

REVIEW

Feeding ecology of free-living aquatic nematodes

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ABSTRACT: The buccal cavity structure of free-living aquatic nematodes indicates 4 feeding groups: deposit feeders, epistrate feeders, scavengers and predators. This is in contrast to a previous classification which united omnivores and predators and separated deposit feeders into selective and non-selective groups. The new classification shows that the previous view that heavy predator pressure plays a major role in the structuring of meiobenthic communities has been much overemphasized. Most predatory species in the previous classification are herein recognized as 'garbage collectors', i.e. species with scavenging feeding habits. The actual feeding behaviour of epistrate-feeding species shows that they are able to break open cell membranes of food items in the buccal cavity and suck out the cell contents (juice feeders), in contrast to deposit-feeding species which swallow the whole food item (particulate feeders), indicating different sets of digestive enzymes. Buccal cavity morphology within predators indicates 2 feeding types. Trans-epidermal uptake of dissolved organic matter is suggested as an additional food supply for thiotrophic species (mainly deposit feeders), hence indicating mixotrophy. Size, shape, quality and quantity of food items may to some extent explain coexistence of congeners. Nematode mobility and mucus release may attract potential food or keep food sources in optimal condition, i.e. gardening.

INTRODUCTION

Studies on food and feeding in free-living aquatic nematodes were in the past approached by various methods all concerned with oral feeding. Wieser (1953) classified nematode feeding groups and types according to their buccal cavity structure, i.e. small vs large, and armed with teeth vs unarmed. Results of this analysis on dead animals showed that (1) nematodes have extremely diversified structures related to food ingestion and obviously adapted to a diversified spectrum of food items, and (2) factors other than buccal cavity morphology must operate in order to explain the co-existence of congeneric species. Tietjen and co-workers and Schiemer (reviews in Alongi & Tietjen 1980, Schiemer 1984) approached nematode feeding through experiments including both quantitative and qualitative aspects. These findings confirmed Wieser's hypothesis that nematodes are highly selective with respect to size, shape and quality of food offered. Selective digestion, i.e. selective enzymatic activity, was shown by Jennings & Colam (1970) and Jennings & Deutsch (1975). Deutsch (1978) and Nuss (1985)

showed morphological and histochemical differences in the intestinal cells related to food absorption in a variety of nematodes. Trans-epidermal uptake of dissolved organic matter (DOM: mainly sugars and amino acids) has not yet been shown in free-living aquatic nematodes but has been suggested by Jensen (1986) as an additional food supply in thiotrophic species because of their relatively larger body surface. Finally, there is also some evidence that the considerable mobility of some nematodes (Meyers et al. 1970, Cullen 1973, Warwick 1981) and their release of organic matter (Riemann & Schrage 1978, Bongers 1983) may attract bacteria and other microbes and maintain them in optimal condition, i.e. gardening. The present paper reviews these findings which are discussed in terms of feeding groups and types, and resource partitioning.

FEEDING GROUPS AND TYPES

From lateral views of the buccal cavity of fixed specimens Wieser (1953) divided marine nematodes into 4 trophic groups: (1A) selective deposit feeders;

(1B) non-selective deposit feeders (both groups encompassing species without teeth, and with small and large buccal cavities, respectively); (2A) epistrate feeders; (2B) omnivore-predators. This classification has been widely used since then and adjusted in subsequent years (e.g. Wieser 1960, Wieser & Kanwisher 1961, Boucher 1973, Platt 1977). Romeyn & Bouwman (1983) as well as Bouwman et al. (1984) even go so far as to include the cephalic setation as an additional

character of importance in nematode feeding strategy; however, no convincing evidence supports such an inclusion. The arbitrary subdivision of deposit feeders was rejected by Jensen (1986) both because experimental evidence is lacking and because the range of sizes of mouth openings and buccal cavities is as large in other feeding groups as in deposit feeders (Fig. 1).

The present classification separates 4 feeding groups of species concerned with oral feeding. Deposit and

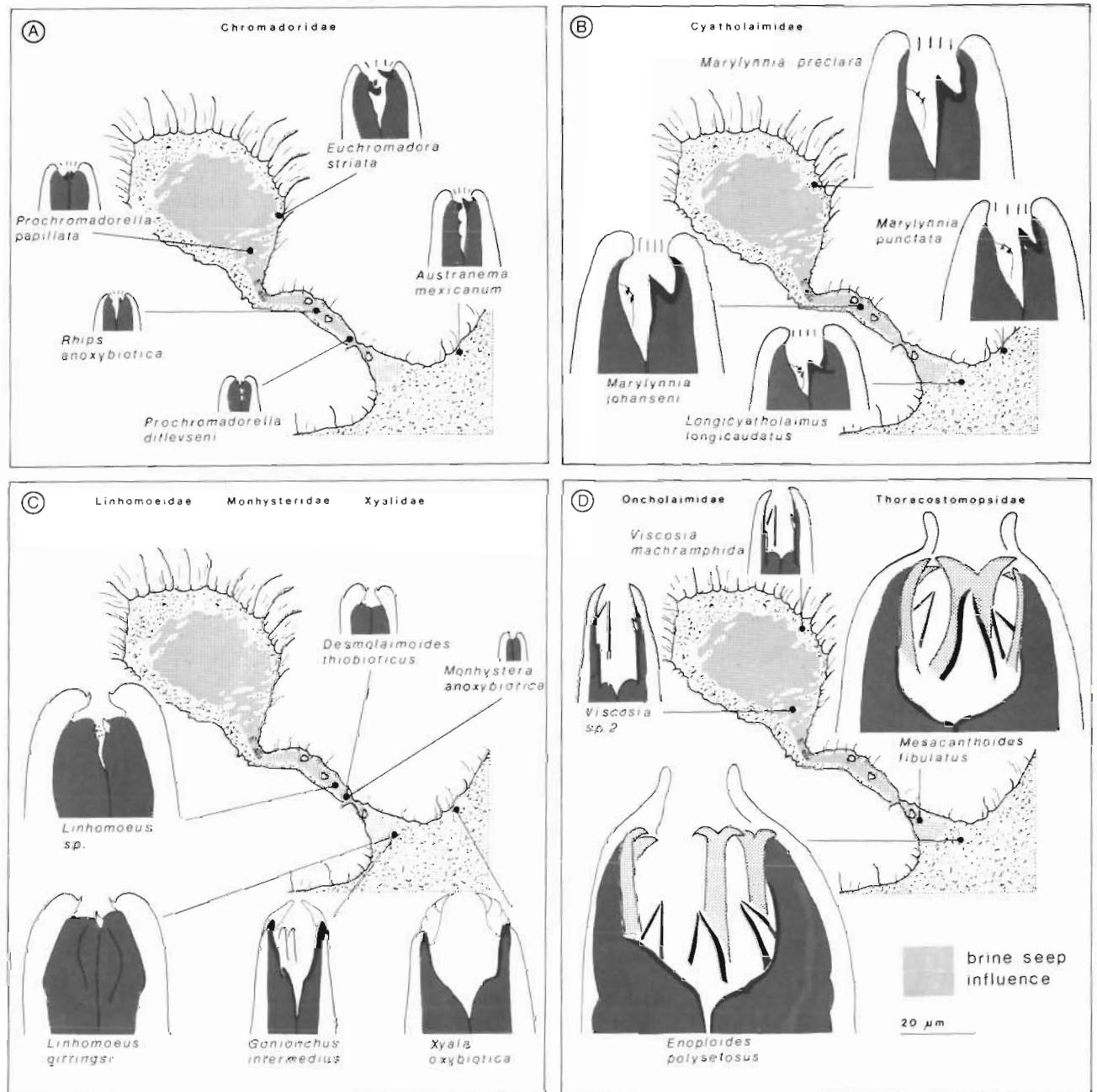


Fig. 1. Location of population maxima, and buccal cavity structure, of most abundant nematodes along an almost 100 m long horizontal brine seep gradient in the East Flower Garden, NW Gulf of Mexico, at 70 m depth shown as feeding groups. (A,B) Epistrate feeders. (C) Deposit feeders. (D) Scavengers (Oncholaimidae) and predators (Thoracostomopsidae). Classified into their systematic relationships. All figures are drawn to the same scale in left lateral view. Adapted from Jensen (1986)

epistrate feeders are distinguished as 2 feeding groups by the absence or presence of a tooth in the buccal cavity, respectively. Consequently, the 2 groups include different feeding types but may exploit the same food source. A third group of species is recognized as scavengers, united by the presence of an onchium (tooth-like structure) in the buccal cavity penetrated by a duct through which the contents of a salivary gland cell empty. Scavengers lack mandibles, claws and articulating plates in the buccal cavity which characterize the fourth group, predators. Finally, trans-epidermal uptake of DOM is likely a significant feeding habit of thiobiotic species (deposit and epistrate feeders), indicating mixotrophy.

Deposit feeders and epistrate feeders

Few publications exist on the feeding habits of free-living aquatic nematodes. However, 3 diatom-feeding types are known. *Chromadorita tenuis* (epistrate feeder) brings the diatom into the buccal cavity (Fig. 2). The 2 valves of the diatom are opened by damaging the girdle with the dorsal tooth and the contents passed to the intestine, where they are found as liquid with lipid droplets (Fig. 3C, D). The empty frustule is then discarded (Fig. 2). The presence of a buccal apparatus in the intestine of a chromadorid should not be taken as an indication of cannibalism as suggested by Allgén (1927) since it may be retained from the preceding developmental stage (Jensen 1983a). *Eudiplogaster pararmatus* (epistrate feeder) holds the diatom firmly with the lips. It apparently punctures the frustule and swallows the cell contents. The empty frustule is dis-

carded (Romeyn et al. 1983). *Daptonema biggi* (deposit feeder) swallows the whole diatom (Jensen 1979). Romeyn & Bouwman (1983) give further examples of species feeding, e.g. *C. guidoschneideri* handles a diatom in the same way as *C. tenuis* does. However, they termed *C. guidoschneideri* a 'cracker' because of the way it breaks the diatom with its teeth. *Linhomoeus gittingsi* (deposit feeder) feeding on the sulphide-oxidizing bacteria *Beggiatoa* spp. was suggested by Jensen (1986) to ingest/suck the bacteria into the intestine like spaghetti. A similar observation was made on a small *Monhystera* species (deposit feeder) ingesting living blue-green bacteria *Oscillatoria okeni* (Fig. 3A, B) isolated from *Potamogeton perfoliatus* in the Finnish archipelago.

Deposit feeders and epistrate feeders thus influence microbial densities directly by their grazing on bacteria, fungi and unicellular algae. The considerable mobility of the high numbers of nematodes in microbial loci (Meyers et al. 1970, Jensen 1986), the expansion by their burrows of sites for microbial activities (Cullen 1973, Warwick 1981), their continuous mucus secretion (Riemann & Schrage 1978, Bongers 1983) and evidence that nematodes may contribute to nutritional recycling (Tietjen 1980) strongly indicate that they maintain microbial populations near exponential state of growth. This is known from the influence of protozoan activities (e.g. Fenchel 1970, Barsdate et al. 1974, Fenchel & Harrison 1976) and more recent evidence with nematodes (Tenore et al. 1977, Gerlach 1978, Bonni & Mitchell 1980, Findlay & Tenore 1982, Pamatmat & Findlay 1983). The quantity and quality of the nematode's food is thereby maximized; this is gardening in its broadest sense, including the effects of intensified grazing.

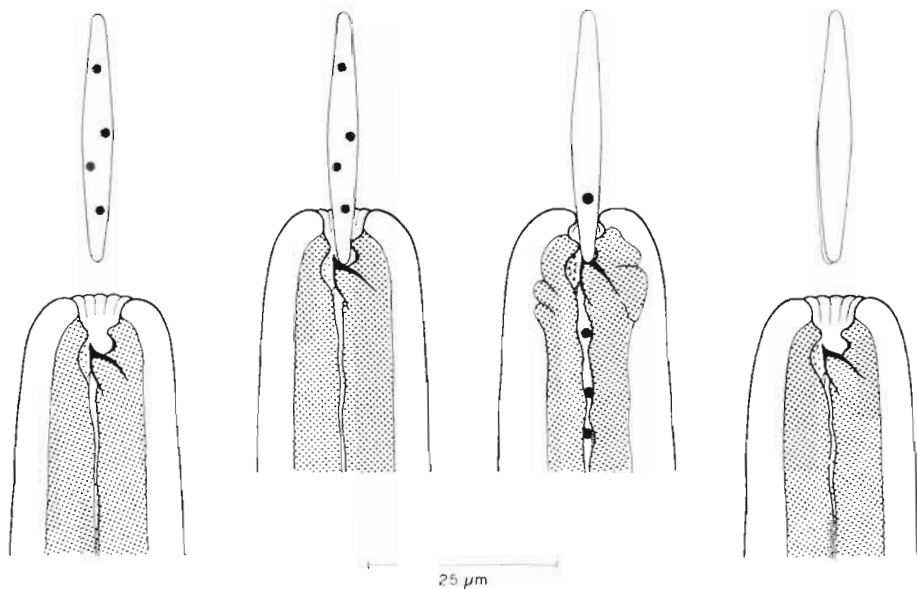
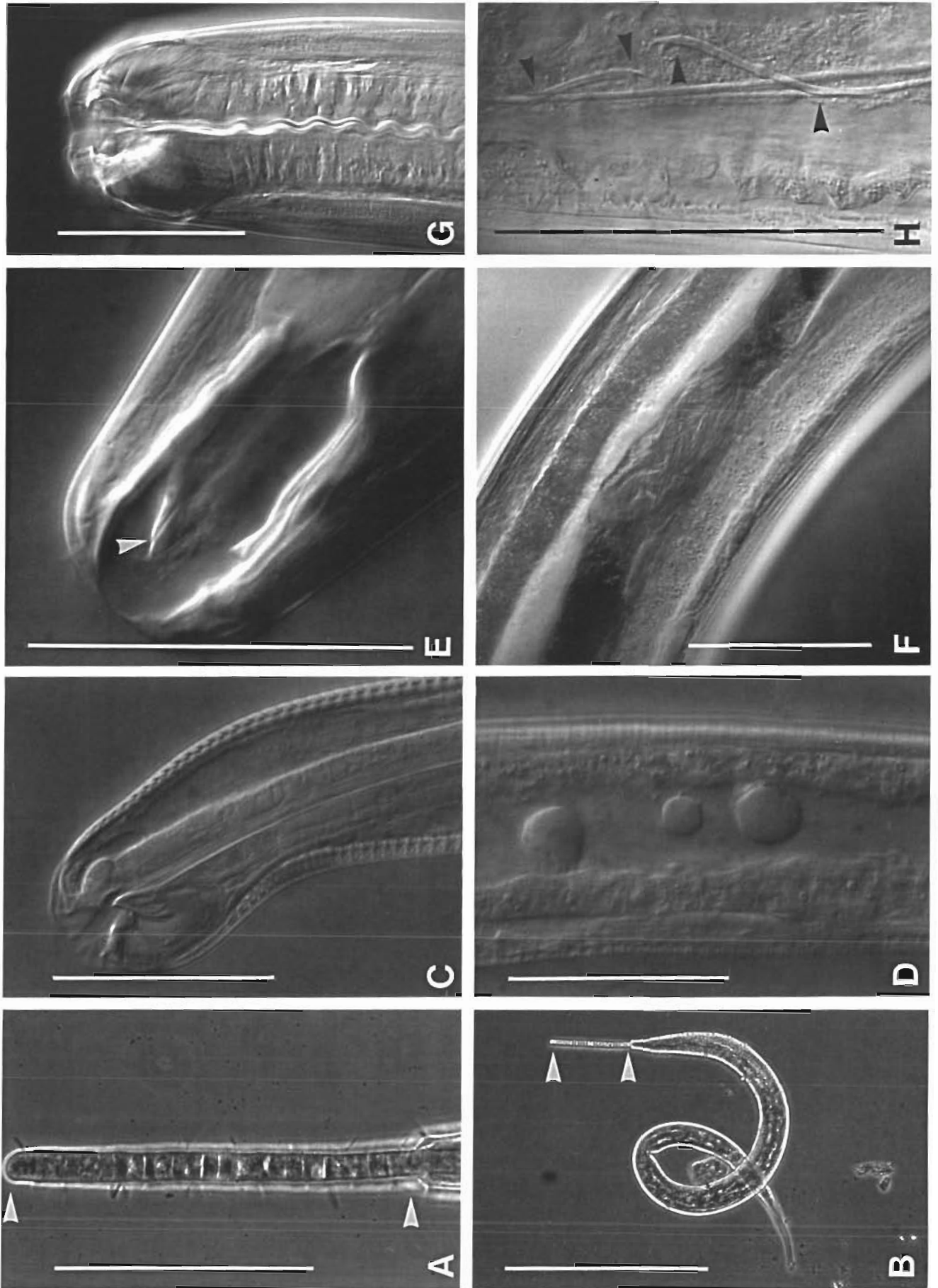


Fig. 2. *Chromadorita tenuis*. Sequence of events when the nematode feeds on the pennate diatom *Nitzschia palea* var. *debilis*. Adapted from Jensen (1982)



Predators

Wieser's Group 2B (omnivore-predators) includes, firstly, predators which catch their living prey by protrusible claws or mandibles (Thoracostomopsidae, Enoplidae, Selachinematidae; Fig. 1D & 3G, H); and those which catch the prey with widely open mouth (Sphaerolaimidae), macerating it in the buccal cavity by means of articulating plates or other sclerotizations. Secretions from oesophageal salivary gland cells begin to digest the prey even before it is swallowed, although it may be found in the intestine still in an identifiable shape. Some adult Selachinematidae species lack an anus (Gourbault & Vincx 1985) indicating a different digestion capacity as compared to Thoracostomopsidae and Enoplidae which have an anus throughout life.

Scavengers

The remainder of Wieser's Group 2B are the omnivores, previously classified with the predator group (Wieser 1953). The taxa of numerical importance (both in terms of species richness and abundance) are Oncholaimidae and Enchelidiidae. Wieser's assumption that these are predator species is based on an analogous type of buccal cavity found in the terrestrial mononchs (Mononchidae), which have a voluminous and sclerotized buccal cavity with one or more teeth and denticles. Adult mononchs are known to feed on a large range of living animals (e.g. Thorne 1927, Nielsen 1949, also confirmed in a more recent study, Grootaert & Maertens 1976). The predatory similitude is indeed apparent at low magnification and from many drawings of species concerned. However, the tooth (teeth) in mononchs is solid and not penetrated by a duct (Baqri & Baqri 1983) whereas the large subventral 'tooth' ('teeth') in oncholaimids and enchelidiids is penetrated by a duct emptying subterminally (Fig. 3E). Jennings & Colam (1970) suggested that the secretions through the ducts penetrating the 2 subventral 'teeth' in *Pontonema vulgare* yield an active enzyme (esterase) when mixed on discharge.

Results of feeding experiments by Thun (1968) and Romeyn & Bouwman (1983) on *Adoncholaimus*

thalassophygas apparently support Wieser's opinion on this species' feeding group and feeding type. They also reported that the buccal cavity is slightly expanded when the prey is swallowed; the prey is punctured by the 'tooth' and its contents sucked out (cf. illustrations in Thun 1968, reproduced in Remmert 1980, Romeyn 1980). Heip et al. (1978) offered live nematodes *Panagrellus redivivus* to *Oncholaimus oxyuris* and concluded that *O. oxyuris* is a predator. However, younger juveniles apparently could not survive on the nematode as prey, but were raised on agar inoculated with bacteria and algae. Moreover, the culture of the older juveniles and adults did not thrive well, probably because manipulations with the fast-growing prey had to be done regularly in order to maintain the cultures (Heip et al. 1978, p. 255–256).

Coomans & Heyns' (1983) analysis of the action of the buccal cavity of *Oncholaimus sahariensis* upon food disagrees with those of Thun (1968) and Romeyn & Bouwman (1983). Coomans & Heyns concluded that when labial muscles – inserting on the labial cuticle and on the walls of the buccal cavity – are contracted, they pull the lips backwards and bring the buccal capsule and tooth forward. However, it seems doubtful whether this action would bring the tooth out of the mouth opening to touch the food item (cf. illustration by Lorenzen 1969 on fixed specimens of the enchelidiid *Calyptonema maxweberi*). My observations from sublateral and subventral views of the buccal cavity of e.g. *Adoncholaimus thalassophygas* (cited in Romeyn 1980), strongly indicate that the walls consist of at least 2 compartments and a sclerotization at the bottom. The posterior portion harbours the subventral 'tooth' (onchium) which I interpret as a sclerotization of the outlet of the salivary gland cell. The 'tooth' is firmly anchored in the oesophageal musculature. The anterior portion is surrounded by a thin sheet of musculature usually not depicted in the literature. The actions of the buccal cavity could be described in the following simplified sequence: (1) detection of released DOM from the food item; (2) transverse expansion of the anterior portion of the buccal cavity; (3) contraction of the oesophageal musculature whereby 2 events are induced: (i) the walls of posterior portion of the buccal cavity glide telescopically along the inner side of the anterior portion so that the 'tooth' reaches outside the mouth opening, and (ii) at the same time the salivary gland cell contents empty and are injected into the food through the hollow 'tooth'; (4) the posterior portion glides backwards inducing a vacuum causing the buccal cavity to be filled with food which is passed into the oesophageal lumen (Fig. 3E, F).

The above hypothesis on the feeding habits and structure of the buccal cavity of oncholaimid and

Fig. 3. Buccal cavity structures and gut contents of 4 nematode feeding groups. (A, B) *Monhystera* sp. (deposit feeder) ingesting a blue-green bacteria *Oscillatoria okeni* (arrows). (C, D) *Chromadorita tenuis* (epistrate feeder): (C) buccal cavity; (D) cell juice including lipid droplets in intestine. (E, F) *Adoncholaimus thalassophygas* (scavenger): (E) buccal cavity showing 'tooth' penetrated by a duct (arrow); (F) gut contents. (G, H) *Enoplus brevis* (predator): (G) buccal cavity; (H) setae (arrows) of Naiididae (Oligochaeta) in intestine. (C, D) from Jensen (1982); others originals. Scale bars:

B = 100 μ m; others = 25 μ m

enchelidiid nematodes is testable through TEM and histological-biochemical studies of the cuticularization of the buccal cavity as well as by chemical analysis of salivary secretions. It is supported by the conclusions of Meyers & Hopper (1973), Riemann & Schrage (1978) and Lopez et al. (1979) that the behaviour of the different oncholaimids studied did not reveal a predatory feeding strategy at all. The oncholaimids were attracted to organic matter in decaying plant material, showed gliding movements along e.g. cotton fibres, and released high amounts of mucus, agglutinating detritus particles from the surroundings. Also *Pon-tonema vulgare* were attracted to a dead shrimp which was ingested within a few hours (Rasmussen 1973, p. 54). A rather similar observation was made by Vran-ken (in Heip et al. 1985, p. 461) of *Oncholaimus oxy-uris* accumulating and feeding on dead gastropods *Hydrobia ulvae*. The Danish biological consultant-firm Marin Idé provided me in 1981 with 0.25 l jar almost filled with large *P. vulgare*. They were retained on a 500 µm screen used to collect the macrofauna in the heavily organically polluted Mariager Fjord in Jyl-land. The successful domination by *P. vulgare* in that polluted sediment could be accounted for by the plen-tiful dead and dying animals. Stekhoven (1933a, b) noted some oncholaimids intensively feeding on bryo-zoans (cf. also observation by Menon 1973). The car-nivorous nature of these nematodes does not conflict with the above hypothesis. The contents of the salivary glands will slowly dissolve the bryozoan after which the juice is ingested mouthful by mouthful, being found in the intestine in the form of feeding balls including also the gut contents of the bryozoan (Jensen 1979, Fig. 153.5). The above observations suggest that Wieser's classification of Oncholaimidae and Enche-lydiidae as predators should be revised. Combining (1) the difficulties in rearing oncholaimids on living nematodes alone with (2) the ¹⁴C experiments by Lopez et al. (1979) and (3) the above hypothesis, it appears most likely that these oncholaimids as juven-iles feed on DOM, including exudates from bacteria and/or algae; older juveniles and adults may also feed on animals. Oncholaimidae and Enchelidiidae may properly be called the 'garbage collectors' among nematodes and the term scavengers would thus be the proper feeding group.

The proportion of juvenile oncholaimids and enchelidiids is high (>70 %) where they are abundant (in previous cited studies and in Jensen 1986). This aspect was completely overlooked when the presumed heavy predator pressure by these nematodes was pre-viously discussed (Heip 1977, Smol et al. 1980). If subsequent studies support the above hypothesis and observations, then it makes no sense to compare, for example, the distribution patterns of oncholaimid with

thoracostomopsid species. A discussion of the pro-portion of Group 2B compared to Wieser's other feed-ing groups also seems out of balance, since the conse-quence of the above discussion is that the proportion of nematodes with predatory feeding habits is much less than previously believed.

I therefore question whether predatory nematodes play an important role in regulating meiofauna densities or diversities. On the other hand, the role played by oncholaimids in stimulating bacterial and fungal metabolism in decomposition of organic matter on the sea bottom has largely been underestimated in the past and ignored in previous feeding schemes.

Trans-epidermal uptake of DOM

Direct evidence for DOM uptake among nematode species is provided by Chia & Warwick (1969), Tietjen & Lee (1975) and Lopez et al. (1979). However, I sus-pect that the species studied by these authors live in normally fully oxygenated habitats and that uptake is probably through oral ingestion. Montagna (1984) experimentally showed DOM uptake by a meiofauna community in which nematodes formed a major com-ponent. Although his study did not distinguish the types of nematodes utilizing DOM, the results proved direct meiofaunal uptake without bacterial involve-ment. Jensen (1986) suggested a trans-epidermal uptake among thiobiotic nematodes (mainly deposit feeders) dwelling in the microenvironmental gradient between oxic and anoxic processes and where micro-bial activity is high. The significantly higher body surface to body volume ratio in thiobiotic nematodes was viewed as an adaptation for DOM uptake from the environment and for respiration. From a view of resource partitioning Jensen (1986) found it very unlikely that a thiobiotic nematode dwelling in this potential source of food would not utilize it in the same way as is known from other marine benthic soft-bodied animals (review in Jørgensen 1976), mainly poly-chaetes (Stephens 1963, 1964, 1968, 1975, Jørgensen 1979, Jørgensen & Kristensen 1980a, b). Organisms suggested to be solely dependent on DOM such as the gutless pogonophores (Southward & Southward 1972, Southward 1982) and possibly also gutless oligo-chaetes (Giere et al. 1982) are known to utilize CO₂ as a carbon source with the fixation of CO₂ by the Calvin cycle intermediated through internal symbiotic chemoautotrophic bacteria (Southward et al. 1981, Fel-beck et al. 1983). The significant release of primary amines from the neighbouring sediment along the burrows of the polychaetes *Capitella capitata* and *Nereis diversicolor* intermediated by their irrigation behaviour (Stephens 1975) might also explain the pre-

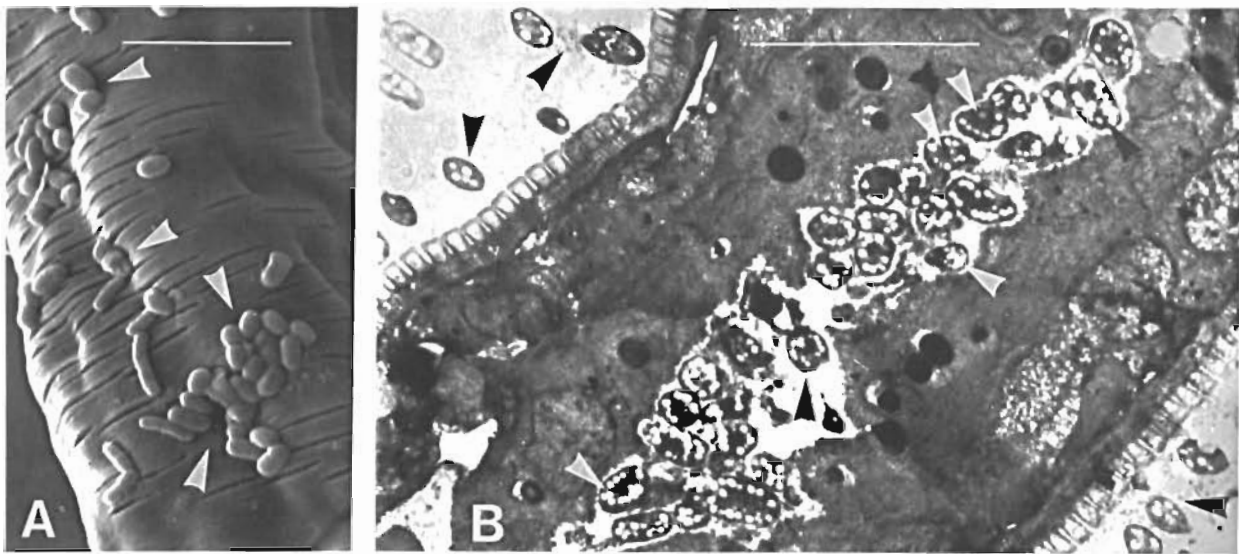


Fig. 4. *Leptonemella aphanothecae* with its symbiotic bacteria (arrows). (A) SEM photograph of cuticle. (B) TEM photograph through body showing bacteria on the cuticle and same undamaged bacteria in intestine. Originals in cooperation with Dr. W. Reichardt and Dr. T. Fenchel, respectively. Scale bars = 10 μ m

sence of the very slender *Spirinia* sp. clinging around the tubes of the polychaete *Sabella* sp. (Jensen 1983b) as well as the presence of the extremely slender and gut-and-mouthless nematode *Astomonema jenneri* attached outside the tubes of the polychaete *Onuphis jenneri* (Ott et al. 1982). The thiobiotic species studied by Jensen (1986, 1987) have a mouth opening and all species have a gut, showing oral feeding; taking this all together indicates that differentiated mixotrophy takes place. I find no clear evidence from bright field microscopic observations that these species have internal procaryotic symbionts similar to those in Siphonolaimidae (Ott et al. 1982). *Desmolaimoides thiobioticus* and *Filitonchoides thiobioticus* (Jensen 1986) and *Paralinhomoeus* sp. (Jensen 1987) all have small globules in their body; TEM analyses and other ultrastructural techniques are, however, necessary in order to know more about 'foreign' inclusions in the nematode bodies and their possible relation to metabolism. There is no structural evidence that thiobiotic nematodes can utilize the energy in sulphide or of how they can avoid the toxic effect of sulphide from their surroundings. Wieser (1959), Hopper & Cefalu (1973) and Ott et al. (1982) described different species of Stilbonematinae with external symbiotic bacteria *Aphanothece* and *Schizothrix* which are thought to trap and oxidize sulphide in the nematode *Eubostrichus diana* and *E. parasitiferus* with the end-product utilizable as an energy source (Powell et al. 1979). This is in contrast to Gerlach (1978) who suggested that *Leptonemella aphanothecae* feeds on its external bacteria (Fig. 4A, B), and provides good environmental conditions by migrating up and down

between oxid and sulphide layers of the sediment (Ott & Schiemer 1973, cited in Gerlach 1978).

RESOURCE PARTITIONING

Experimental evidence has shown that deposit and epistrate feeders discriminate between bacteria and unicellular algae, and among each type of food, select the proper size for ingestion (Tietjen & Lee 1973, Alongi & Tietjen 1980, Romeyn & Bouwman 1983, Trotter & Webster 1984). This primary discrimination of a diverse food source may allow 3 abundant deposit and epistrate feeders to coexist: *Austranema mexicanum*, *Marylynnia punctata* and *Xyala oxybiotica* (Fig. 1A to C) (Jensen 1986a). That study has also pointed out that food-size selection may effectively minimize interspecific competition; otherwise it is hard to explain how the 2 deposit feeders *Desmolaimoides thiobioticus* and *Monhystera anoxybiotica* can obtain their population maxima at the same place. Jensen (1981, 1983b) showed that European congeneric *Sabatieria* species (deposit feeders) had different microhabitats in the sediments thereby minimizing interspecific competition. From faunistic information Schiemer (1984) concluded that the actual habitat selection of *Caenorhabditis briggsae* and *Plectus palustris* shows only weak overlap. This habitat separation agrees with observed differences in the food dependence of energetics and population parameters.

The co-existence of 2 pairs of closely related epistrate-feeding species *Rhyps anoxybiotica*/*Marylynnia*

johanseni and *Euchromadora striata*/*M. preclara* in a thiobiotic and an oxybiotic habitat respectively (Fig. 1A, B) might be explained by resource partitioning of a common food source made possible by their different buccal cavity structures. *Rhyps* and *Euchromadora* species have moveable teeth close to the mouth opening, whereas *Marylynnia* species have one large tooth deep in the buccal cavity indicating different feeding behaviour (Jensen 1986).

CONCLUSION

Four feeding groups are recognized. Deposit feeders and epistrate feeders feed on bacteria and unicellular eucaryotes in different modes. Deposit-feeding species have no teeth and swallow the whole food undamaged (particulate feeders), whereas the epistrate-feeding species puncture the cell membrane with their teeth and ingest only the cell contents (juice feeders). Their considerable mobility, burrows and mucus secretion maintain more indirectly microbial populations near exponential state of growth. Thiobiotic species may even benefit from the intense microbial activity in the chemocline by obtaining food by uptake of DOM through the skin, hence supporting the idea that a differentiated mixotrophy takes place. Scavengers feed on dead animals or suck the cell contents of injured animals while releasing enzymes; these are placed in a separate group. Juvenile scavengers may take up DOM. Two types of predators are recognized by their equipment for catching or swallowing the whole prey. Resource partitioning in free-living aquatic nematodes is accomplished by food size, shape and quality selection and by means of differentiated structures in the buccal cavity.

Observations on actual feeding and histochemical studies of digestive enzymes in nematodes are scarce. Such studies, and better knowledge of grazing efficiency on specific microbes, will undoubtedly improve present understanding of nematode nutrition and their role in trophic dynamics.

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