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DIATOM-FEEDING BEHAVIOUR OF THE FREE-LIVING MARINE NEMATODE *CHROMADORITA TENUIS*

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The feeding behaviour of the marine nematode *Chromadorita tenuis* on the pennate diatom *Nitzschia* sp. in agar culture is described and depicted. The two valves of the diatom are opened by damaging the girdle with the dorsal tooth and the contents sucked out. The empty frustule is then left in the substrate. Characteristic lipid droplets from the diatom cell can be observed in the intestine of the nematode in both living and fixed specimens. In the wild, patches of bacteria may be seen in the anteriormost part of the nematode's intestine. These findings confirm that the nematode is an epistrate feeder, with a preference for diatoms as food.

Wieser (1953) reviewed the feeding habits of free-living aquatic nematodes, and divided the animals into groups according to their buccal cavity morphology. This schema is now widely accepted and few alterations have subsequently been made (Wieser, 1960; Boucher, 1974; Riemann & Schrage, 1978). Further information on feeding habits have been derived from gut content analysis (Perkins, 1958; Hopper & Meyers, 1967; von Thun, 1968; Tietjen, 1967; Deutsch, 1978). However, as Overgård Nielsen (1949), Tietjen (1967) and McIntyre (1969) pointed out, gut content analysis alone may be misleading. Studies on the nutrition of some selected bacteria and diatom feeding nematodes by Tietjen and co-workers (see Tietjen, 1980; Alongi & Tietjen, 1980) as well as van Es *et al.* (1980) and Bouwmann & Romeyn (1981) demonstrated successful growth of certain species on well-defined food media; the actual feeding habits remain, however, largely unknown.

The studies of von Thun (1968) and Lopez *et al.* (1979) show feeding behaviour in nematodes by direct observations of the buccal cavity and the oesophagus of living material. This paper deals with the mechanism involved when the nematode *Chromadorita tenuis* feeds on the pennate diatom *Nitzschia* sp.

This study is part of the project on the behaviour and ecology of Baltic Sea nematodes (see e.g. Jensen, 1981 and 1982).

MATERIAL AND METHODS

A laboratory population of *Chromadorita tenuis* (G. Schneider, 1906) (adult length ca. 1 mm) was successfully cultured through several generations for more than two years. The culture was kept on agar plates in 87 and 50 mm

Petri dishes, inoculated with a diatom (*Nitzschia* sp. train Tv 102, isolated by G. Hällfors) which grew in association with at least one species of slow-growing bacteria. The laboratory population of *C. tenuis* was started with animals from phytal substrates in the Tvärminne area (Jensen, 1979). It was lost at the end of 1981.

The culture medium was a modified Erd-Schreiber medium based on seawater from the Tvärminne area (salinity ca. 6‰) enriched with 100 mg $NaNO_3$, 0.5 mg NH_4Cl, 10 mg K_2HPO_4, ca. 10 mg $Na_2SiO_3 \cdot 9H_2O$, ca. 10 µg thiamine, ca. 1 µg cobalamine, and 10 ml soil extract per litre, and solidified with 0.8% agar (G. Hällfors, pers. comm.).

Among several food items tested, including bacteria, blue-green algae, diatoms and green algae (all algae isolated by G. Hällfors), strain Tv 102 was selected because it best sustained the nematode. Furthermore, it grew and spread rapidly, and was confined to the surface of the agar plates which facilitated direct observations of the animals. Due to its slenderness, the diatom could be utilized even by the smallest, newly hatched nematodes. The average dimensions of the diatom were 5 × 35 µm.

The observations were made with a Wild M 5 stereomicroscope at a magnification of 50 ×, and a Leitz Dialux microscope at a magnification of 1000 ×. Fig. 1 is also based on a cine film of the feeding behaviour; Figs. 2 and 3 B & C were made with the aid of interference contrast microscopy, and Fig. 3 A & D are SEM micrographs.

RESULTS

The mechanism used by *Chromadorita tenuis* to feed on *Nitzschia* sp. can be described as follows (Fig. 1A-F):

a. the nematode locates one end of the diatom;
b. the nematode brings the diatom into the buccal cavity placing it between the dorsal tooth and the dorsal wall of the buccal cavity;
c. the lips and vestibulum close, holding the diatom firm;
d. the dorsal tooth moves 1-3 times against the diatom, damaging the girdle and causing the two valves to separate;
e. the cell is emptied by 1-2 pumping movements of the oesophagus, the oesophageal lumen being filled with the cell contents which are then passed to the intestine;
f. the emptied frustule is left in the substrate undamaged, apart from the dislocation of the girdle (see also Fig. 3A, D).

Gut contents of *Chromadorita tenuis* never showed fragments of the frustules of *Nitzschia* sp. Observations of the gut at high magnification showed presence of lipid droplets (Fig. 2B); the shape of the droplets, particularly in the anterior-most portion of the gut, resembled closely those of the diatom. Fused lipid droplets, 10 µm × 30 µm, are found more frequently in the midpart of the gut.

Such lipid droplets are also commonly in living and formalin-fixed specimens; solid particles were observed only infrequently in specimens in the wild, but patches of bacteria were sometimes present in the gut.

DISCUSSION

Chromadorita tenuis is classified as an epistrate feeder according to the schema of Wieser (1953): this study confirms it. The slightly S-shaped dorsal tooth and the sclerotized dorsal border of the buccal cavity act like a parrot's bill while

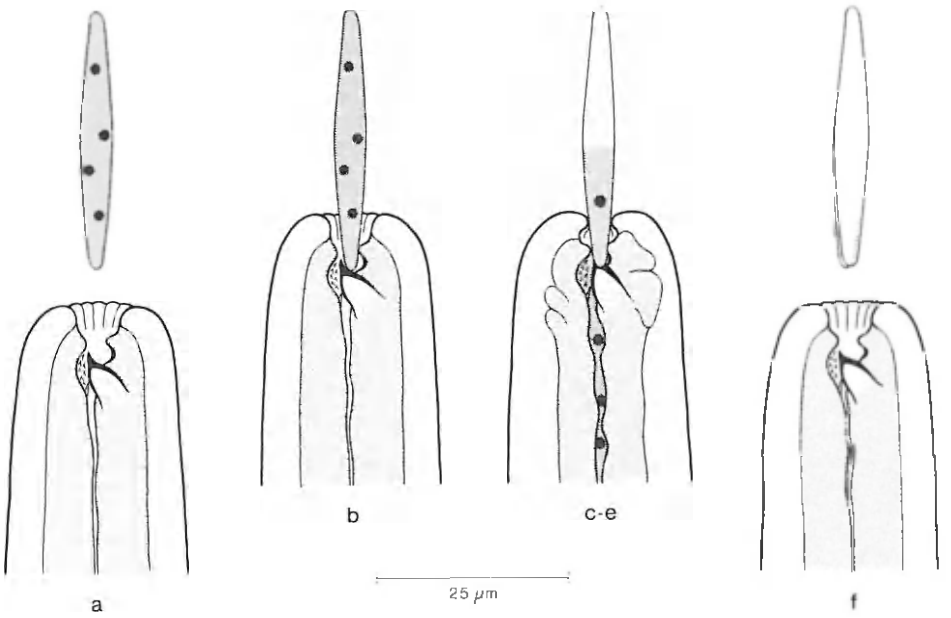

Fig. 1. *Chromadorita tenuis*. Sequence of events when the nematode feeds on the diatom *Nitzschia* sp. See text for further explanation.

the sclerotized ribs in the vestibulum hold the diatom firm (Fig. 1). *C. tenuis* may also graze on other epiphytes than diatoms such as bacteria in which case the denticles on the ventral border of the buccal cavity are thought to act as scrapers (Fig. 2A).

The unpublished observations by von Thun (1968) (reproduced by Remmert, 1980 Fig. 28). on the nematode *Hypodontolaimus balticus*, which has a similar buccal cavity to *Chromadorita tenuis*, in many respects agree with the present study. However, *C. tenuis* is only able to ingest pennate diatoms from one end, and not from the side as shown for *H. balticus* ingesting *Navicula* sp. (von Thun *op cit.* Fig. 7). Moreover, *C. tenuis* empties the diatom by action of the dorsal tooth on the girdle connecting the two valves, thereby opening the two valves and sucking out the contents. *H. balticus* is reported to use the dorsal

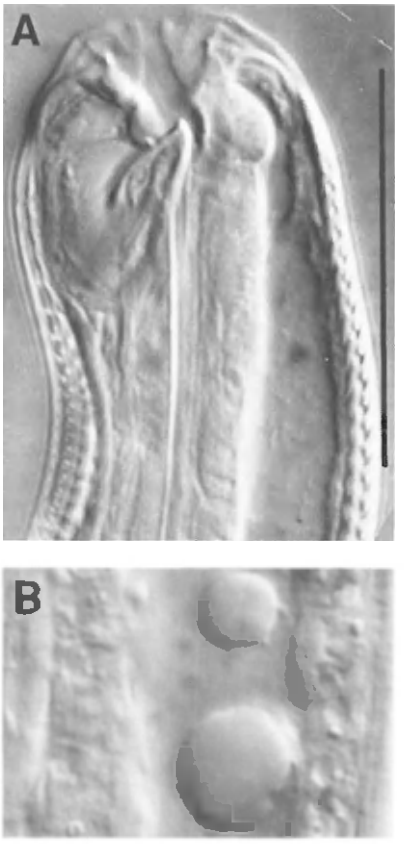

Fig. 2. *Chromadorita tenuis*. A: Buccal cavity; B: Lipid droplets in the gut. Scale = 25 μm.

tooth to puncture the diatom frustule after which the cell contents are removed. Physically it is unlikely that the cell contents can be sucked out of only one opening, and the pore perforations, a few nanometres in diameter allow diffusion, but not physical flow of seawater. Based on present findings, it seems possible that the feeding habits of *H. balticus* upon *Navicula* sp. may also involve dislocation of the girdle and not simply damage to the frustule.

Chromadorita tenuis leaves the emptied diatom in the substrate; which was observed, too, for *Hypodontolaimus balticus* when feeding on large diatoms, whereas smaller ones were swallowed in fragments. It is obvious that by not ingesting the frustule, but only the cell contents, more space is left in the gut for digestable products. The presence of fragments of diatom frustules in the gut as in some *Theristus* and *Daptonema* species should not be taken as the only means of showing that the nematode feeds on diatoms. The presence of identifiable diatom lipid droplets can also act as an excellent indication of diatom feeding.

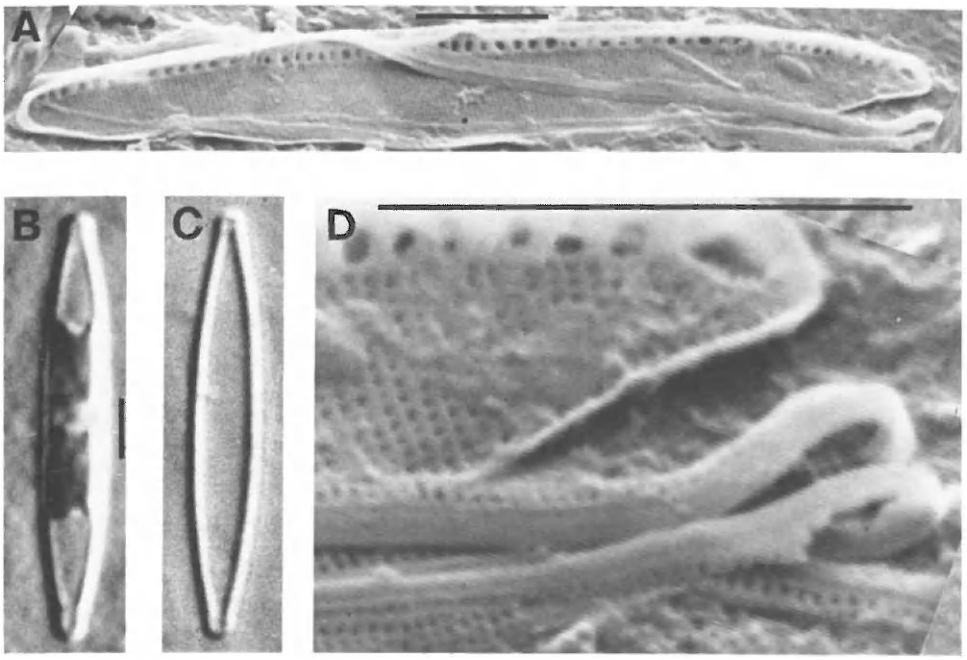

Fig. 3. *Nitzschia* sp. A: Valve with dislocated girdle; B: Living specimen; C: Emptied specimen; D: Detail of dislocated girdle. Scale = 5 μm

Occasionally, sclerotized parts of a nematode feeding apparatus (buccal cavity, oesophageal lumen or both) have been found in the gut of *Chromadorita tenuis* in both laboratory and natural populations. This could be interpreted as a predatory feeding habit. However, these findings are correlated with the moulting process of the animal itself; moulting animals ingest their own sclerotized linings of the buccal cavity and the oesophageal lumen, leaving the old body cuticle in the medium (Jensen, unpubl.).

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ZUSAMMENFASSUNG

Das Verhalten des Meeresnematoden Chromadorita tenuis *beim Fressen von Diatomeen*

Das Verhalten des Meeresnematoden *Chromadorita tenuis* bei der Aufnahme einer pennaten Diatomee (*Nitzschia sp.*) in Agarkulturen wird beschrieben und dargestellt. Die beiden Schalen-

hälften der Diatomee werden durch eine Zerstörung des Gürtels mit Hilfe des dorsalen Zahnes geöffnet und dann der Inhalt aufgesaugt. Die leere Schale wird im Substrat zurückgelassen. Charakteristische Lipidtröpfchen aus der Diatomeenzelle können im Darm lebender und fixierter Nematoden beobachtet werden. Unter natürlichen Bedingungen können Gruppen von Bakterien im vordersten Abschnitt des Nematodendarmes auftreten. Diese Ergebnisse bestätigen, daß der Nematode ein Epistratfresser mit einer Vorliebe für Diatomeen ist.

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