

AN ESSAY ON THE EVOLUTION OF CILIOPHORAN ORAL CYTOARCHITECTURE BASED ON DESCENT FROM WITHIN A KARYORELICTEAN ANCESTRY

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Abstract. A description of how two basically dissimilar oral cytoarchitectures of ciliates, one prostomial, the other ventrostomial, might have evolved is presented. The evolutionary sequence for these types of oral organization may well have been derived from within a karyorelictean ciliate ancestry. A truly gymnostomatous condition, similar to the morphology of oral areas in extant *Tracheloraphis* species, is postulated to have preceded the evolution of oral types in which kinetids have come to support the ingestatory areas. The precursor to the *Tracheloraphis* stage is argued to have been similar to the flan-like condition of the extant ciliate genus *Kentrophoros*. Thus, it is proposed that ciliate oral architecture had its origin from within the group of karyorelictean ciliates rather than from some flagellate ancestor.

1. Introduction

In recent years, there has been a growing awareness of the existence of psammobiotic ciliates that show a diverse array of morphological types (Dragesco, 1960, 1963) most, if not all, of which also possess distinctive nondividing diploid macronuclei. These macronuclei differentiate at each division from micronuclear division products (Raikov, 1969, 1975, 1982). This has led Corliss (1974, 1979; Corliss and Hartwig, 1977) to establish a new taxon, the order Karyorelictida. Electron microscopical studies (Gerasimova and Seravin, 1976; Nouzarède, 1977; Raikov, 1975) have revealed that the ultrastructure of the somatic kinetid is similar to that of the heterotrichine heterotrichs. Following Lynn's (1981) recent review of somatic kinetid ultrastructure, Small and Lynn (1981) have proposed a new macrosystem for the phylum Ciliophora in which karyorelictean ciliates are given class status and have been recognized as central to the evolution of the phylum (see Figure 1 in Small and Lynn, 1981).

The karyorelicteans are indeed not only karyorelicts but also, in my thinking, corticorelicts as well. Unlike other ciliates, their somatic kinetids consist of dikinetids that lack parasomal sacs. The cell membrane surface has neither the well developed alveoli typical of so many ciliates nor the perilemme of some spirotrichous groups. Contractile vacuoles (expulsion vesicles) and a well-defined cytoproct are also wanting.

Yet these same ciliates (with their unique form of nuclear duality) still possess, like other ciliates, oral attributes that run the gamut of diverse expression – all within the same class! And a whole range of feeding types may be found, filling diverse ecological niches (as pointed out by Fenchel, 1969). Oral morphological types corresponding to diverse ecological types are represented within the class by:

(1) forms that are only prostomatous, both raptorial and nonraptorial, within the genus *Trachelocera*;

(2) forms that have well developed ventral cytostomes bordered by heterotrich-like polykinetids (e.g., the proheterotrich genera *Avela* and *Geleia*: see Nouzarède, 1977);

(3) forms that have well developed ventral cytostomes bordered by multiple left- and right-sided oral dikinetid configurations (e.g., *Loxodes* and *Remanella*: see Dragesco, 1960; de Puytorac and Njiné, 1971); and

(4) forms, like *Kentrophoros*, that are completely astomatous, in which ingestion of attached epicommensal bacteria or diatoms takes place by simple membrane infolding (see Fenchel, 1968) in a fashion that is reminiscent of amoeboid pseudopodial engulfment.

If one excludes, for the moment, the highly evolved ciliates that have very specialized modes of ingestion – like the apostomatids, astomates, and suctoria – major oral strategies (morphologies) are obvious. One group, represented in Small and Lynn (1981) in part by the subphylum Rhabdophora, is essentially prostomial. None is truly gymnostomatous. Each has a specialized oral ciliature of oral dikinetids many of which, like the litostomean Haptoria, possess transverse microtubular ribbons orally directed on which specialized toxicysts insert. Another group, represented in Small and Lynn (1981) by the subphylum Cyrtophora, possesses ventral cytostomy, and, except for certain groups (e.g., the astomates, suctoria, etc.), has specialized oral kinetid morphologies. Fauré-Fremiet (1950) long ago recognized these two different strategies when he originally erected for the now archaic systematic group, the gymnostomes, the two major subdivisions Rhabdophorina and Cyrtophorina. Ever since reading this heuristic work, my question has been to understand the possible origin(s) of these two basically different stocks of ciliates.

Orias (1976) has proposed that the karyorelictean astome *Kentrophoros* might be looked on as primitive among all ciliates since the cell surface is organized into a flange of kinetid units on one side with ingestion taking place from the other nonciliated surface. In his view, the rounding up of the ciliated surface from the outside, thus enclosing the ingestive surfaces on the inside, would create a tube-like ciliate with digestive vacuoles located internally and somatic flange locomotory ciliature located externally. It is true that in species of the genus *Kentrophoros* there is no evidence of oral ciliature, and the whole cell surface is bound by only one cell membrane, capable of infolding to form internal cytoplasmic food vacuoles without necessarily rounding up (Raikov, 1973a, 1974). Unfortunately, Orias did not take into account two other genera of karyorelictean ciliates that are equally enigmatic: *Trachelonema* and *Tracheloraphis*.

Species of both of these two ciliate genera seem at first glance to be prostomatous since the anterior ends appear enlarged and the somatic kineties terminate in such a fashion that an anterior area, devoid of ciliature, is *almost* completely enclosed. This would suggest that these phagotrophic ciliates are prostomatous. Examination by light microscopy of diverse genera shows that, indeed, some species within the genus *Tracheloraphis* are capable of ingesting very large food substances, such as copepods (Hartwig, 1973) or large pennate diatoms (Raikov, 1962; Raikov and Kovaleva, 1968);

and a multitude of others (35 described species in the genus *Tracheloraphis* alone) are able to feed on diverse foodstuffs, including bacteria, microflagellates, diatoms, and small ciliates (Fenchel, 1968, 1969).

It is of interest to note that, in all of the published literature on such ciliates, no one has actually observed the act of ingestion itself. Dragesco, Fenchel, Raikov, and Borrer (personal communications) all suggest that the ingesta of these forms may include sand grains, among which the ciliates live, which would thus make microscopical observations of the process difficult.

Frequently overlooked as an additional possible feeding surface in these organisms is the 'dorsal' glabrous zone, an area often continuous with the anterior nonciliated surface and extending to the posterior end of the cell. This zone is barren of structure, save the external limiting plasma membrane.

2. How Ciliate Oral Evolution May Have Proceeded

It has occurred to me that species of the genus *Tracheloraphis* might ingest phagotrophically from the anterior end, from the glabrous stripe, or from both. *Trachelonema* species may feed in the same fashion, since they have essentially the same cortical morphological features but are more ribbon-like and possess fewer kineties and an even broader glabrous area. Evidence in support of the glabrous zone as a feeding surface in species of the genus *Tracheloraphis* has recently been found by Lenk *et al.* (1984) working with cultures of species from North American marine and estuarine sands. When fed cooked egg yolk, these ciliates have been observed ingesting the yolk granules directly through their glabrous surfaces.

A second idea is also suggested. Ciliate prostomatous oral specializations and ventral oral specializations may well have evolved from a single *Tracheloraphis*-like ancestral stock. In the first instance, the anteriormost kinetid paratene would have become specialized for raptorial feeding from a dome-like configuration. Some extant *Tracheloraphis* species possess that kind of oral architecture, with a demonstrable 'coronne ciliaire' of oral dikinetids (e.g., see the description of *T. teissleri* in Dragesco, 1960, 1969). Observations on living species feeding prostomially have been made by but two observers, to my knowledge. Fenchel (1968) describes the process very briefly; and Spoon (personal communication) states that he has observed it, too, when some of these organisms have been feeding on small scuticociliates. Spoon's samples were taken directly from the living coral reef exhibit tanks at the Smithsonian Institution's National Museum of Natural History in Washington, D.C.

Ciliated ventral oral structures could have evolved from the glabrous stripe region of a *Tracheloraphis*-like ancestral stock, in the second instance, Protargol-stained preparations of local *Tracheloraphis* species confirm Dragesco's earlier observations that kinetosomes barren of both cilia and the microtubular postciliodesmata are to be found on both sides of the zone. In an evolutionary sense, these kinetosomes could well have given rise to the oral di- and polykinetid configurations that are found in those ciliates bearing nongymnostomatous ventral cytostomes and oral ciliature and

infraciliature. This kind of regional oral differentiation would have thus produced the recognizable ventral cytostomy so characteristic of geleid and loxodid karyorelicteans. The striking ultrastructural similarity noted by Nouzarède (1977) between the ventral polymerized, densely packed serial paracytostomal monokinetids of *Avela* and *Gelia* and the serial, adoral polykinetids of heterotrichine heterotrichs further supports this contention. The left and right specialized oral dikinetids of *Loxodes* and *Remanella*, two other genera of karyorelicteans with ventral cytostomes, would lend additional support for his contention. A corollary of Lynn's (1976) structural conservatism hypothesis could be that, since dikinetids are less polymerized, less specialized than polykinetids, free-living ciliates possessing only oral dikinetids are primitive. Likewise, ciliates possessing no oral kinetid specialized structural organization would be even more primitive and thereby represent the most likely primitive stock, provided, of course, that the nonoral cortical structures were homologous and the nuclear features were homologues, as indeed they all are in karyorelicteans.

Again, *Tracheloraphis* appears to be primitive since species in the genus that have been thus far examined ultrastructurally by Raikov have no oral kinetid specialization (Raikov, personal communication with respect especially to *T. Dogieli*). In my opinion, this appears to be a truly gymnostomatous (naked mouth) condition: the total absence of orally specialized kinetids and ciliation.

The predecessor to the *Tracheloraphis-Trachelonema* prostomial and ventrostomial ciliate-like types may have been *Kentrophoros*-like. As Orias (1976) suggested, this would be a simple flat flan, ciliated on one surface only, with ingestion taking place on the nonciliated surface by membrane infolding. Contrary to Orias' point of view, however, I suggest that the next step in the sequence would not be the coiling or closing up (as is exhibited by *Kentrophoros fistulosum*: see Raikov, 1973a) of the nonciliated surface so that it becomes internal. In my view, *K. fistulosum* is a specialized form, since many other *Kentrophoros* species are known that also feed by presumed pseudopodial engulfment but do not coil up. Fenchel (1968) alludes to one species, found in Danish sands, that contained diatom tests. The transitional state, from a flat ribbon-like form to one that is cylindrical in cross-section, is rather to be found in a *Tracheloraphis*-like form in which the glabrous area might be considered homologous to the nonciliated surface of *Kentrophoros* and/or *Kentrophoros*-like forms. The tubular shape of *Tracheloraphis*-like species could be accounted for by increase in cell volume concomitant with increased numbers of somatic kinetid units that are aligned into kineties in such a way that the kinetid organization gradually expands to enclose an ever-increasing amount of nonciliated, glabrous cortex. Again, within the known species of the genus *Tracheloraphis*, evidence is found to support this idea:

(1) Some species with relatively low kinety numbers possess glabrous stripes that are broad, whereas other species with relatively high kinety numbers possess glabrous stripes that are relatively narrow.

(2) Branching kineties are known for at least one species (*T. striatus* Raikov, 1962). On transverse division, these incomplete kineties could become complete, thereby giving rise to progeny with an increased number of kineties.

(3) Some *Tracheloraphis* species have incomplete kineties to the left of the glabrous stripe (if the glabrous stripe, a feeding surface, can be considered ventral, rather than dorsal). Here again the numbers of kineties could increase with each transverse division that first bisected preexistent partial kineties, which were then left to replicate additional kinetids after division. Since karyorelicteans are known to recover remarkably from merotomy caused by the grinding action of sand grains in their habitats, it is certainly likely that kinetidal replications do occur with or without nuclear divisions; well recognized cortical patterns are always reproduced or reconstituted following such damage.

The next stage in this phylogenetic sequence would be to 'zipper up', or have the kineties come together in the region just posterior to or as a part of the slightly bulbous anterior end. This morphological picture is seen, though only in the genus *Tracheloraphis*. Complete absence of a glabrous stripe is found solely in the genus *Trachelocerca*, and all of the species described for this genus are exclusively prostomial feeders. If one turns to examine other *Tracheloraphis* species, however, the intermediate condition can be noted. In some of these forms (e.g., *T. prenanti* Dragesco, 1960, and *T. remanei* Dragesco, 1960), the anterior 'neck region' does not contain a glabrous zone but is closed by the encircling kineties.

3. Postulated Sequence of Stages

Stage 1(a). The advent of multiple kinetids in more than one kinety (see Figure 1). A single-kinety protist is not to be found in the ciliates, and one could assume that a multiple-kinetid single kinety must have originated in a flagellate ancestor. Certainly a flagellate with a highly organized cortex like that found in *Colponema loxodes* (Mignot and Brugerolle, 1976), but with nuclear endomitosis, might provide the ancestral type. Or, a simple unarmored gymnodinioid flagellate with an endomitotic nuclear apparatus is equally appealing. Replication of the nonapical kinetid in the absence of karyokinesis and cytokinesis could then give rise to a form similar to species of

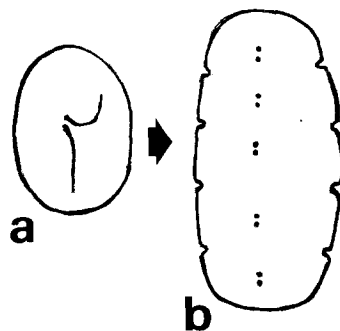


Fig. 1. The possible evolution of a single kinety with multiple paired-kinetosome kinetids from a single kinetid-bearing organism by means of kinetid replication in the absence of karyokinesis and cytokinesis.

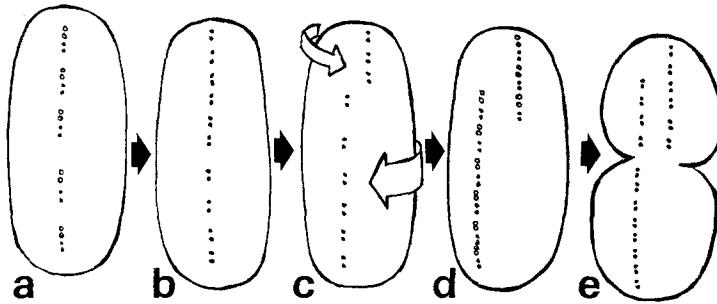


Fig. 2. A sequence of minimal steps by which an organism with but one kinetid could become multikinetid. a. Replication. b. Torsion and fragmentation of the kinetid. c. Further replication within each kinetal fragment. d. Perkinetal cytokinesis. e. Resultant filial cell separation in which the proter bears two kinetids.

Polykrikos extant today, again with eukaryotic nuclei and endomitoses. It is interesting to note the recently published observations by Raikhel *et al.* (1981) that *Stentor*, a heterotrich in the subphylum Postciliodesmatophora of Small and Lynn (1981), has its nuclear, mitotic microtubules external to the nuclear envelope during division, thereby resembling the condition in the dividing nuclei of dinoflagellates more than it resembles the endomitosis of most other ciliates. Another important reason for selecting this hypothetical original flagellate ancestry would be that the cytokinetic fission plane would divide the cell transversally, through the replicated kinetid(s), as indeed the process occurs in extant dinoflagellates today.

State 1(b). Replication of one kinetid to form multiple kinetids (see Figure 2). It is known, but little recognized, in cloned ciliates studied in mass culture, that frequently unequal torsion of the anterior end of a cell (Figure 2b) may produce a spatial disjunction between the two previously connected ends of a single kinetid. These kinetal fragments with their kinetids may continue to replicate kinetosomes (Figure 2c), so that by the next cell division (Figure 2d) the anterior division product (the proter) could then possess one kinetid and a second kinetal fragment. If the fragment continued to replicate kinetids in the absence of all division, the ultimate outcome of this sequence of

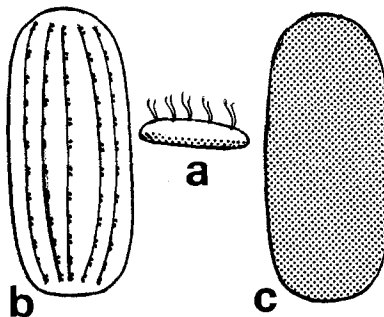


Fig. 3. The flat flange stage. a. Hypothetical cross-section in which the ingestory surface (stippled) is separate from the kinety-bearing surface. b. Kinety-bearing surface. c. Ingestory surface (stippled).

events would be the uneven production of multiple kineties in at least one fission product (Figure 2e). Ciliates, like the flagellate *Polykrikos*, replicate their kinetids within the kinety, and the fission plane is perkinetal in this type of transverse or oblique division.

Stage 2. The flan condition of the Orias (1976) hypothesis (see Figure 3). Continued fragmentation of a few kineties into even more numerous kinetal fragments, coupled with continued replication of the kinetids within the fragments as shown in Stage 1 (d), could result in a flan-like organism that could have been the original *Kentrophoros*-like organism. Such an organism – to be a ciliate – would have had to meet several conditions. Firstly, this organism would have had to have a ciliate kinetid like all other ciliates, and in this primitive condition the kinetosomes would be paired within the kinetid (see Lynn, 1981; Lynn and Small, 1981; and Small and Lynn, 1981, on this point). Secondly, like *Colponema loxodes*, there would be phagocytosis of particulate food from a nonkinetidal surface, as ingestion does occur in known extant *Kentrophoros* species (Figure 3c). Thirdly, the number of kineties would be necessarily few, as is the case for extant *Kentrophoros* and *Trachelonema* species studied in recent years (see Figures 2a and 2b). No examples are known for *Kentrophoros* or *Trachelonema* with more than six kineties. Fourthly, as one finds in *Kentrophoros*, directionality of cell movement in this simple organism is determined by the way it moves and not by where its ‘mouth’ is. Direction of movement is again linked to the anterior-posterior orientation of the kinetids and not to a positional relationship with the oral area. Lastly, the nonkinetidal surface, the oral area that extends the length of the nonciliated cell surface, could be considered homologous to the glabrous region of *Trachelonema* and the more confined glabrous stripe of *Tracheloraphis*.

Stage 3. The *Tracheloraphis*-like stage: expansion of cell volume with increased cell biomass and increased numbers of kineties (see Figures 4a and 4b). In an evolutionary sense, a *Tracheloraphis*-like ancestral organism would have been the next step in this sequence, since at this stage one might expect to see organisms with increasing numbers of kineties. Such increased kinetal numbers could have resulted in the ribbon-flan-shaped cells becoming increasingly rounded, with the flan ingestatory surface remaining from anterior to posterior. Such *Tracheloraphis* species exist, and this morphological pattern was the very reason for Dragesco’s (1960) creation of the genus *Tracheloraphis*. Again, Lenk *et al.* (1984) have observed macrophagous ingestion through this glabrous zone in several species of *Tracheloraphis*.

Stage 4. Closure of the *Tracheloraphis* glabrous stripe (see Figure 4c). Continued kinetid proliferation and increasing kinety numbers in the now *Tracheloraphis*-like tubular-body organization could, by simple constriction of the anterior region, result in two separate glabrous ‘oral’ areas at this stage: one would thus be anterior and prostomial and the other ‘ventral’ and more posterior. Again, this condition is seen in some of the known species of the genus *Tracheloraphis*. The curious apical cortical cleft, always in line with the more posteriorly separated and now ventral glabrous region, lends support to this glabrous zone closure idea (see Figures 4c, 5a and b, 5f and h).

Stage 5. Further closure of either the anterior or ventral glabrous regions so that

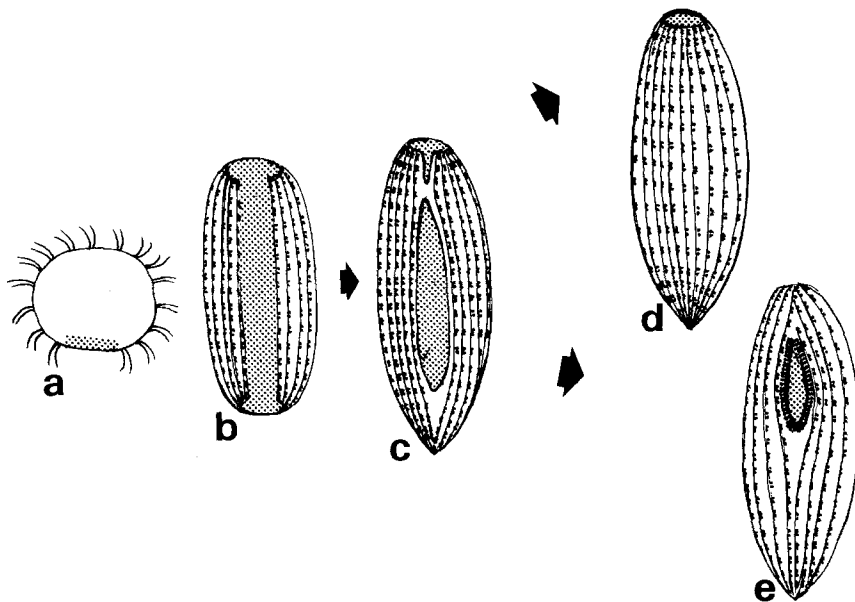


Fig. 4. The sequential steps involved in the transition from a *Tracheloraphis*-like stage to the prostomial and ventrostomial forms of more structurally complex karyorelicteans. a. A hypothetical cross-section of a *Tracheloraphis*-like form. b. A longitudinal view of a *Tracheloraphis*-like form with a continuous glabrous stripe from anterior to posterior. c. A longitudinal view of a *Tracheloraphis*-like form with a constriction of the stripe into two regions. d. A ciliate with only a prostomial ingestatory area (stippled) in which dikinetids surround the ingestatory area. e. A ciliate with only a ventrostomial ingestatory area (stippled) in which dikinetids surround the ingestatory area.

prostomial and ventrostomial ciliate stocks result (see Figures 4d and 4e). At this stage, if only the anterior glabrous region were to remain, a *prostomial* form would result. Such a condition exists in species of *Trachelocerca* (Dragesco, 1960; and see Figure 4d). Such anterior oral organization patterns of *Trachelocerca* (Figure 5l, m, and n) are perhaps not that basically different from the anterior prostomial regions of some *Tracheloraphis* forms, in which closure of the glabrous stripe within the neck region has also resulted in the apparent evolution of anterior oral specialization (see Figure 5j and k). Other *Tracheloraphis* species possess domed-like oral areas (Figures 5c, e, and h) reminiscent of the *Trachelocerca* of Figure 5m. Perhaps these are the *Tracheloraphis* and *Trachelocerca* species, noted by other authors, which feed raptorially, as do haptorid domed ciliates such as *Didinium*, *Chaenea*, and *Lacrymaria* (to mention just a few). Unfortunately, for most karyorelictean forms no ultrastructure studies have yet been carried out that would permit comparisons of their domed condition with that of the litostomial rhabdophoran species. If complete closure of the anteriormost region of this tubular *Tracheloraphis*-like primitive stock occurred, a ciliate with a *ventral* oral area would be the result (see Figure 4e). Coincident with this closure, the evolution or differentiation of specialized oral kinetids could have evolved.

Known representatives with ventral oral architecture are represented by several

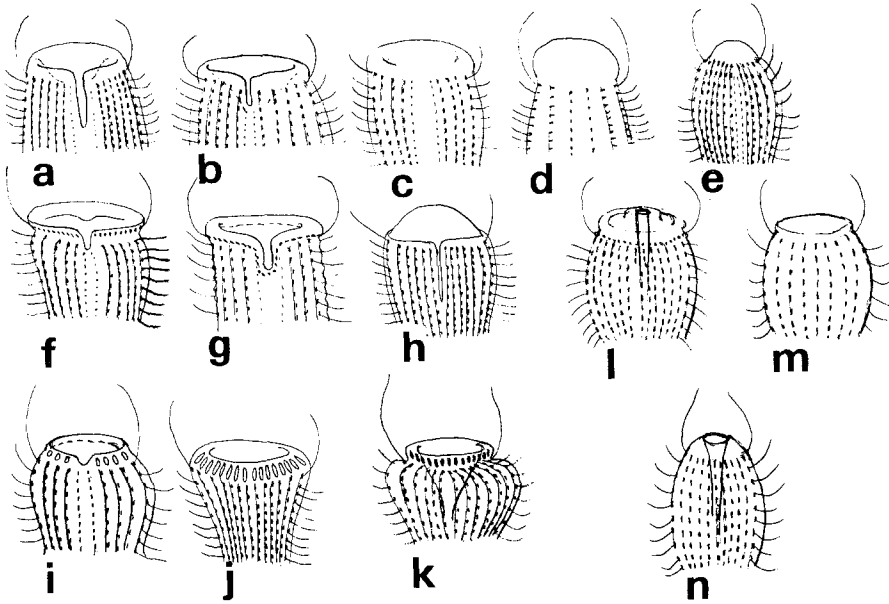


Fig. 5. The anterior ends of some *Tracheloraphis* and *Trachelocerca* species illustrating some of the diversity in presumed 'oral' morphology. a.-k., *Tracheloraphis* spp.; l.-n., *Trachelocerca* spp. a. *T. dogieli* (after Dragesco, 1963). b. *T. margaritaceus* (after Dragesco and Raikov, 1966). c. *T. prenanti* (after Dragesco, 1960). d. *T. bodiani* (after Dragesco, 1963). e. *T. stephani* (after Dragesco, 1965). f. *T. hyalinum* (after Dragesco, 1960). g. *T. teisserieri* (after Dragesco, 1963). h. *T. phoenicopterus* (after Raikov and Kovaleva, 1978). i. *T. remanei* (after Dragesco, 1960). j. *T. incaudatus* (after Dragesco, 1960). k. *T. swedmarki* (after Dragesco, 1960). l. *Trachelocerca entzi* (after Dragesco, 1960). m. *T. binucleata* and n. *T. lacrylmariae* (after Dragesco, 1960) m. The oral cleft, visible in Figures a, b, c, f, g, h, and i, always appears anterior to the glabrous stripe. Some species in both genera lack the cleft. A presumably domed oral configuration can be seen in both *Tracheloraphis* spp. d, e, and h, and in *Trachelocerca* sp. m. Likewise, a prostomial cytostome-cytopharynx is observable in *Tracheloraphis* sp. k and *Trachelocerca* spp. l and n. These arrays of prostomial morphology suggest to the author that the prostomial ciliates shared a common ancestry with these karyorelicteans.

genera of karyorelicteans, each of which can be characterized, in part at least, by its oral kinetal morphology. See Figures 6a and b of *Loxodes* and *Cryptopharynx*, respectively; both have oral dikinetids adjacent to or bordering the oral regions. Curiously, in these two genera, oral dikinetids are to be found in the area that one would think of as the cytopharynx, an internal cell surface. The structural, functional, and developmental significance of this type of cytopharyngeal kinetid remains unknown. Other karyorelictean genera with multiple-kinetosome kinetids to the right, left, anterior, or posterior in position with respect to the cell 'mouth' are illustrated in Figures 6c, d, and e. Figure 6c is a figure of a *Remanella* species with polykinetids to the left and a serial oral dikinetid to the right of and anterior to the cytostome; this is morphologically similar to the oral architecture of *Loxodes*, as illustrated in Figure 6a. Figure 6d is a figure of the oral region of a species of *Protocruzia* with six preoral serial polykinetids and a paroral, right dikinetid.

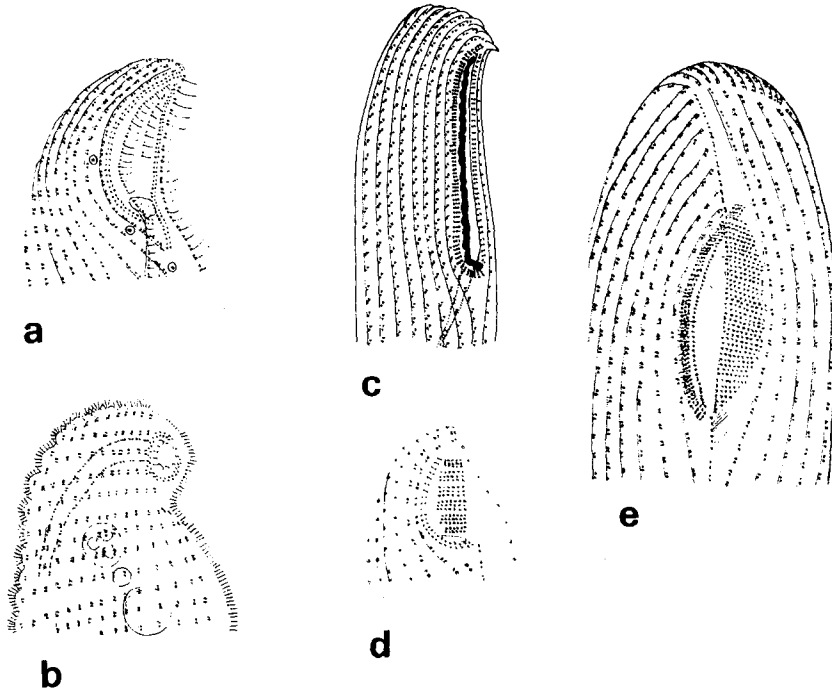


Fig. 6. Examples of karyorelictean ciliates with ventral oral configurations: a. *Loxodes vorax*, multiple and oral dikinetid both to the left and to the right, preoral and endoral kinetal fragments. b. *Cryptopharynx* sp., perioral and endoral kinetal fragments. c. *Remanella* sp. Right side, single oral polykinetid; left side, single oral dikinetid segment. d. *Protocruzia* sp., six preoral serial polykinetids, right oral dikinetid, and single postoral dikinetid kinetosomal pair. e. A geleiid sp., right side, oral monokinetid and polykinetid; left side, single oral polykinetid. Note the absence of postciliodesmata from pre- and post-oral 'somatic' kinetids and the presence of presumed nematodesmata underlying the right oral polykinetid and the postoral 'somatic' dikinetal fragment.

Figure 6e is a figure of a species of a new geleiid genus found in the Chesapeake Bay estuary. Like species of other geleiid genera, it possesses polykinetids to the right and to the left of the ventral oral region. Preliminary observations on the feeding behavior of live organisms of this new form and related *Geleia* species (see Lenk and Small, 1983) have shown that these ciliates can and do actively ingest large cooked egg yolk particles through this oral region, in a manner quite similar to the ingestion of the same foodstuff, through the glabrous stripe in species of *Tracheloraphis* (Lenk *et al.*, 1984). The difference between the two forms is the confinement of the area in the former and the addition of oral ciliature in the latter. These observations are noteworthy in light of the ultrastructural similarity noted by Nouzarède (1977) between the left oral single polykinetid of *Geleia* and *Avela* and the multiple oral polykinetids of heterotrichine heterotrichs. The actual feeding mechanisms, however, do not appear to be the same. Clearly an additional evolutionary morphological step was taken in the evolution of heterotrich spirotricheans from geleiid proheterotrichid karyorelicteans, both considered subgroups of the subphylum Postciliodesmatophora (Small and Lynn, 1981, 1983).

4. Conclusion

An account of how two basically dissimilar oral morphological strategies might have evolved within a karyorelictean ancestry from a single karyorelictean stock of flan-like ciliates has been presented. Supporting the overall idea is our laboratory observation of macrophagous particle-ingestion by a ventral nonciliated region, the glabrous stripe, in species of *Tracheloraphis*. The present hypothesis of ciliate evolution, while utilizing the flan condition, a term and concept suggested by Orias (1976), differs from that worker's by not considering the 'rolling up' process of a few *Kentrophoros* species as crucial to the entire evolutionary sequence. Rather, the more generalized body plans of extant karyorelicteans are here considered to reflect the early evolutionary process by which both prostomial and ventrostomial cytoarchitectures could have evolved within the Karyorelictea.

Beyond the subphylum Postciliodesmatophora, two other subphyla (ranks accorded by Small and Lynn, 1981, 1983) are to be found: the Rhabdophora, with essentially prostomial cytoarchitectural morphologies; and the Cyrtophora, with essentially ventrostomial cytoarchitectural morphologies. Both of these subphyla could have evolved their oral apparatus, as well as their complex nuclear conditions, from a single karyorelictean stem group. A remaining challenge is to find a rational explanation for the transition to the more structurally conservative somatic kinetid states of the six ciliate classes (two rhabdophoran and four cyrtophoran) of these two subphyla. It is possible that continued ultrastructural analyses of both cortical and oral morphologies of the diverse karyorelictean species may supply answers to these intriguing unresolved questions as well as answers to questions that have not yet been imagined.

Ciliate 'oralness', as overwhelmingly diversified as it first appears to the student of the Ciliophora, can possibly be explained, then, as having originated from within a karyorelictean ancestral group. I have postulated that this stem group was initially gymnostomatous and that it preceded kintal elaboration and differentiation to evolve into the two major oral lineages recognized today within the total ciliate assemblage. These two lineages, prostomial and ventrostomial, have extant examples in both karyorelictean and nonkaryorelictean taxa.

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