extended; posterior portion abruptly narrowed forming distinct straight or slightly curved tail (Figs. 1, 4-6, 27-30, 38). Head trumpet-shaped when fully extended (Figs. 3, 27, 43), cylindroidal when contracted (Figs. 28-30, 31), bright because hollowed by 20-40 µm deep oral cavity lined by brown extrusomes, very fragile, often quickly dissolving under cover glass (Figs. 2, 3, 28, 30, 37; Table 1). Oral bulge conspicuous because packed with brown extrusomes, interrupted at brosse cleft about half as deep as oral cavity, main part of cleft covered by head cortex, as indicated by SEM micrographs (Figs. 43, 44), cleft margin thickened by gelatinous plasm (Figs. 2, 3, 19, 20, 31, 37).

Macronuclei globular to slightly ellipsoidal, number highly variable (Table 1), individually arranged left of midline, forming long strand in middle third of cell (Figs. 1, 6); occasionally clustered to indistinct groups (Fig. 5). Micronuclei globular to slightly ellipsoidal, near and between macronuclei. No contractile vacuole.

Cortex very flexible and gelatinous, about 2 μ m thick (Figs. 7, 48), tuberculate in contracted cells (Fig. 45), contains two types of conspicuous, extrusive granules, whose fine structure and genesis were investigated by Kovaleva and Raikov (1972); both extrusome types brilliant brown to darkbrown and thus well-recognizable in living cells (Figs. 46, 47), impregnate heavily with protargol (Figs. 49, 50), make cortex knobby in light and scanning electron microscope (Figs. 31, 41, 45). Large extrusomes about 2 x 1-1.5 μ m, ellipsoidal to pyriform, contain nail-shaped structure after protargol impregnation (Figs. 7, 9, 52, 53), globular with slightly knobby surface when extruded (Fig. 54), arranged in single (rarely two) row between each two somatic kineties, in loose rows on glabrous stripe, except for

longitudinal groove, packed in oral bulge and cortex of oral cavity, absent in head cortex (Figs. 2, 3, 8, 10, 28, 30, 46, 47, 49, 50), provide cells with dark, punctate appearance at low magnification (Figs. 27-30). Small extrusomes about 0.4 μ m across, elongate to about 1 μ m long rods when extruded, arranged in narrowly spaced rows in whole cortex, including head and longitudinal furrow on glabrous stripe (Figs. 3, 8, 10, 31, 37, 49-51).

Cytoplasm colourless, packed with about 2 x 1 μ m sized, highly refractile (crystalline ?) granules, fat globules, and some food vacuoles containing diatoms (Figs. 7, 10, 48). Glides and winds elegantly between sand grains and organic debris.

Somatic infraciliature (Figs. 10-26, 31, 32, 35, 38-42, 45): Kovalevaia sulcata 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 is occasionally slightly curved to the right and has condensed, i.e. more narrowly spaced dikinetids. Usually, the condensation is inconspicuous or even lacking in some kineties. One to three 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. 11-14). In other words, an anterior and posterior secant system are formed at the margins of the cell where some ciliary rows abut to the bristle kinety. Thus, the head, neck and tail have slightly fewer kineties than the trunk (Table 1). The ciliary rows neighbouring the right branch of the bristle kinety are unshortened anteriorly and thus run alongside the glabrous stripe (Figs. 13, 14).

The entire infraciliature consists of ciliated dikinetids, except for 0-2 dikinetids at the anterior end of the kineties and the dikinetids in the posterior half of the tail, where only the anterior basal bodies are ciliated (Figs. 11, 12, 20, 24). The dikinetids are associated with various distinct fibres, all very likely originating from the posterior basal bodies (Figs. 15-18, 35). My observations largely agree with the transmission electron microscopic investigations by Kovaleva (1974), who, however, did not recognize the subkinetal microtubule arrays and some site-specific differences. On the other hand, the transverse microtubule ribbons and the kinetodesmal fibres did not stain in my 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 microtubule ribbons form a thin, but sharply impregnated bundle underneath or close to the left of the kineties. They are more intensively impregnated in the neck region and do not or hardly overlap so that their commalike shape can be recognized (Figs. 15-18). No oralized somatic dikinetids were recognizable, asin *Tracheloraphis longicollis* (Foissner and Dragesco 1996b).

The contractile apparatus of *K. sulcata* consists of a myoneme close to the left of each kinety (Figs. 15-18, 35). As in the other species investigated (Foissner and Dragesco 1996b), the distinctiveness of the myonemes varies highly, depending on preparation conditions. The myonemes are flattened ribbon-like and commence as very thin bundles in the neck region (Fig. 17), gradually thickening posteriorly (Figs. 18, 35). No myonemes impregnated in the glabrous stripe and along the bristle kinety.

The glabrous stripe extends along the whole body length and width, except on the anterior neck region and head, where it gradually narrows, occupying only about one third of the head's width (Figs. 19-22, 24-26, 38, 42). The glabrous stripe is bordered by the bristle kinety which extends in a narrow groove and consists, like the ordinary ciliary rows, of individual dikinetids having about 12 µm long, rather stiff cilia (Figs. 10, 11-14, 38, 41, 45). However, the bristle kinety is easily distinguished from ordinary somatic ciliary rows because its dikinetids are more widely spaced, except in the right anterior portion (Figs. 22, 26), and more irregularly arranged and either lack or have very inconspicuous postciliary microtubule ribbons, too small to be recognized with the light microscope; the subkinetal microtubule bundles are conspicuous (Figs. 20-22, 24, 26, 32). The bristle kinety is continuous at the posterior end of the cell (Fig. 42), whereas its anterior end appears covered by a short, arched kinety ("anterior arch of bristle kinety", see Foissner and Dragesco 1996b for detailed explanation). The ciliation of the bristle dikinetids is as described in other trachelocercids (Foissner and Dragesco 1996a, b), 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; at the site where the right end and the anterior arch of the bristle kinety abut, the ciliation of the bristle kinetids is opposed by about 180° (Figs. 20, 24). A fuzzy structure, possibly composed of basal bodies connected by some fibrous material, is found, in about half of the specimens, between the anterior arch of the bristle kinety and the vertex of the circumoral kinety (Figs. 24, 26).

Oral infraciliature (Figs. 3, 19, 20, 22-26, 31-34, 36, 40): the oral infraciliature of K. sulcata consists of a circumoral kinety and a minute brosse, difficult to recognize in living specimens. The circumoral kinety extends in the flat furrow separating the oral bulge from the head and is continuous along the brosse cleft, thus obtaining a characteristic, key-hole-like shape (Figs. 20, 26, 36). The rear portion of the kinety, which extends along the posterior vertex of the brosse cleft, was lacking in about half of the specimens (Figs. 22, 24, 34); however, this was possibly caused by insufficient impregnation and/or artificial spreading of the cleft by the preparation procedures. The circumoral kinety is composed of a single row of obliquely oriented dikinetids having only the posterior basal body ciliated (Fig. 40); the anterior, barren basal body is slightly smaller in protargol preparations (Fig. 23). Each circumoral dikinetid is associated with a comparatively short nematodesma obliquely extending into the head. The nematodesmata of neighbouring dikinetids unite to small bundles, forming a slightly cone-shaped oral basket (Fig. 19). As in the other species investigated (Foissner and Dragesco 1996b), the circumoral kinety of K. sulcata is very likely composed of several fragments, as indicated by small gaps, 1-2 dikinetids wide, and the bundled arrangement of the nematodesmata.

The brosse is located in a rather deep cavity, the brosse pocket, which extends underneath the anterior half of the brosse cleft. It invariably consists of a single, short kinety composed of closely spaced dikinetids having only the posterior basal body ciliated (Figs. 20, 22, 24, 26, 32, 34; Table 1).

Distribution and ecology: *Kovalevaia sulcata* was discovered by Kovaleva (1966) at the coast of the Black Sea, where this species is widespread in fine (grain size 0.25-0.30 mm), slightly polluted sand (Kovaleva and Golemansky 1979). Later, mass populations were found by Raikov and Kovaleva (1968) in fine, aerobic sands of the Posjet Gulf (Japan Sea, Pacific Basin). The present record from Roscoff (France) is the first from the Atlantic Basin. The species could be transported from Roscoff to the Salzburg laboratory, where it was one of the few trachelocercids surviving some months in the sampling jar, obviously tolerating microaerobic conditions. Furthermore, I found *K. sulcata* at the coast of Cape Town, South Africa, where it inhabited the upper, muddy sand layer of a beach (Figs. 38-45). Again, it



Figs. 55-63. *Trachelocerca incaudata* from life (55-61) and after protargol impregnation (62, 63). 55, 56 - typical specimen extended and contracted (drawn to scale); 57 - the head is claviform and contains minute, drumstick-shaped structures, possibly extrusomes; 58 - transverse section of trunk, which is slightly flattened in fully extended specimens; 59 - usually, 8 macronuclei and 2 micronuclei form a nuclear capsule; 60, 61 - surface view and optical section of cortex; 62, 63 - Arrangement of ciliary rows on left and right side. About half of the kineties are shortened and abut to the left branch of the bristle kinety, forming an anterior and posterior secant system. A - anterior secant system, BK - bristle kinety, EC - ellipsoidal (crystalline ?) inclusions, FG - fat globule, G - cortical granules, GS - glabrous stripe, NA - nuclear apparatus, NU - nucleoli, PC - (protein ?) crystal, PD - postciliodesma. Scale bar division 100 μm



Figs. 64-66. *Trachelocerca incaudata*, oral and somatic infraciliature after protargol impregnation. 64, 65 - left and right side view of anterior body portion. Arrows mark bristle kinety bordering very narrow glabrous stripe; 66 - somatic fibrillar system in left anterior trunk region of an excellently prepared specimen (cp. Fig. 87). Arrows mark minute, laterally directed fibre originating from the ciliated basal body of the bristle dikinetids. Arrowheads denote unciliated argyrophilic granules (basal bodies ?) within and near the bristle kinety. C - cilia, CK - circumoral kinety, CR - ciliary row, M - myoneme, N - nematodesmata, OB - oral bulge, PD - postciliodesma, SK - subkinetal microtubule ribbon. Scale bars 20 µm

survived transport to the Salzburg laboratory despite anaerobic conditions in the jar. These data indicate that *K. sulcata* is a cosmopolite tolerating microaerobic and anaerobic conditions, at least for some time.

Redescription of *Trachelocerca incaudata* Kahl, 1933 (Figs. 55-88, 109-118; Table 1)

Improved diagnosis (including literature data): fully extended cells *in vivo* 400-1000 x 30-40 μ m. Slender, neck rather distinctly set off from slightly flattened, fusiform trunk, head claviform and whitish or dark, posterior end rounded. 6-10, usually 8 macronuclei and 2 micronuclei forming tight cluster in centre of trunk. 25-40, usually about 32 somatic ciliary rows and 40-95, on average 68 circumoral dikinetids; glabrous stripe narrow, about one quarter of body width. Cortical granules about 1 x 0.5 μ m, yellowish, form stripes between ciliary rows and narrowly spaced rows in glabrous zone. 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. incaudata* has been mentioned in the literature. Thus, I have deposited three 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.

Description of Roscoff population: size of fully extended specimens *in vivo* about 800-1,000 x 30-40 μ m, highly flexible and contractile, size and shape thus poorly preserved and highly variable in protargol slides (Table 1; Figs. 55, 62, 70, 81); about 1.5:1 flattened laterally (Fig. 58). Grey to blackish in dissecting and bright-field microscope due to innumerable, about 4 x 2 μ m sized, refractile (crystalline ?) inclusions in trunk



Figs. 67-69. *Trachelocerca incaudata*, somatic infraciliature after protargol impregnation. 67, 69 - left side of anterior body portion showing variability of bristle kinety; 68 - posterior end showing bristle kinety (arrowheads) extending around glabrous stripe. A - anterior secant system, BK- bristle kinety, CK - circumoral kinety, GS - glabrous stripe. Scale bar division 20 µm



Figs. 70-80. *Trachelocerca incaudata* from life (70-79) and after protargol impregnation (80). For sizes, see text and Table 1. 70, 71 - extended and slightly contracted specimen. Note rounded posterior end; 72, 73, 74 - left anterior body portion of partially contracted specimen. Arrows mark claviform cortex blisters; 75 - ellipsoidal, highly refractile cytoplasmic inclusions making cells dark at low magnification (Fig. 70); 76, 78, 79, 80 - nuclear capsules, individual macronuclei (arrowheads) become recognizable only in squashed (79) or stained (80) capsules; 77- surface view of posterior body portion showing cortical granule stripes. A - anterior secant system, C - cilia, G - cortical granules, GS - glabrous stripe, NA - nuclear apparatus, NU - nucleoli, OB - oral bulge, PC - protein (?) crystals



Figs. 81-88. *Trachelocerca incaudata*, somatic and oral infraciliature after protargol impregnation (81-87) and in the scanning electron microscope (88). For sizes, see text and Table 1. 81 - general left side view (cp. Fig. 62); 82, 83, 84, 85 - right and left side views of anterior body portion. Arrows mark condensed dikinetids at anterior end of kineties. 86, 87 - left side views showing details of somatic kineties and bristle kinetids at high magnification (cp. Fig. 66). Arrows mark fibre originating from ciliated basal body of bristle dikinetids, which are composed of three minute granules (arrowheads); 88 - anterior body portion of contracted specimens showing conspicuous, claviform cortical blisters. A - anterior secant system, BK- bristle kinety, C - cilia, CK - circumoral kinety, GS - glabrous stripe, M - myoneme, N - nematodesmata, NA - nuclear apparatus, OB - oral bulge, PD - postciliodesma

(Figs. 55, 58, 61, 70, 75). Fully extended specimens needle-shaped with neck rather distinctly set off from head and cylindroidal trunk; no tail, i.e. posterior region only slightly tapering and narrowly rounded (Figs. 55, 70). Head about 20 µm wide, claviform when fully extended, usually, however, cylindroidal and indistinctly set off from neck, whitish in undisturbed specimens, dark in disturbed and thus frequently contracting cells due to shifting of ellipsoidal inclusions described above from trunk to head (Figs. 57, 71, 72, 74). Oral bulge inconspicuous because indistinctly set off from head, surface flat (Figs. 57, 74, 88), centre in one specimen filled with 2-3 µm long, drumstick-shaped structures, possibly extrusomes (Fig. 57); Dragesco (1960) observed "navicular trichocysts" around the oral opening. Slightly contracted cells cylindrical or claviform (Fig. 71), fully contracted specimens fusiform and about 300 µm long in vivo (Fig. 56); glabrous stripe neither protruding nor distinctly tuberculate (Figs. 73, 77). Macronuclei globular, form conspicuous, about 20 µm sized capsule in centre of trunk (Figs. 55, 59, 62, 76, 80), individual nuclei recognizable only in strongly squashed capsules (Fig. 79); each nucleus contains some small and large nucleoli and, usually, one cuboid protein crystal, which often occupies more than half of the nucleus' volume and does not stain with protargol (Figs. 59, 78, 79). Micronuclei globular, in centre of macronuclear cluster. No contractile vacuole. Cortex highly flexible, about 1.5 µm thick, forms columnar tubercles between, and many small claviform blisters along ciliary rows in contracted specimens (Figs. 61, 73, 74, 88). Cortical granules about 1 x 0.5 µm in size, yellowish, arranged in broad stripes between kineties and in narrowly spaced rows in glabrous stripe (Figs. 58, 60, 61, 77). Cytoplasm packed with ellipsoid inclusions as described above, and some 3 µm sized fat globules (Figs. 58, 61, 75, 76). Movement like in other trachelocercids, i.e. elegantly gliding and winding between sand grains and organic debris.

Somatic infraciliature (Figs. 62-69, 81-88): the surface of *T. incaudata* is densely ciliated, leaving blank an only about 10 μ m wide zone, the glabrous stripe, extending the whole body length in the midline of the left side (Figs. 58, 62, 81). The cilia, which are rather stiff and can be spread, are about 10 μ m long and 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 (Figs. 67, 69, 82, 83). About 16 ciliary rows are gradually shortened in the anterior trunk region and on the neck abutting to the left branch of the bristle kinety. Thus, the head has about half the kineties present in the centre of the trunk (Table 1). The posterior secant system consists of only about 6 short-ened kineties because the body narrows only slightly, i.e. is tailless. The ciliary rows neighbouring the right branch of the bristle are unshortened anteriorly and posteriorly (Figs. 62, 66, 69, 73, 87).

The entire infraciliature consists of dikinetids which, however, have a specialized ciliation. 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 subkinetal microtubule ribbon extends underneath each ciliary row (Figs. 66, 86, 87). Only the anterior basal body of the dikinetids is ciliated, except in the neck region, where both are ciliated.

The contractile apparatus of *T. incaudata* consists of a myoneme close to the left of each kinety (Figs. 66, 86, 87). 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 from the neck to the posterior end of the cell becoming slightly thicker from anterior to posterior. No myonemes were found in the glabrous stripe.

The glabrous stripe, which extends along the whole length of the body, widens gradually from the head to the trunk, where it obtains its full width corresponding to an area occupied by 2-3 kineties. 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 irregularly and loosely arranged and either lack or have very inconspicuous postciliary microtubule ribbons too small to be recognized with the light microscope (Figs. 58, 62, 63, 66, 73, 86, 87). 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 (Foissner and Dragesco 1996b; Fig. 68). Both ends of the bristle kinety are very close together subapically, where some irregularly arranged



Figs. 89-107. Comparison of *Kovalevaia sulcata* (89 - 99) and *K. teissieri* (100-107). Figs. 89-99. *Kovalevaia sulcata* from life (89-91, 93, 94, 96-98), after Feulgen reaction (92, 95), and in a light green preparation (99). Russian Black Sea population (type, Figs. 89-94, from Kovaleva 1966); Bulgarian Black Sea population (Figs. 95-98, from Kovaleva and Golemansky 1979); Japan Sea population (Fig. 99, from Raikov and Kovaleva 1968). 89, 90, 96, 97 - typical gliding and swimming specimens; 91, 98 - heads, arrows mark brosse cleft; 92, 95 - nuclear apparatus; 93, 94, 99 - surface views showing cortical granulation. Figs. 100-107. *Kovalevaia teissieri* from life (100-102, 104, 105, 107), after Feulgen reaction (103), and protargol impregnation (106). Roscoff population (type, Figs. 100-105, from Dragesco 1960); Roscoff population (Fig. 106, from Dragesco 1963); Somalian population (Fig. 107, from Ricci et al. 1982). 100 - general view of typical specimen; 101 - left and right side view of posterior body portion; 102- surface view showing cortical granulation; 103 - nuclear apparatus; 104, 107 - heads; 105 - left side view of frunk region; 106 - infraciliature of anterior left side. Arrowhead marks circumoral kinety extending at margin of brosse cleft. Abbreviations: CR - ciliary row, DMA - developing macronucleus, GS - glabrous stripe, LE - large extrusomes (cortical granules), LG - longitudinal groove on glabrous stripe, M - myoneme, MA - macronuclei, MI- micronuclei, NA - nuclear apparatus, SE - small extrusomes (cortical granules). Scale bar division 100 µm

dikinetids occur (Figs. 64, 67, 69, 83, 84). 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. Nonciliated granules are scattered within the bristle kinety. In the best preparations, the *ciliated* dikinetids are composed of three granules forming minute triangles, and the ciliated basal body of the bristle dikinetids is associated with a short fibre directed, like the third granule, laterally towards the somatic kineties (Figs. 66, 86, 87).

Oral infraciliature (Figs. 57, 64, 65, 67, 69, 72, 74, 82-85, 88). The oral infraciliature of *T. incaudata* is very simple and consist 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 15 short fragments, as indicated by small gaps, 1-2 dikinetids wide, and the bundled arrangement of the nematodesmata. The circumoral dikinetids have 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.

Distribution and ecology: there are numerous records of *T. incaudata* from Eurasia, but none from South America and Australia (for reviews, see Agamaliev 1967, Hartwig and Parker 1977, Hartwig 1980). However, this does not prove a restricted geographic distribution but very likely only reflects the highly limited data available from these regions. *Trachelocerca incaudata* prefers, like most trachelocercids, sand with a grain size of 0.1-0.25 mm (Agamaliev 1967, Burkovsky 1970).

DISCUSSION

Identification and synonymy of Kovalevaia sulcata

My observations on *K. sulcata* match the original description (Kovaleva 1966) very well and, especially so, those on a population from the Posjet Gulf (Japan Sea), later reported by Raikov and Kovaleva (1968). Thus, there is no doubt about the identification (cp. Figs. 1-10, 27-31, 46-54, 89-99). As mentioned by Raikov and Kovaleva (1968), the Posjet specimens are striking in being, with respect to the number of ciliary rows, intermediates between the type population of *K. sulcata* from the Black Sea and *Tracheloraphis poljanskyi*

(Raikov, 1963) comb. n.¹ from the Japan Sea. The Posjet specimens have, similarly to those from Roscoff (Table 1), 10-16 kineties and are in this respect nearer to *T. poljanskyi* (12 kineties) than to the Black Sea form of *K. sulcata*, which has 16-24 (\overline{x} 20) ciliary rows (Kovaleva 1966, Kovaleva and Golemansky 1979). Thus, I agree with Raikov and Kovaleva (1968) that the presence, respectively, absenceof a longitudinal groove on the glabrous body side should be considered as the main distinctive character between *K. sulcata* and *T. poljanskyi*. Whether or not *T. poljanskyi* belongs to the genus *Kovalevaia* needs investigation of silver-impregnated specimens (see below).

Tracheloraphis grassei (Dragesco, 1960) Foissner and Dragesco, 1996b is also rather similar to *K. sulcata* because it possesses large, brown extrusomes and a longitudinal groove on the glabrous body side. However, *T. grassei* has a unique apical prominence and a different body shape, i.e. narrows gradually to the tail. Furthermore, the small extrusomes of *T. grassei* are colourless. I thus agree with Kovaleva (1966) that *T. grassei* and *K. sulcata* are different species.

Kovalevaia as a new genus and its systematic position

The somatic infraciliature of the trachelocercids shows a great similarity, although some details, for instance, the ciliation of the dikinetids and the fine structure of the bristle kinety vary (Table 2). Thus, Foissner and Dragesco (1996b) used the shape and structure of the brosse and circumoral kinety for the generic classification of trachelocercid karyorelictids (Fig. 108, Table 2).

Kovalevaia has a "simple" circumoral kinety made up of a single row of dikinetids. Thus, it belongs to the family Trachelocercidae Kent, 1881 as defined by Foissner and Dragesco (1996b). The circumoral kinety of *K. sulcata* surrounds not only the head but also the brosse cleft, producing a unique, key-hole-shaped pattern (Figs. 20, 26, 36, 108). Admittedly, at first glance, this is a rather inconspicuous generic character. However, many *Tracheloraphis* species, although also having a brosse cleft, show a differently shaped, i.e. sigmoidal circumoral kinety (Fig. 108; Foissner and Dragesco 1996b), indicating that brosse cleft and shape of the circumoral kinety are independent from each other or, in other words, that trachelocercids with a key-hole-shaped circumoral kinety very likely represent a particular

¹This species is transferred from *Trachelonema* to *Trachelonaphis* because *Trachelonema* is a junior, subjective synonym of *Tracheloraphis* (Foissner and Dragesco 1996b)

evolutionary branch. Thus, separation at genus level seems justified. Furthermore, some simple morphological grouping of this large assemblage (70 described and, very likely, many undescribed species; Foissner 1997b) is of practical value.

The observation on the occurrence of a key-holeshaped circumoral kinety in trachelocercids is, in fact, not entirely new. Dragesco (1963) showed it for the first time in protargol-impregnated specimens of *Tracheloraphis* *teissieri* (Fig. 106), which is thus transferred to the new genus: *Kovalevaia teissieri* (Dragesco, 1960) comb. n. (basionym: *Tracheloraphis teissieri* Dragesco, 1960). *Kovalevaia teissieri* has, like *K. sulcata*, minute brown extrusomes, while large brown extrusomes and a longitudinal groove on the glabrous body side are lacking. Further differences concern the body shape, which is much more slender in *K. teissieri* than in *K. sulcata* (cp. Figs. 1, 27, 89, 96, 100), and the nuclei, which are

Table 2. Genus distinction in trachelocercia karvore
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Character	Trachelocerca	Trachelolophos	Kovalevaia	Tracheloraphis	Prototrachelocerca
Brosse Ciliary tuft in oral cavity Circumoral kinety, structure Circumoral kinety, shape ⁴ Bristle kinety ⁵	absent absent ³ simple circular simple	absent ² present simple circular simple	present absent simple key-hole-shaped simple	present absent simple sigmoidal simple or complex	present absent complex sigmoidal mixed
Glabrous stripe	usually $\leq 1/3$ of body width	≤ /3 of body width	of body width	usually $\geq 1/3$ of body width	about 1/3 of body width

¹ Modified from Foissner and Dragesco (1996b)

² Very likely, the ciliary tuft within the oral cavity is a highly modified brosse

 3 Simple = single row of dikinetids; complex = two or more rows of dikinetids. See Foissner (1996) for details

⁴ See Figure 108

 5 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



Fig. 108. Genus distinction in trachelocercid karyorelictids. For explanation, see text and Table 2

more irregularly arranged in *K. teissieri* than in *K. sulcata* (cp. Figs. 5, 6, 89, 103). The number of ciliary rows is rather similar (8-12 vs. 10-24) in both species, if the whole range reported in the literature is taken into account (Dragesco 1960, 1963; Agamaliev 1968; Ricci et al. 1982).

Kovalevaia sulcata has a very conspicuous oral cavity (Figs. 2, 3, 37, 43, 44), distinctly different from the flat oral bulge surface found in *Trachelocerca* (Fig. 88). However, *K. teissieri* apparently lacks such an oral cavity (Figs. 104, 107). Thus, the generic significance of this feature remains doubtful. Very likely, some of the numerous *Trachelocerca* and *Tracheloraphis* species in the older literature belong to *Kovalevaia*, too, especially *Tracheloraphis grassei* (Dragesco, 1960) and *T. poljanskyi* (Raikov, 1963), as indicated by their general organization and the conspicuous brown extrusomes. However, a definite transfer should await the investigation of silver-impregnated specimens, because neither the brosse cleft nor the extrusomes and the groove on the glabrous stripe are unambiguous generic characters. Large, brown extrusomes occur, for instance, also in supposedly rather distant trachelocercids, *viz. Trachelocerca margaritata* Kahl,



Figs. 109-118. *Trachelocerca incaudata* from life (109-114, 117, 118) and after hematoxylin staining (115, 116). 109 - left side views, length up to 500 µm (from Kahl 1933, 1935); 110 - left side view, length 500 µm (from Kiesselbach 1936); 111, 112, 113, 114 - total left side view (bar division 100 µm), head with navicular extrusomes, left side view of posterior body portion, and surface view showing cortical blisters and granules (from Dragesco 1960); 115, 116 - arrangement of ciliary rows on left side and nuclear apparatus (from Raikov and Kovaleva 1968); 117, 118 - extended and contracted specimens (very likely misidentified, as indicated by broad glabrous stripe; from Czapik and Jordan 1976). GS - glabrous stripe, NA - nuclear apparatus

1930 (see also Kahl 1935) and *T. binucleata* Dragesco, 1960. The extrusomes of *K. sulcata* have a unique structure (Figs. 9, 51-54) and origin (Kovaleva and Raikov 1972) and thus possibly represent an additional generic character. However, this can not be reliably assessed at the present state of knowledge, because the other species mentioned above have not yet been studied in this respect.

Trachelocerca incaudata

The following review shows that my observations largely agree with previous reports, i.e. that identification is beyond all doubt. However, all former data are entirely based on live observations and/or conventional histological techniques. Thus, they lack details of the infraciliature and accurate morphometrics. Furthermore, all authors obviously observed only slightly contracted specimens (cp. Figs. 55, 70, 71, 109-111).

The original description of T. incaudata is rather incomplete, as also mentioned by Dragesco (1960): "Extended specimens (rarely found) up to 500 µm long; shape very constant, trunk ribbon-like, slightly narrowed and rounded posteriorly; invariably only one nuclear bleb; cytoplasm darkly granulated; glabrous stripe very narrow and difficult to recognize, bordered by a row of bristles on both sides; common in marine sands at Kiel, Germany (Kahl 1933, 1935; Fig. 109). Kiesselbach (1936) found two specimens at the Adriatic coast of Italy. They had a size of 500 x 45 µm and were strongly contractile (Fig. 110). Dragesco (1960), who found T. incaudata at the same site as I did, i.e. at Roscoff, not only confirmed Kahl's observations but also added some important characteristics (Figs. 111-114): length 400-650 µm, very fragile; posterior end rounded; 6 macronuclei and 2 micronuclei forming tight cluster (capsule); cytoplasm packed with various inclusions; 32 meridional somatic kineties; glabrous stripe narrow, corresponding to an area occupied by about 4 kineties, contains conspicuous, highly refractile, brownish protrichocysts found also between ciliary rows; head as usual, oral opening bordered by navicular trichocysts. Raikov and Kovaleva (1968) confirmed Dragesco's observations and described a variety with 4 micronuclei and 24-30 ciliary rows. Furthermore, they extended the variation of the nominal species, which occurred concomitantly with the variety quadrimicronucleata in the Japan Sea, by reporting that it has 6-8 macronuclei, 2 very small (1-1.5 µm) micronuclei, and 28-32 ciliary rows (Figs. 115, 116). Czapik and Jordan (1976) studied specimens from the Baltic coast and noted a brown colour and high fragility (Figs. 117, 118). Wright (1983), who found *T. incaudata* in marine sands from the south coast of England, confirmed Dragesco (1960). His specimens were 400-800 µm long (average 600 µm) and had 6-8 macronuclei, 2 micronuclei, 28-32 ciliary rows, and a narrow glabrous stripe, corresponding to an area occupied by 2-3 kineties.

Borror (1973) suggested uniting several closely related forms to a "*Trachelocerca incaudata* complex", *viz. T. incaudata, T. monocaryon, T. gracilis, T. stephani,* and *T. swedmarki.* This view is consistent with my data, which show that the infraciliature of *T. incaudata* is extremely similar to that of *T. sagitta* and, especially, *T. ditis,* as redescribed by Foissner and Dragesco (1996b), differing only in some morphometric details. Thus, species separation cannot be based entirely on silverimpregnated material but needs also conventional techniques, i.e. detailed live observation, and characters like body size and shape, arrangement, colour and shape of the extrusomes (cortical granules), and number and arrangement of the nuclei.

The present investigations show that *T. incaudata* lacks a brosse (Figs. 64, 82-84). Thus, it belongs to the genus *Trachelocerca* (Table 2, Fig. 108). Dragesco (1960) transferred *T. incaudata* to *Tracheloraphis* because it possesses a glabrous stripe. However, the glabrous stripe is an ordinal character of trachelocercid karyorelictids and thus cannot serve for genus distinction (Foissner and Dragesco 1996b).

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

REFERENCES

- Agamaliev F. G. (1967) Faune des ciliés mésopsammiques de la côte ouest de la mer Caspienne. *Cah. Biol. mar.* **8:** 359-402
- Agamaliev F. G. (1968) Materials on morphology of some psammophilic ciliates of the Caspian Sea. *Acta Protozool.* 6: 225-244 (in Russian with English summary)
- Borror A.C. (1973) *Tracheloraphis haloetes* sp. n. (Ciliophora, Gymnostomatida): description and a key to species of the genus *Tracheloraphis. J. Protozool.* **20:** 554-558
- Burkovsky I. V. (1970) Ciliates of the sand littoral and sublittoral of Kandalaksha Gulf (White Sea) and the analysis on the fauna of

benthic ciliates of other seas. *Acta Protozool.* **8:** 183-201 (in Russian with English summary)

- Carey P. G. (1992) Marine Interstitial Ciliates. Chapman & Hall, London, New York, Tokyo, Melbourne, Madras
- Corliss J. O. (1979) The Ciliated Protozoa. Characterization, Classification and Guide to the Literature. 2nd ed. Pergamon Press, Oxford, New York, Toronto, Sydney, Paris, Frankfurt
- Czapik A., Jordan A. (1976) Les ciliés psammophiles de la mer Baltique aux environs de Gdañsk. *Acta Protozool.* **15**: 423-445
- Dragesco J. (1960) Ciliés mésopsammiques littoraux. Systématique, morphologie, écologie. Trav. Stn biol. Roscoff (N.S.) 12: 1-356
- Dragesco J. (1963) Compléments a la connaissance des ciliés mésopsammiques de Roscoff. I. Holotriches, II. Hétérotriches. *Cah. Biol. mar.* **4**: 91-119, 251-275
- Fauré-Fremiet E. (1951) The marine sand-dwelling ciliates of Cape Cod. Biol. Bull. mar. biol. Lab., Woods Hole 100: 59-70
- Foissner W. (1991) Basic light and scanning electron microscopic methods for taxonomic studies of ciliated protozoa. *Europ.* J. Protistol. 27: 313-330
- Foissner W. (1996) Updating the trachelocercids (Ciliophora, Karyorelictea). II. *Prototrachelocerca* nov. gen. (Prototrachelocercidae nov. fam.), with a redescription of *P. fasciolata* (Sauerbrey, 1928) nov. comb. and *P. caudata* (Dragesco & Raikov, 1966) nov. comb. *Europ. J. Protistol.* 32: 336-355
- Foissner W. (1997a) Updating the trachelocercids (Ciliophora, Karyorelictea). IV. Transfer of *Trachelocerca entzi* Kahl, 1927 to the Gymnostomatea as a new genus, *Trachelotractus* gen. n. (Helicoprorodontidae). Acta Protozool. 36: 63-74
- Foissner Ŵ. (1997b) The karyorelictids (Protozoa: Ciliophora), a unique and enigmatic assemblage of marine, interstitial ciliates: a review emphasizing ciliary patterns and evolution. In: Evolutionary Relationships among Protozoa (Eds. A. Warren & G. Coombs) (in press).
- Foissner W., Dragesco J. (1996a) 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. J. Euk. Microbiol. 43: 12-25
- Foissner W., Dragesco J. (1996b) Updating the trachelocercids (Ciliophora, Karyorelictea). III. Redefinition of the genera *Trachelocerca* Ehrenberg and *Tracheloraphis* Dragesco, and evolution in trachelocercid ciliates. *Arch. Protistenk.* **147**: 43-91
- Hartwig E. (1980) The marine interstitial ciliates of Bermuda with notes on their geographical distribution and habitat (1). *Cah. Biol. mar.* **21:** 409-441
- Hartwig E., Parker J. G. (1977) On the systematics and ecology of interstitial ciliates of sandy beaches in north Yorkshire. J. mar. biol. Ass. U. K. 57: 735-760

- Kahl A. (1930) Urtiere oder Protozoa I: Wimpertiere oder Ciliata (Infusoria) 1. Allgemeiner Teil und Prostomata. *Tierwelt Dtl.* 18: 1-180
- Kahl A. (1933) Ciliata libera et ectocommensalia. Tierwelt Nordund Ostsee 23 (Teil II, c_x): 29-146
- Kahl A. (1935) Urtiere oder Protozoa I: Wimpertiere oder Ciliata (Infusoria) 4. Peritricha und Chonotricha. *Tierwelt Dtl.* 30: 651-886
- Kent W. S. (1880-1882) A Manual of the Infusoria: Including a Description of all Known Flagellate, Ciliate, and Tentaculiferous Protozoa British and Foreign, and an Account of the Organization and Affinities of the Sponges. Vols. I-III. D. Bogue, London (Vol. I 1880: 1-432; Vol. II 1881: 433-720, 1882: 721-913; Vol. III 1882: Plates)
- Kiesselbach A. (1936) Zur Ciliatenfauna der nördlichen Adria. Thalassia 2: 1-53
- Kovaleva V. G. (1966) Infusoria of the mesopsammon in sand bays of the Black Sea. *Zool. Zh.* **45:** 1600-1611 (in Russian with English summary)
- Kovaleva V. G. (1974) The fine structure of ciliary and cortical organoids and some structures of the ectoplasm and endoplasm of *Trachelonema sulcata* (Ciliata, Holotricha). *Tsitologiya* **16**: 217-223 (in Russian with English summary)
- Kovaleva V. G., Golemansky V. G. (1979) Psammobiotic ciliates of the Bulgarian coast of the Black Sea. Acta Protozool. 18: 265-284 (in Russian with English summary)
- Kovaleva V. G., Raikov I. B. (1972) Saccules énigmatiques en "soucoupes" et leur relation avec les protrichocystes chez le cilié holotriche *Trachelonema sulcata* Kovaleva. *Protistologica* 8: 413-425
- Raikov I. B. (1963) Ciliates of the mesopsammon of the Ussuri gulf (Japan Sea). Zool. Zh. 42: 1753-1767 (in Russian with English summary)
- Raikov I. B., Kovaleva V. G. (1968) Complements to the fauna of psammobiotic ciliates of the Japan Sea (Posjet gulf). Acta Protozool. 6: 309-333
- Ricci N., Santangelo G., Luporini P. (1982) Researches on the coast of Somalia. Sand-dwelling ciliates. *Monitore zool. ital.*, *Suppl.* (N. S.) 17: 115-148
- Wright J. M. (1983) Sand dwelling ciliates of South Wales. Cah. Biol. mar. 24: 187-214

Received on 23rd May, 1997; accepted on 10th July, 1997