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The karyorelictids (Protozoa: Ciliophora), a unique and enigmatic assemblage of marine, interstitial ciliates: a review emphasizing ciliary patterns and evolution

Wilhelm Foissner

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

ABSTRACT

This review updates morphology, ecomorphology, and evolution of karyorelictids, a small (~135 described species, but many more very likely exist) but unique assemblage of mainly marine, interstitial ciliates having paradiploid, non-dividing macronuclei originating from micronuclei. Thus, they have been widely considered to represent an ancestral state of the dimorphic ciliate nuclear apparatus. Most of the gross morphological peculiarities of the karyorelictids (e.g. filiform shape, high regeneration capacity) are apparent adaptations to the spatial structure and unstable conditions of their preferred biotope, coastal sands. Cladistic analysis, based on a reinvestigation of most main groups of karyorelictids, produced two major branches, one containing geleiids and another with loxodids and trachelocercids. The geleiids are completely ciliated, like the supposed ancestors (heterotrichs) of the karyorelictids, and have unique monokinetidal oral structures very different from those of other karyorelictids. The loxodid/trachelocercid clade has a very strong synapomorphy, viz. a highly specialized ciliary row (bristle

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kinety) surrounding a glabrous (unciliated) stripe on the left side of the cell. Ultrastructural and molecular data have suggested a close relationship between karyorelictids and heterotrichs s. str. (e.g. *Stentor*). Surprisingly, such a relationship is hardly recognizable in the somatic and oral ciliary pattern, which shows some (analogous?) characters (e.g. the trachelocercid oral apparatus) highly reminiscent of those found in haptorid gymnostomes and especially prostomatids (e.g. *Coleps*). Stomatogenesis of *Loxodes* is buccokinetal and thus links karyorelictids with oligohymenophorans rather than with heterotrichs. The karyorelictid infraciliature is rather complex and diverse. Thus, the nuclear peculiarities are very likely not ancestral but derived and probably evolved several times, as indicated by the quite different organization of geleiids and loxodids/trachelocercids.

17.1 INTRODUCTION

Ciliates are unicellular, heterokaryotic organisms having a macronucleus and a micronucleus of distinctly different size and function within the same cytoplasm (Raikov, 1982). The macronucleus, which is usually highly polyploid, divides amitotically during asexual reproduction and controls mainly somatic functions (e.g. RNA synthesis, morphogenesis, regeneration). The diploid micronucleus is active mainly during sexual reproduction (conjugation), although recent experiments indicate that it also plays an important role during asexual morphogenesis (Ng, 1990). However, the macronuclei of a restricted group of ciliates, the Karyorelictea, are diploid or nearly diploid (paradiploid) and cannot divide but differentiate from micronuclei during and after cell division (Raikov, 1958, 1982). These peculiarities were interpreted by Corliss (1974, 1979) as being ancestral (relict), and thus he named the whole group 'Karyorelictea'. However, recent molecular evidence (see chapter 18) and the morphological data summarized in this paper indicate that the special nuclear features of the karyorelictids could be derived (apomorph), i.e. evolved secondarily from polyploid ciliate nuclei.

Morphological analysis of the karyorelictids was limited for a long time by their extreme fragility, although many basic features were explored in the pioneering studies by Dragesco (1960), Dragesco and Dragesco-Kernéis (1986), Raikov, Gerassimova-Matvejeva and Puytorac (1975), and Wilbert (1986). Using a new, very 'strong' fixative and Wilbert's protargol technique, Foissner (1995, 1996a–c) and Foissner and Dragesco (1996a,b) obtained excellent preparations from all main groups of karyorelictids, showing a world of new details.

The present paper is a brief overview of the group, emphasizing recent morphological data, phylogeny, and possible relationships between karyorelictids and other ciliates. The very restricted space allowed does not permit much detail, but I hope to summarize the main points in a way attractive to both beginners and specialists. Although outdated in some respects, the last comprehensive reviews on karyorelictids by Corliss and Hartwig (1977) and Raikov (1982, 1994) are still useful and should be consulted, especially for details on their nuclear features and ecology.

17.2 COMPARATIVE MORPHOLOGY, CLADISTICS, AND CLASSIFICATION OF KARYORELICTIDS

The karyorelictids are a small group comprising about 135 species classified into two subclasses, three orders, six families and 11 genera (Table 17.1). I agree with the supraordinal classification suggested by Puytorac (1994) and Puytorac *et al.* (1987), however, with *Protocruzia* excluded because it has mitotically dividing macronuclei and recent molecular data group it with the hypotrichs (Hammerschmidt *et al.* 1996). It is thus doubtful whether this enigmatic genus (see Grolière *et al.* (1980) and Raikov (1982) for detailed accounts) can serve as a model for the origin of nuclear dimorphism in ciliates, as suggested by Bardele and Klindworth (1996); rather, it seems to be a dead and/or specialized route like that of the karyorelictids. *Stephanopogon*, another 'eociliate' classified by Corliss (1979), Corliss and Hartwig (1977) and others near the karyorelictids, has been proven to be a flagellate (Lipscomb and Corliss, 1982).

Our studies on the infraciliature provide a rather clear picture of the evolution within the karyorelictids, at least as concerns the main groups. Consideration of the evidence extends only to family level (Figure 17.1); see Foissner (1996a) and Foissner and Dragesco (1996b) for details on genera.

Using heterotrichs s. str. as outgroup, as suggested by the ultrastructural and molecular data, the karyorelictids can be founded as a monophyletic group by two unique characters (apomorphies), viz. the loss of adoral membranelles and of dividing macronuclei (see final section for detailed discussion). The cladogram then splits into two major branches, one containing loxodids and trachelocercids and the other with geleiids (Figure 17.1).

The geleiids are a very conspicuous component of the interstitial ciliate fauna because some attain a length of up to 5 mm and most have brown pigment granules in the cortex making them dark at low magnification (Figure 17.7). Comparatively little is known about the infraciliature of the geleiids, the most important studies being those of Dragesco and Dragesco-Kernéis (1986) and Nouzarede (1977). These investigations showed that geleiids, unlike all other karyorelictids, are completely ciliated and have oral monokinetids forming a right and left oral ciliary field (Figure 17.9). These 'paracytostomal' monokinetids are

Table 17.1 Classification of karyorelictids and number of species within taxa

Taxa[a]	*Number of species*[b]
Class Karyorelictea Corliss, 1974	135
Subclass Protoheterotrichia Puytorac *et al.*, 1987	20
Order Protoheterotrichida Nouzarede, 1977	20
Family Geleiidae Kahl, 1933	20
Genera *Avelia* Nouzarede, 1977	3
Geleia gen. nov.[c]	17
Subclass Trachelocercia Puytorac *et al.*, 1987	65
Order Loxodida Jankowski, 1978	45
Family Kentrophoridae Jankowski, 1980	14
Genus *Kentrophoros* Sauerbrey, 1928	14
Family Cryptopharyngidae Jankowski, 1980	7
Genera *Apocryptopharynx* Foissner, 1996	2
Cryptopharynx Kahl, 1928	5
Family Loxodidae Bütschli, 1889	24
Genera *Loxodes* Ehrenberg, 1830	6
Remanella Foissner, 1996	18
Order Trachelocercida Jankowski, 1978	65
Family Trachelocercidae Kent, 1881	62
Genera *Trachelocerca* Ehrenberg, 1840[d]	15
Trachelolophos Foissner & Dragesco, 1996	2
Tracheloraphis Dragesco, 1960	45
Family Prototrachelocercidae Foissner, 1996	3
Genus *Prototrachelocerca* Foissner, 1996	3

Incertae sedis: *Ciliofaurea* Dragesco, 1960 (4 species), and *Corlissia* Dragesco, 1960 (monotypic). Both possibly belong to the Protoheterotrichia or Loxodida.

[a] Authorship and dating is controversial in some taxa. Most nomenclatural problems were discussed and solved by Foissner (1995, 1996a–c) and Foissner and Dragesco (1996b). Generic classification is also according to these papers. Most genera do not have taxonomic synonyms. Only *Trachelonema* Dragesco, 1960 has been synonymized with *Tracheloraphis* by Foissner and Dragesco (1996b).

[b] Mainly according to Carey (1992). Note that the actual number is very likely much higher in most genera (see ecomorphology section).

[c] Kahl (1933) founded *Geleia* with three new species, without, unfortunately, designating a type. The genus is thus invalid according to the ICZN. This was overlooked not only by Kahl (1935) but also by later workers. I thus declare *Geleia* Kahl, 1933 to be a nomen nudum, but reinstall *Geleia* as new genus to avoid an inflation of names. Furthermore, I fix *Geleia fossata* (Kahl, 1933) nov. comb. as type species of the new genus.

[d] Dating of this genus is uncertain and needs special investigation.

the most important autapomorphy of the geleiids (Figure 17.1). Further unique features are an enigmatic kinety in a groove near the anterior end and the distinct preoral suture caused by the subapical position of the oral apparatus (Figure 17.8).

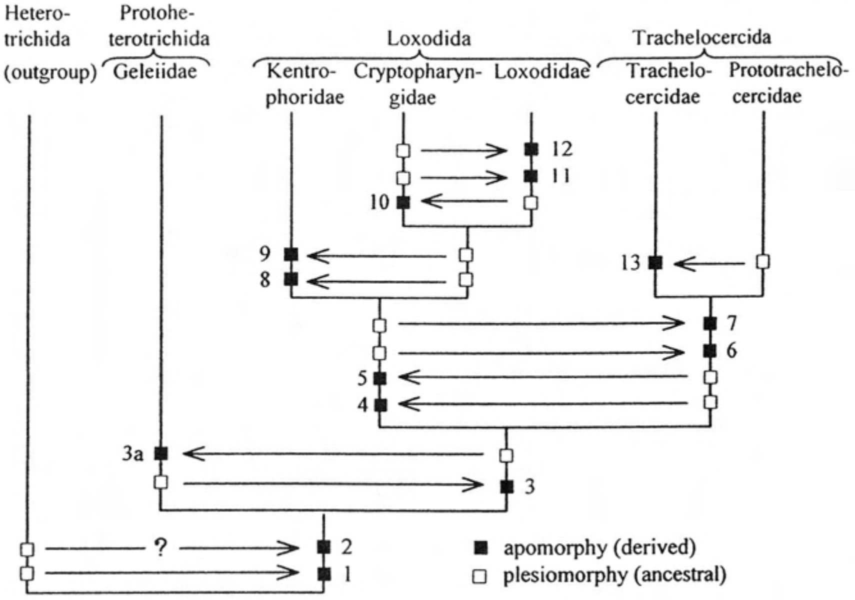
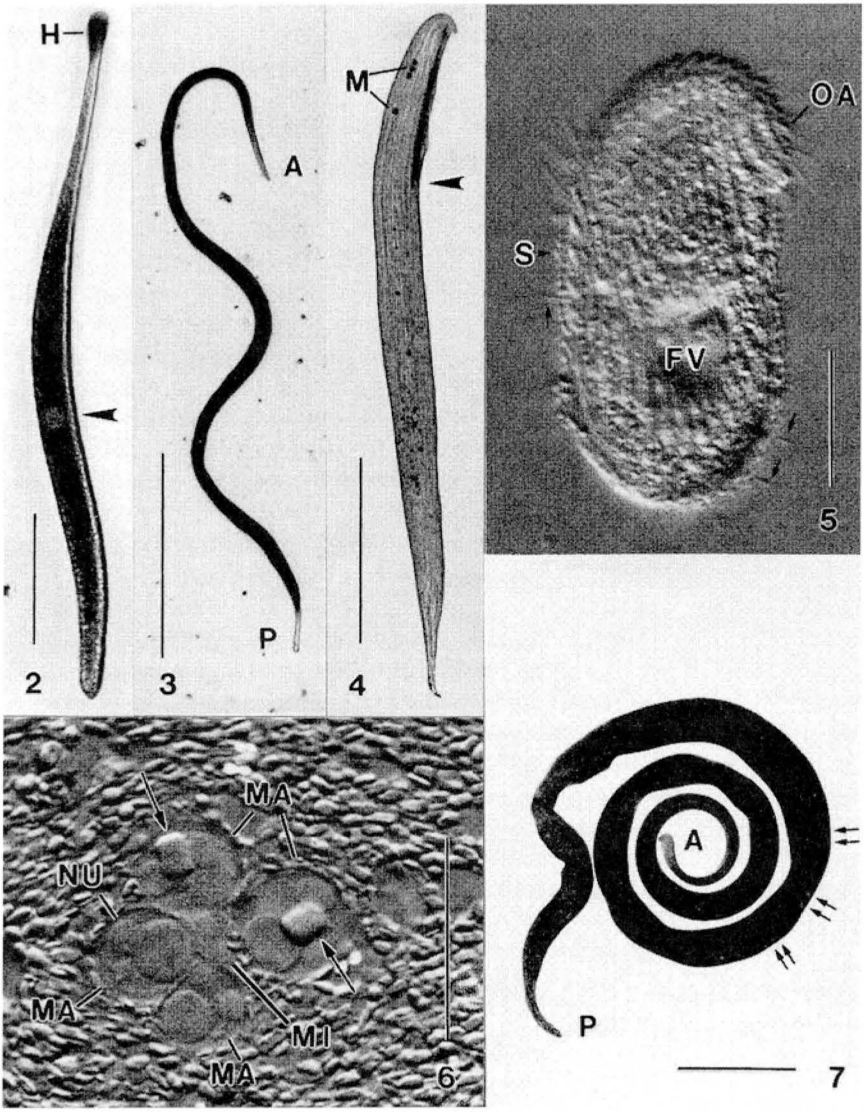


Figure 17.1 A phylogenetic (cladistic) system of karyorelictid ciliates. The analysis was restricted to classical morphological traits because ontogenetic data are lacking for most taxa. The heterotrichs were chosen as outgroup because ultrastructural data and molecular trees argue for a sistergroup relationship with the karyorelictids. Character states (apomorph/plesiomorph): 1, adoral membranelles highly modified or reduced/of typical structure; 2, macronucleus nondividing/dividing; 3, highly specialized bristle kinety framing glabrous stripe/without, i.e. completely and uniformly ciliated; 3a, paracytostomal monokinetids; 4, epipellicular scales or mucilage/without; 5, dorsolateral kinety/without; 6, brosse/without; 7, oral apparatus apical/ventrolateral; 8, epibiontic/symbiotic bacteria on glabrous stripe/without; 9, oral apparatus almost completely reduced/complete; 10, dorsolateral kinety elongated to ventral side/restricted to dorsal and posterior margin of cell; 11, Müller organelles/without; 12, buccal kineties interrupted at anterior buccal vertex/uninterrupted, Figure 17.25; 13, circumoral kinety (ciliature) simple/compound.

The loxodid/trachelocercid clade has a strong synapomorphy, viz. a highly specialized (bristle) kinety surrounding a more or less wide glabrous (nonciliated) stripe on the left side of the cell (Figures 17.1, 17.10, 17.13, 17.14, 17.16, 17.19, 17.20, 17.22, 17.26). The ontogenesis of the bristle kinety is not known. However, light and electron microscopical investigations showed that its fibrillar associates are distinctly different from those of the somatic kineties and that it very likely



Figures 17.2–17.7 Living karyorelictids (from Foissner, 1995, 1996a,b; Foissner and Dragesco, 1996b). 17.2, 17.6: *Trachelocerca ditis*. Arrowhead marks nuclear capsule containing four macronuclei (Figure 17.6). Arrows mark crystalloid inclusions. 17.3: *Kentrophoros fistulosus* is black due to the symbiotic bacteria lawn growing on its left surface. 17.4: *Remanella multinucleata*. Arrowhead marks posterior end of oral apparatus. 17.5: *Apocryptopharynx hippocampoides*. Arrows mark bristles of bristle kinety. 17.7: A very long (3 mm), still undescribed geleiid having many nuclear groups (arrows). A, anterior end; FV, food vacuole; H,

consists of a small anterior and a large, U-shaped posterior fragment (Foissner and Dragesco, 1996b). The site where the fragments of the bristle kinety abut is clearly marked at the right margin of the glabrous stripe. Here, the dikinetids of the anterior segment have the anterior basal bodies ciliated, whereas those of the posterior segment have the posterior basal bodies ciliated (Figures 17.13, 17.14, 17.22, 17.26).

The loxodids are ventrostome, almost acontractile, usually leaf-like flattened ciliates preferring microaerobic habitats. Most *Loxodes*, *Remanella*, and *Kentrophoros* species are slender or filiform (Figures 17.3, 17.4), whereas cryptopharyngids are elliptical (Figures 17.5, 17.19). The left side is unciliated, except near the margin where the bristle kinety extends (Figures 17.15, 17.16). The oral apparatus commences at the anterior end and extends as a narrow slit posteriorly on the thin side of the cell. The oral ciliature is composed of several dikinetidal ciliary rows forming a complex pattern (Figure 17.15). Literature on loxodids is rather voluminous, the most important contributions being those by Bardele and Klindworth (1996), Fenchel and Finlay (1986), Foissner (1995, 1996a,b), Klindworth and Bardele (1996), and Raikov (1971, 1978).

The loxodid clade is defined by two comparatively inconspicuous synapomorphies, viz. epipellicular scales or mucilage and, more importantly, a unique dorsolateral kinety (Figure 17.1). Complex epipellicular scales occur in the Cryptopharyngidae (Figure 17.5), whereas a thick layer of mucous material is used by kentrophorids to attach the symbiotic 'kitchen garden' on the unciliated left side of the cell (see ecomorphology section). *Loxodes* and *Remanella* apparently lack scales and mucus. The dorsolateral kinety is present on the dorsolateral margin of the cell as a ciliary row which is more or less distinctly shortened anteriorly. The kinetids of this kinety are more closely spaced than those of the neighbouring somatic kineties and are associated with special fibres (Figure 17.17). *Kentrophoros* has such a kinety too, at least the fibres are clearly identifiable (Figure 17.18). Thus, the order Protostomatida Small and Lynn, 1985, uniting the Kentrophoridae and Trachelocercidae but excluding the Loxodidae, is very likely artificial. The Kentrophoridae are distinguished from the other loxodids by their highly reduced oral apparatus (Foissner, 1995) and the symbiotic kitchen garden (Raikov, 1971; Foissner, 1995). The Loxodidae have a unique apomorphy associated with the bristle kinety, viz. the Müller organelles (Figures 17.4, 17.10) used for gravity perception (Fenchel and Finlay, 1986). The Cryp-

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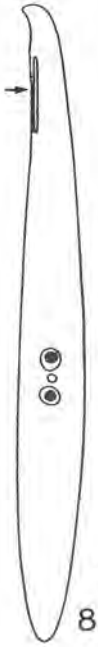
head; M, Müller organelles; MA, macronuclei; MI, micronucleus; NU, nucleoli; OA, oral apparatus; P, posterior end; S, epipellicular scales. Scale bars 20 μm (Figures 17.5, 17.6), 200 μm (Figures 17.1, 17.4, 17.7), 500 μm (Figure 17.3).



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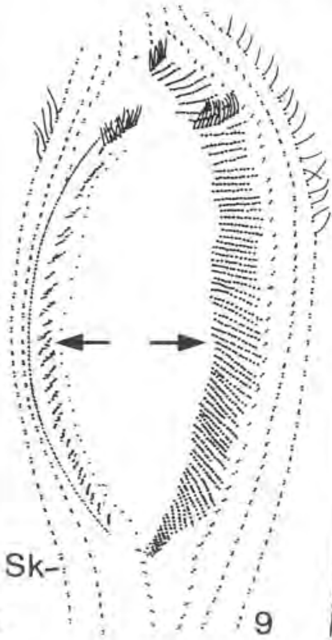

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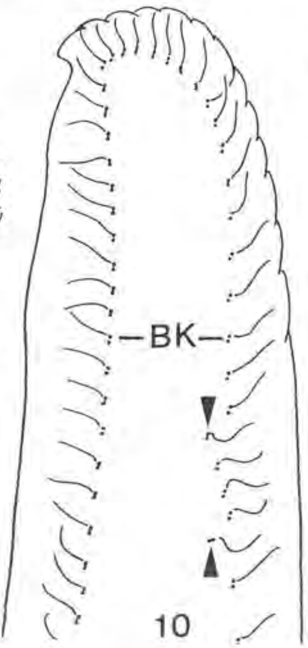

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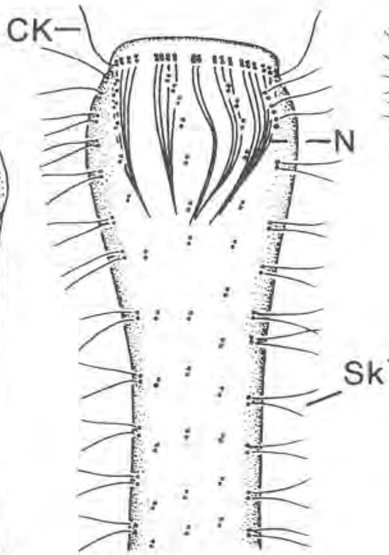

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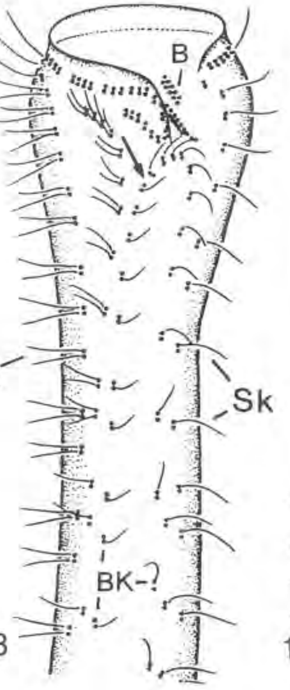

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topharyngidae are very near the Loxodidae and provide an example of how the complex loxodid oral infraciliature may have evolved (Figures 17.15, 17.19, 17.25).

All trachelocercids are filiform, highly contractile organisms, typically composed of a globular head bearing the oral apparatus, a thin neck, and a more or less distinctly flattened, rounded or tapered trunk (Figures 17.2, 17.11). Trachelocercids are widespread in coastal sands and the most characteristic component of the interstitial ciliate fauna. Benchmark studies include papers by Dragesco (1960), Dragesco and Dragesco-Kernéis (1986), Foissner (1996c), Foissner and Dragesco (1996a, b), Raikov (1958, 1982), and Raikov, Gerassimova-Matvejeva and Puytorac (1975).

The trachelocercid clade is defined by two strong synapomorphies, viz. the apicalization of the oral apparatus and the brosse (Figures 17.1, 17.12, 17.13, 17.20–17.24, 17.26). Admittedly, the first character is rather speculative and partially based on Eisler's (1992) hypothesis that ancestral ciliates had ventrolaterally located oral structures as, for instance, found in *Remanella* (Figures 17.4, 17.15). However, there is also direct support for an apicalization of the trachelocercid oral apparatus, viz. the location of the site where the ends of the bristle kinety meet. In trachelocercids, this site is close beneath the circumoral kinety because the anterior arch of the bristle kinety is short or, as in *Trachelocerca*, even lacking (Figures 17.13, 17.20, 17.22, 17.26). In the sister group, the loxodids, the right anterior branch of the bristle kinety is much longer and extends along the oral slit and thus meets the other end only at the level of the posterior buccal vertex (Figure 17.14). It is easy to imagine

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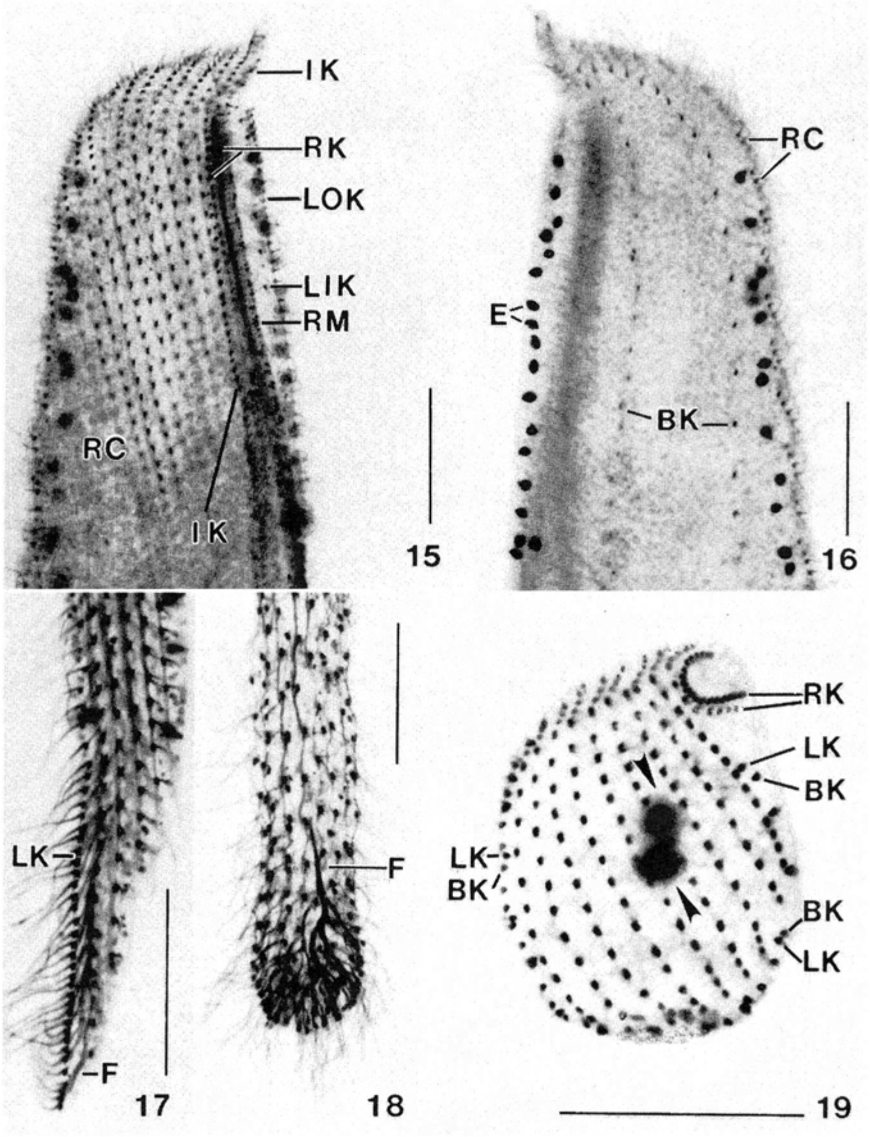
Figures 17.8-17.14 Somatic and oral infraciliature (ciliary pattern) of geleiid, loxodid, and trachelocercid karyorelictids after protargol impregnation. 17.8, 17.9: *Geleia decolor*, length 500 μm (from Dragesco and Dragesco-Kernéis, 1986). The oral ciliary fields (arrows) consist of rows of single basal bodies (monokinetids), unlike those in all other karyorelictids. 17.10, 17.14: *Remanella multinucleata*, left side infraciliature (from Foissner, 1996b). The left side is glabrous (unciliated), except for the bristle kinety whose fragments meet at the level of the proximal buccal vertex, as evident from the opposed ciliation of the dikinetids (Figure 17.14). Arrowheads mark bristle kinetids, slightly out of line, associated with the Müller organelles (cp. Figure 17.4). 17.11-17.13: *Tracheloraphis longicollis*, length about 800 μm (from Foissner and Dragesco, 1996b). Right and left side view of head, which bears distinct oral structures composed of a circumoral kinety (CK), nematodesmata (N) and brosse kineties (B). Arrow marks site where the ciliation of the bristle kinety is opposed (cp. Figure 17.14). B, brosse composed of two short, oblique kineties; BK, bristle kinety; CK, circumoral kinety; N, nematodesmata; Sk, somatic kineties.



Figures 17.15-17.19 Infraciliature of loxodid karyorelictids after protargol impregnation (from Foissner, 1995, 1996a,b). 17.15, 17.16: *Remanella multinucleata*, right and left side view of anterior oral region. 17.17, 17.18: Posterior end of *R. multinucleata* and *Kentrophoros fistulosus* showing fibres (F) originating from the dorsolateral kinety. 17.19: *Cryptopharynx setigerus*, a very flat species, showing dorsolateral kinety (LK) extending around posterior half. Arrowheads mark macronuclei. BK, bristle kinety; E, extrusomes; F, fibres; IK, intrabuccal kinety; LK,

that a trachelocercid pattern arises if, for instance, the oral apparatus of *Remanella* is shifted anteriorly, i.e. apicalized (Foissner and Dragesco, 1996b). The second apomorphy, the brosse, is a highly distinctive character. Usually, the brosse consists of 1–3 short, oblique dikinetidal kineties located beneath the circumoral kinety in a more or less deep cavity (Figures 17.13, 17.22, 17.26). The brosse has been modified to a tuft of cilia in *Trachelolophos* (Figure 17.23) and, very likely, has been secondarily reduced in *Trachelocerca* (Figure 17.20).

Evolution within trachelocercids is difficult to follow for several reasons (Foissner and Dragesco, 1996b). *Prototrachelocerca* was separated at family level because of its unique circumoral ciliature, which consists of 2–3 closely spaced dikinetidal rows, somewhat reminiscent of the loxodid oral structures (Figure 17.24).

17.3 ECOMORPHOLOGY OF KARYORELICTIDS

Comprehensive reviews on the ecology of marine micrometazoa and protozoa, including karyorelictids, were published by Fenchel (1987), Patterson, Larsen and Corliss (1989), and Remane (1933). The reader is referred to these publications for details and specific literature. Here, I want to highlight only some peculiarities and problems relating to the karyorelictids.

Karyorelictid ciliates are marine, benthic organisms, except for some *Loxodes* species, which are widespread in microaerobic freshwater habitats. Most karyorelictids are obligate interstitial inhabitants, i.e. they live in sheltered microporal (grain size 120–400 μm) and mesoporal (400–1800 μm) coastal sands, preferring the tidal zone, particle sizes between 120 μm and 250 μm, and the upper, well-oxygenated, nutrient-rich 10 mm of the sediment. Here, they may reach high abundances of up to 5000 individuals per cm^2. Thus, in some sediments ciliates play an important role in the benthic energy transfer and are at least as important as metazoa as consumers (Fenchel, 1987).

The most conspicuous morphological features of the karyorelictids are the large size (some species attain a length of 5 mm; Figure 17.7), the vermiform shape often combined with leaf-like lateral flattening, the high contractility and regeneration capacity (geleiids, for instance, can regenerate the oral body half within 3–4 hours), and the ability to attach firmly to the sand grains (thigmotactism) by means of the cilia (Figures

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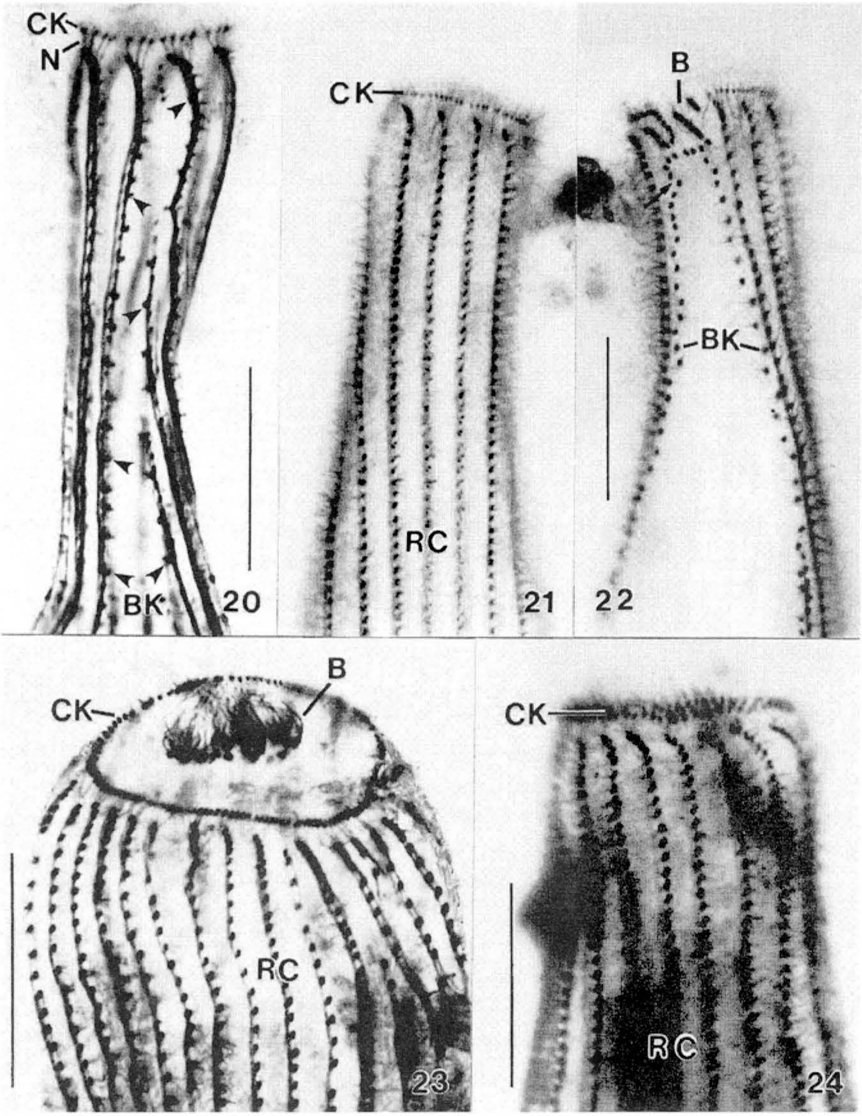
dorsolateral kinety; LIK, LOK, left inner and outer buccal kinety; RC, ends of right lateral ciliary rows; RK, right buccal kineties; RM, right margin of buccal overture. Scale bars 20 μm.



Figures 17.20-17.24 Infraciliature of trachelocercid karyorelictids after protargol impregnation (from Foissner, 1996c; Foissner and Dragesco, 1996a, b). All figures show the anterior (head) region with the oral apparatus. 17.20: *Trachelocerca sagitta*, left side view. Arrowheads mark bristle kinety close to somatic kineties. 17.21, 17.22: *Tracheloraphis longicollis*, right and left side view. Note distinct brosse. Arrow marks site where fragments of bristle kinety abut. 17.23: *Trachelolophos gigas* has the brosse in a pit near the centre of the oral field. 17.24: *Prototrachelocerca caudata* has a compound circumoral ciliature composed of closely

17.2–5, 17.7). Thus, the marine sand ciliate community is distinctly different, both morphologically and ecologically, from the ciliate communities found in freshwater and soil (Table 17.2). Very likely, most of these peculiarities evolved as adaptations to the porous structure and unstable conditions of the biotope. For instance, the risk of being washed out is minimized by thigmotactism and by long, flattened shapes entangling the organisms between the sand grains. Furthermore, a vermiform shape allows them to exploit the fine pores for food and other resources. Thus, this shape type is common also in mesopsammal micrometazoa (Remane, 1933) and among soil ciliates (Foissner, 1987). A high regeneration capacity is advantageous in a biotope which exerts strong mechanical forces by moving sand grains during tides and storms.

Freshly collected karyorelictids are usually packed with large food vacuoles containing a variety of algae, ciliates, and even micrometazoa such as rotifers and harpacticoid copepods. Surprisingly, the mode of food uptake is not known in most species; nobody has ever seen how a trachelocercid ingests these large food items. *Ad hoc*, one would expect that ingestion occurs via the oral apparatus because all karyorelictids, except for kentrophorids, have more or less elaborate oral structures comparable to those found in other ciliates (Figures 17.9, 17.12, 17.13, 17.15, 17.19–24). However, Lenk, Small and Gunderson (1984) and Lenk, Hollander and Small (1989) claimed that ingestion in at least some trachelocercids occurs via the glabrous stripe. In my opinion, this is not very likely because the glabrous stripe is rather narrow in many species and Lenk's micrographs do not show the process unequivocally. On the other hand, Lenk's observations cannot be denied entirely because *Kentrophoros*, which has the oral structures reduced to inconspicuous vestiges (Foissner, 1995), does indeed use the glabrous stripe for food uptake. *Kentrophoros* spp. are unique in having a symbiotic kitchen garden of sulphur bacteria on the left side (Raikov, 1971). The bacteria, which are embedded in a mucous substance, divide on the ciliate and are phagocytosed through the glabrous stripe (Raikov, 1971; Foissner, 1995).

Karyorelictids have a huge variety of extrusomes, some of which are highly reminiscent of hydrozoan cnidocysts (Foissner, 1996a,b; Raikov, 1978; Figure 17.16). Their function is not known. Possibly, they are used for prey capture and/or attachment to solid particles. *Loxodes* and *Remanella* have unique organelles, the Müller vesicles (Figures 17.4, 17.10) for gravity perception (Fenchel and Finlay, 1986).

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spaced dikinetidal rows. B, brosse; BK, bristle kinety; CK, circumoral kinety; N, nematodesmata; RC, right side ciliary rows. Scale bars 20 μm.

Table 17.2 A comparative description of the ciliate communities in freshwater, soil, and marine sand[a]

Character	*Freshwater*	*Soil*	*Marine sand*[f]
Mean biomass (mg) of 10^6 individuals	1076 (n = 200)[b]	98 (n = 238)	872 (n = 200)
Mean body length (μm)	162 (n = 200)	110 (n = 238)	424 (n = 200)
Mean body width (μm)	56 (n = 422)	36 (n = 238)	54 (n = 200)
% Colpodea	5 (n = 422)	18 (n = 238)	0 (n = 292)
% Hypotrichida	11 (n = 422)	37 (n = 238)	20 (n = 292)
% Peritrichida	21 (n = 422)	3 (n = 238)	0.3 (n = 292)
% cyst forming species	⩽80	>95	<2
% species with reduced ciliature[c]	41 (n = 182)	53 (n = 229)	53 (n = 200)
% species with nodulated macronucleus[d]	8 (n = 200)	25 (n = 238)	43 (n = 200)
Ploidy of macronucleus	generally high	generally high	often low
Body shape	often cylindrical	often flattened, elongated, worm-like	often flattened, elongated, worm-like
Caudal prolongation	uncommon	common	very common
'Cephalization'	very rare	very rare	rare
Contractility	generally low	generally low	generally high
Fragility	generally low	generally low	generally high
Cytological peculiarities	cytoplasm seldom strongly vacuolated	cytoplasm seldom strongly vacuolated	cytoplasm often strongly vacuolated; skeletal rodlets
Movement	thigmotactic creepers common only in the Aufwuchs; sessile forms common	thigmotactic creepers common; sessile forms nearly absent	thigmotactic creepers common; sessile forms nearly absent
Nutrition	great majority of common species are bacterivorous, or macrophagous	great majority of autochthonous species are bacterivorous predaceous, or mycophagous	great majority of autochthonous species are macrophagous (predaceous)
Symbiotic bacteria on the body surface of species within the sulfide system	present	unknown	present
Number of species	about 4000	about 400	about 1000
Abundance[e] range m^{-2}	$5 \times 10^4 - 5 \times 10^6$	$0 - 4 \times 10^6$	$5 \times 10^6 - 3 \times 10^7$

[a] From Foissner (1987). See this publication for literature on data sources.

[b] n refers to the number of species considered.

[c] Peritrichs and suctorians were excluded because of their high degree of specialization. Calculated from the same data set as used for 'mean biomass'.

[d] Only species with more than two nodules have been considered as having a nodulated macronucleus. Two nodules are 'normal' in many groups (e.g., hypotrichs). Calculated from the same data set as used for 'mean biomass'.

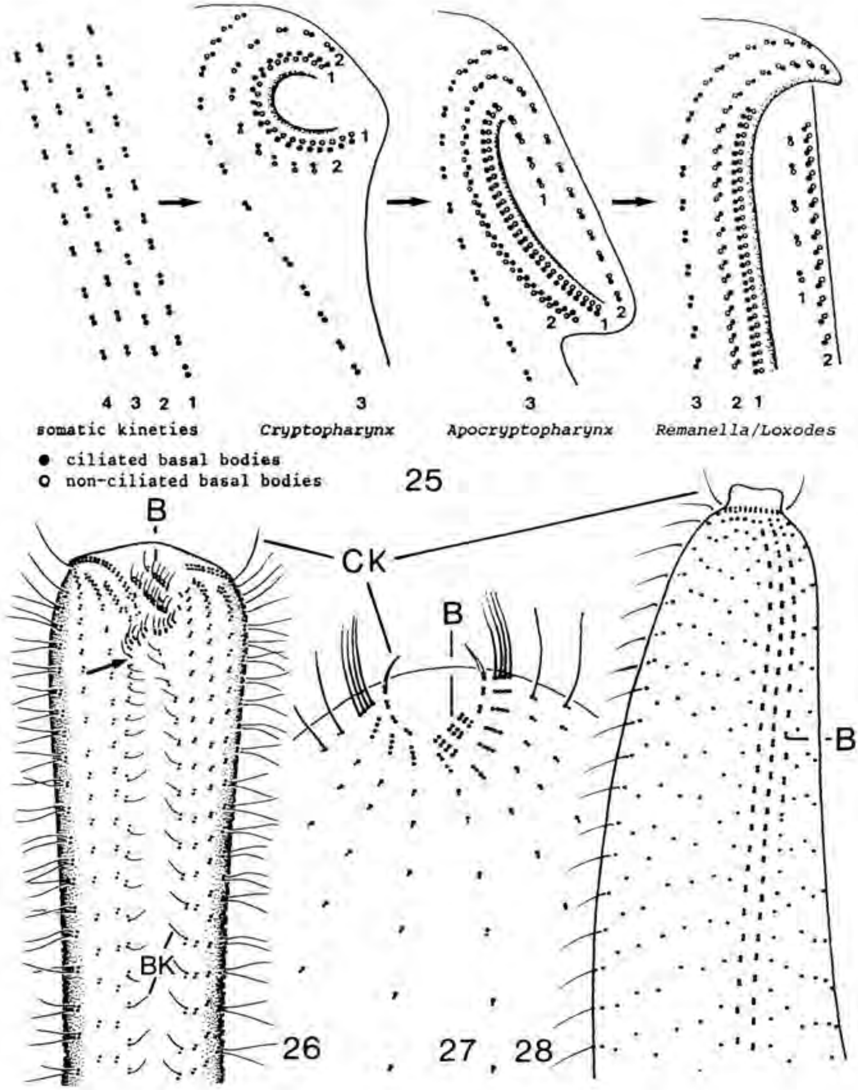
[e] These are only a few, perhaps not representative, examples from mesosaprobic rivers, alpine grassland soils, and marine sands.

[f] Includes not only karyorelictids but also other ciliates inhabiting marine sands.

The diversity of karyorelictids is apparently small, i.e. only 135 species have been described (Table 17.1), most of which are assumed to be cosmopolitan. Some species are believed to have a restricted geographic range, for instance, *Geleia murmanica* to Europe, and *Avelia martinicense* to Martinique. However, I agree with Patterson, Larsen and Corliss (1989) that 'Statements relating to the distribution of species must be viewed with some (I would say, great) caution because of uncertainty over taxonomic practice and because of undersampling'. Although the diversity of karyorelictids is undoubtedly small as compared with the rest of the ciliates, many more species than are presently known very likely exist. New species are being described continuously and I expect that, when our new fixative and silver impregnation are more widely used, the number of known species will quickly and greatly increase, as happened with the soil ciliates (Foissner, 1987). Dragesco and I found at least two new genera (Foissner 1996a; Foissner and Dragesco, 1996a) and several new species during two weeks of work at Roscoff, a well-investigated site, although we did not particularly look for new taxa. And the geleiid depicted in Figure 17.7 is also a new species, having, unlike all described species, several groups of macronuclei. Furthermore, karyorelictids are very patchily distributed and many of them are, as usual, rare. Thus, I would not be surprised if forthcoming generations of scientists established that we knew only 10% of the species actually existing at the turn of the millenium.

17.4 RELATIONSHIPS OF KARYORELICTIDS WITH OTHER CILIATES

Structural similarities of the SSUrRNA gene sequences of several heterotrichs s. str. (e.g. *Stentor*, *Climacostomum*), heterotrichs s. l. (*Metopus* spp.), trachelocercids (*Tracheloraphis*, *Loxodes* spp.), and *Protocruzia* sp. were analysed with parsimony and distance algorithms (Baroin-Tourancheau *et al.*, 1992; Hirt *et al.*, 1995; Hammerschmidt *et al.*, 1996). The results showed, with strong bootstrap support, the karyorelictids as a sister group of the heterotrichs s. str., while *Protocruzia* clustered with the hypotrichs and *Metopus*, surprisingly, with the haptorid gymnostomes; however, bootstrap values were weak for *Protocruzia* and *Metopus* and their phylogenetic relationships are thus still open for discussion (Hirt *et al.*, 1995). A close relationship between heterotrichs s. str. and karyorelictids was proposed long ago also by Raikov, Gerassimova-Matvejeva and Puytorac (1975) because of distinct similarities in the somatic cortical ultrastructure. Surprisingly, such a close relationship is not evident from our studies of the somatic and oral infraciliature, and not even from the few reliable ontogenetic data available (Bardele and Klindworth, 1996).



Figures 17.25–17.28 Relationships within karyorelictids and between karyorelictids and other ciliates. 17.25: Origin and evolution of the loxodid oral ciliature from somatic ciliary rows (cp. Figures 17.15, 17.19; from Foissner, 1996a). 17.26–17.28 *Tracheloraphis phoenicopterus* (26, Karyorelictea, from Foissner and Dragesco, 1996b), *Coleps hirtus* (27, Prostomatea, from Foissner, 1984), and *Enchelyodon terrenus* (28, Gymnostomatea, from Foissner, 1984) have a dikinetidal circumoral kinety and a brosse. Arrow marks site where fragments of bristle kinety abut. B, brosse; CK, circumoral kinety; BK, bristle kinety.

The somatic and oral infraciliature of the karyorelictids is distinctly different from that of the proposed sister group, the heterotrichs s. str., except for some general similarities, like somatic dikinetids and oral structures composed of elements which might be interpreted as paroral and/or adoral ciliature. Specifically, all karyorelictids lack classic adoral membranelles, as typical for heterotrichs, composed of several closely spaced ciliary rows; even the geleiids have the left oral ciliary field, which is densely ciliated and thus reminiscent of an adoral zone of membranelles, composed of single (monokinetidal) ciliary rows (Figure 17.9). On the other hand, the heterotrichs lack the glabrous stripe and the bristle kinety (Figures 17.10, 17.13, 17.16, 17.19, 17.20, 17.22), which are so conspicuous in all loxodids and trachelocercids, but absent in geleiids, indicating that they might be more ancestral than trachelocercids and loxodids.

The oral structures of the Geleiidae and Loxodida are unique, hardly bearing any resemblance to those of other ciliates, although there is some evidence that the loxodid oral kineties have somatic progenitors (Figure 17.25). This contrasts with the trachelocercid oral infraciliature (Figure 17.26), which strongly resembles that found in haptorid gymnostomes (e.g. *Enchelyodon*, Figure 17.28) and especially in prostomes (e.g. *Coleps*, Figure 17.27). All have a circumoral kinety composed of dikinetids, and a brush or brosse, i.e. some small kineties near the oral opening. In prostomatids, the brosse is interpreted as adoral ciliature (Huttenlauch and Bardele, 1987). Similarly, the trachelocercid brosse kineties could be remnants of heterotrich adoral membranelles. There is also another remarkable similarity between prostomatids and karyorelictids, viz. the rectangular or hexagonal cortical fibrillar system found in prostomatids and hymenostomes such as *Urotricha* (Foissner and Pfister, 1997) and *Paramecium* (Wichtermann, 1986) and karyorelictids like *Geleia swedmarki* (Dragesco, 1960) and *Trachelolophos gigas* (Foissner and Dragesco, 1996a).

Unfortunately, the molecular and morphological investigations can hardly be compared with ontogenetic data because these are almost completely lacking for karyorelictids. Only *Loxodes* has been recently studied in some detail. Bardele and Klindworth (1996) showed that stomatogenesis of *Loxodes* is buccokinetal, i.e. the daughter oral structures originate by direct participation of the parental oral apparatus. Thus, stomatogenesis of *Loxodes* at least is quite different from that of heterotrichs s. str. and of prostomatids, which form the daughter oral apparatus parakinetally or telokinetally, i.e. from parental somatic infraciliature (Foissner, 1996d). Typically, buccokinetal stomatogenesis is found in the Oligohymenophorea, a large group of ciliates comprising hymenostomatids (e.g. *Tetrahymena*, *Paramecium*), scuticociliates (e.g. *Uronema*, *Pleuronema*) and, possibly, also prostomatids (e.g. *Urotricha*, *Coleps*).

Thus, as with morphology, ontogenesis indicates some link between karyorelictids and oligohymenophorans, especially when the prostomatids are included in the latter. However, the molecular data do not indicate any relationship between karyorelictids and oligohymenophoreans/prostomatids (chapter 18).

Karyorelictids were frequently used as model organisms for the origin of nuclear dimorphism and oral structures in ciliates (Corliss, 1974, 1979; Orias, 1976; Small, 1984; Herrick, 1994). None of these hypotheses gained wide acceptance and most were based on incomplete data. Orias (1976), for instance, proposed *Kentrophoros* to be most primitive among all ciliates, partly because of its supposed mouthlessness. However, recent observations showed that *Kentrophoros* very likely has vestiges of an oral infraciliature, suggesting that it became secondarily mouthless due to its highly specialized mode of nutrition (Foissner, 1995). Likewise, Small (1984) based his hypothesis on the origin of the ciliate oral apparatus on the assumption that orally specialized kinetids and ciliation are 'totally absent in *Tracheloraphis*'. This has been clearly disproved by later investigations (Figures 17.12, 17.13, 17.20–17.24, 17.26). In the light of the highly specialized somatic and oral infraciliature, as well as the molecular evidence, I agree with Hirt *et al.* (1995) and (chapter 18) and Hammerschmidt *et al.* (1996), that the specific nuclear features of the karyorelictids are not ancestral but derived. I would not even be too surprised if non-dividing macronuclei had evolved twice, possibly due to ecological constraints (Fauré-Fremiet, 1961), considering the highly different somatic and oral infraciliatures of the Protoheterotrichida and Trachelocercia.

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