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The enigmatic mineral particle accumulations on the cuticular rings of marine desmoscolecoid nematodes – structure and significance explained with clues from live observations

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Abstract

The majority of Desmoscolecoidea are characterized by ring-shaped accumulations of mineral particles on the cuticle resulting in the impression of a peculiar body articulation. Live observations made during the extraction of desmoscolecoids from mud sampled in the Swedish Gullmar fjord suggested new ideas pertinent to the particle accretion and the likely functional significance of the prominent rings. Undisturbed desmoscolecoids were observed to perform perpetual, vigorous, stationary undulations with their body. In our opinion these undulations affect the distribution of particles adhering to the cuticle by pushing them from soft, pliable cuticular sections to comparably stiff rings thus generating distinct concretion rings and naked interzones. The prominent concretion rings are assumed to increase positive mechanical effects of the undulations on the productivity of ubiquitous microbial populations residing on ambient sediment particles. The microbial production boosted by this kind of bioturbation may be of nutritional importance for the desmoscolecoids. – An electron-microscopic investigation (TEM) of *Tricoma* sp. from the Gullmar fjord revealed the concretion rings to consist of stacks of clay mineral platelets in the submicrometer size range. A perusal through contributions of other authors suggests that such clay mineral aggregates are the basic component (“granular component” sensu Timm 1970) in the concretion rings of all desmoscolecoids. In a number of species these aggregates contain a specifically determined admixture of conspicuous other mineral grains.

Keywords: *Desmoscolex*, *Tricoma*, *Quadricoma*, clay mineral accretions.

Introduction

Desmoscolecoidea are small, often minute, spindle-shaped benthic nematodes, the majority of which are characterized by a strong annulation of the cuticle. All or many of the rings of these species are covered in the adults by accumulations of foreign bodies that are included in a hyaline matrix. The presence of these conspicuous rings may give the appearance of a peculiar body articu-

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lation, reminiscent of the contours of polychaetes or caterpillars. Most species occur in marine habitats, but a few species live in freshwater habitats or soils. A comparatively high population density has been found in the deep sea and in brackish soils of meadows at coastal fringes. Comprehensive, general synopses on Desmoscolecoidea have been presented by Timm (1970), Freudenhammer (1975) and Decraemer (1985). Lorenzen (1994) revised the classification of the Desmoscolecoidea and the systematic position of this superfamily (suborder Desmoscolecina, order Chromadorida) within the Nematoda. The classification of De Ley & Blaxter (2002) gives the Desmoscolecina the rank of an order, Desmoscolecida.

The number of annules covered by particle accumulations ('main rings') varies between 12 (mostly 17) in the genus *Desmoscolex* Claparède, 1863 and 270 in the genus *Tricoma* Cobb, 1893. The ring-like covering (called 'concretion rings' by Timm 1970, or 'desmen', singular: 'desmos', by Freudenhammer 1975) is generally considered to consist of secretions from the nematode containing inclusions of particles derived from the ambient sediment. The attachment of these coverings on defined areas of the cuticular surface has been related to cuticular tiny spines or pores (Timm 1970, critical remarks by Freudenhammer 1975).

The great majority of publications on Desmoscolecoidea are taxonomic descriptions with little detailed information about the composition of the concretion rings other than describing the grain size of the foreign particles. Deep-sea specimens are said to bear larger and more numerous particles than species from other regions (Timm 1970); an example is *Desmoscolex lapilliferus* Freudenhammer, 1975. Obviously, there is selectivity concerning the kind and size of the included particles and Freudenhammer (1975) stated, that deep-sea species living in *Globigerina* oozes never include shells from the Foraminifera. Timm (1970, p. 5-6) identified two different kinds of particles in the rings: "Concretion rings are not build solely of concretion particles but the main substance is an internal granular component which is typical for each species." The context of Timm's statement suggests an external source of the concretion particles and an endogenous origin of the 'granular component'. It is not clear, however, whether this component is actually a granular form of secretion of the desmoscolecoids or an accumulation of fine granular particles from another source. The optical limits of light microscopy prevented the identification. Since Soetaert (1989) and Soetaert & Decraemer (1989) described some aggregations of bacteria around the body of deep-water desmoscolecoids, these microorganisms have also been taken by us into consideration as likely components of the cuticle surface covering.

In contrast to the adults the few juvenile desmoscolecoids observed so far never showed definite concretion rings; the formation of these characteristic, localized particle accumulations takes place only after the final moult. The juveniles have a homogeneously annulated cuticle covered by a flimsy, hyaline layer, in which small, irregularly distributed, unidentified particles are embedded (Lorenzen 1971a, Decraemer 1977, 1978, 1996). Lorenzen (1971a) described a juvenile of *Desmoscolex balticus* Lorenzen, 1971 moulting to the adult stage. He observed the adult body under the larval exuvia that showed small definite crevices in the narrow space between larval and adult cuticle indicating the position of the 17 future main rings. Lorenzen related the crevices to the presence of a secretion which would contribute to the construction of the main rings in the adult. The further development of particle accumulation on the cuticle immediately after hatching of the adults remained unknown.

In our present study we provide evidence for explaining the formation of the particle accumulations on the main rings of desmoscolecoids and their functional significance. We base our arguments on live observations, light-microscopic observations at high magnifications of glycerin-mounted preserved specimens and on transmission electron microscopy. Particular attention was paid to a small *Tricoma* species, which showed no distinct mineral particles on the cuticle, because we expected to receive information on the nature of the 'granular component' in the concretion rings.

Material and Methods

The field work and live observations were made by the senior author (F. R.) under the guidance of Sievert Lorenzen (University of Kiel, Germany) at the Swedish Gullmar fjord. Laboratory facilities were used at the Klubban Biological Station (University of Uppsala) in Fiskebäckskil between 12-17 June 2003. An opportunity was provided to retrieve one sediment sample from the fjord with the kind help of Jarl-Ove Strömberg, the former director of the Kristineberg Marine Research Station (University of Göteborg), who made it possible for us to participate on a students' ship excursion on 13 June arranged by that institution, which is located close to the Klubban Station.

The sampling site was near by the Kristineberg Station in the mouth area of the Gullmar fjord in the Skagerrak, between Gåsö and a point 200 m north of Stockevik, in 40 m depth. By means of an Ockelmann dredge we retrieved the sediment, homogeneous gray mud, without smell, obviously oxic, containing a dense colony of Pennatularia. Two hours later the mud sample (about 10 litres) was thoroughly stirred in the Klubban Station after the addition of the same amount of cold oceanic water available from the deep-water supply system of the station. The sample then was stored for 20 hours in the cold laboratory in order to enrich the meiofauna at the sediment surface. Small subsamples (about 1 ml) were siphoned off from the sediment surface during the following three days and rinsed with cold seawater through sieves with a 50-µm mesh size. The sieve residue was inspected in petri dishes under the stereomicroscope using 100x-magnification and the desmoscolecoids were extracted using pipettes or hook-bent needles. About 10 desmoscolecoids belonging to the genera *Tricoma* Cobb, 1893, *Desmoscolex* Claparède, 1863 and *Quadricoma* Filipjev, 1922 were found in each subsample.

After observing their behaviour the nematodes were fixed in a mixture of fixatives containing 5 % formaldehyde, 0.5 % propionic acid and 28 % ethanol. This mixture was replaced by a 4 % formaldehyde solution after 30 min. Permanent microscopic mounts were made in glycerin after the slow evaporation method (Riemann 1988). Microscopic observations were made with a Zeiss WL and a Zeiss Axioplan microscope equipped with Nomarski optics. Photographs were taken with the digital camera Nikon Coolpix 5000. The ultrastructural study (TEM) was performed after opening one glycerin mount and transferring the selected specimens into Na-cacodylate buffer. Postfixation was made with 1 % solution of osmium tetroxide, dehydration via an acetone series, the embedding was in araldite. The electron microscope used was a ZEISS EM 940. – Voucher specimens of the Gullmar nematodes are deposited at the Zoological Museum, University of Hamburg.

Observations and Discussion

Live Observations

The first impression when observing active desmoscolecoids is that they are extremely flexible and sticky short worms. They belong to the most pliable aquatic nematodes we ever have seen; their cuticle appears to be soft and slack. The body can perform narrow bendings in the median plane, alternating to the dorsal and the ventral side. During this activity the worm may be attached to sediment particles with the tail end or it may remain unattached. By means of secretions from the large caudal glands desmoscolecoids may stick firmly to the substratum. Other sources for stickiness are glands emanating their secretions through the tips of certain body setae and, possibly, secretions from the pharyngeal glands (compare Riemann & Helmke 2002). Detrital aggregates may stick to the cuticle. Because of the stickiness, the extraction of living desmoscolecoids from the sediment with pipettes and needles was difficult, resulting in the loss of many specimens during the sorting of the sample.

The ability of *Desmoscolex* sp. to walk on the dorsal side, stalking with the aid of the thick, sticky subdorsal setae, was observed by Stauffer (1924) and Timm (1970). We could confirm these descriptions of the peculiar, caterpillar-like locomotion in the course of the present studies. Besides the stalking movement, desmoscolecoids display the normal nematode locomotion by the serpentine undulatory propulsion with undulations running in the dorsoventral plane, whereby the worm, after rotating around the body axis, often crawls on the lateral side on the substrate. During the observation of these turning movements we noticed that one *Desmoscolex* sp. is dorsoventrally flattened like an isopod crustacean. To our knowledge, a dorsoventral flattening has never been described so far to occur in desmoscolecoids.

After storing a collection of Gullmar-fjord desmoscolecoids overnight in the laboratory (estimated temperature below 18 °C) in a Boveri dish (3 ml) containing sea water and a small amount of detrital aggregates and mineral grains, we in the next morning observed peculiar stationary swinging movements of the worms. The desmoscolecoids displayed perpetual, vigorous undulations of their body, with a standing-wave movement, being either attached with the tail to the substrate or unattached.

It appears that Timm (1970 p. 5) referred to the same kind of stationary undulations performed by desmoscolecoids when he wrote: “It is often considered that the Desmoscolecida are very sluggish because of their short plump bodies. However, if living specimens are kept at low temperature (6 °C) and then examined before they warm up they will be seen to make vigorous sinuous movements. Panceri (1876) referred to such movements.” These undulations present a puzzling constituent of the bionomics of desmoscolecoids, and we will come back to this point when we discuss the likely development and significance of the concretion rings.

Microscopy: Structure of the Concretion Rings

Tricoma sp.

Figs. 1A-D

Taxonomic remarks: The male has 78 concretion rings; the body length is 332 µm. The female has 79 concretion rings; body length 382 µm. The species resembles *Tricoma lobata* Juario, 1974, described from the German Bight. – 11 preserved specimens were investigated.

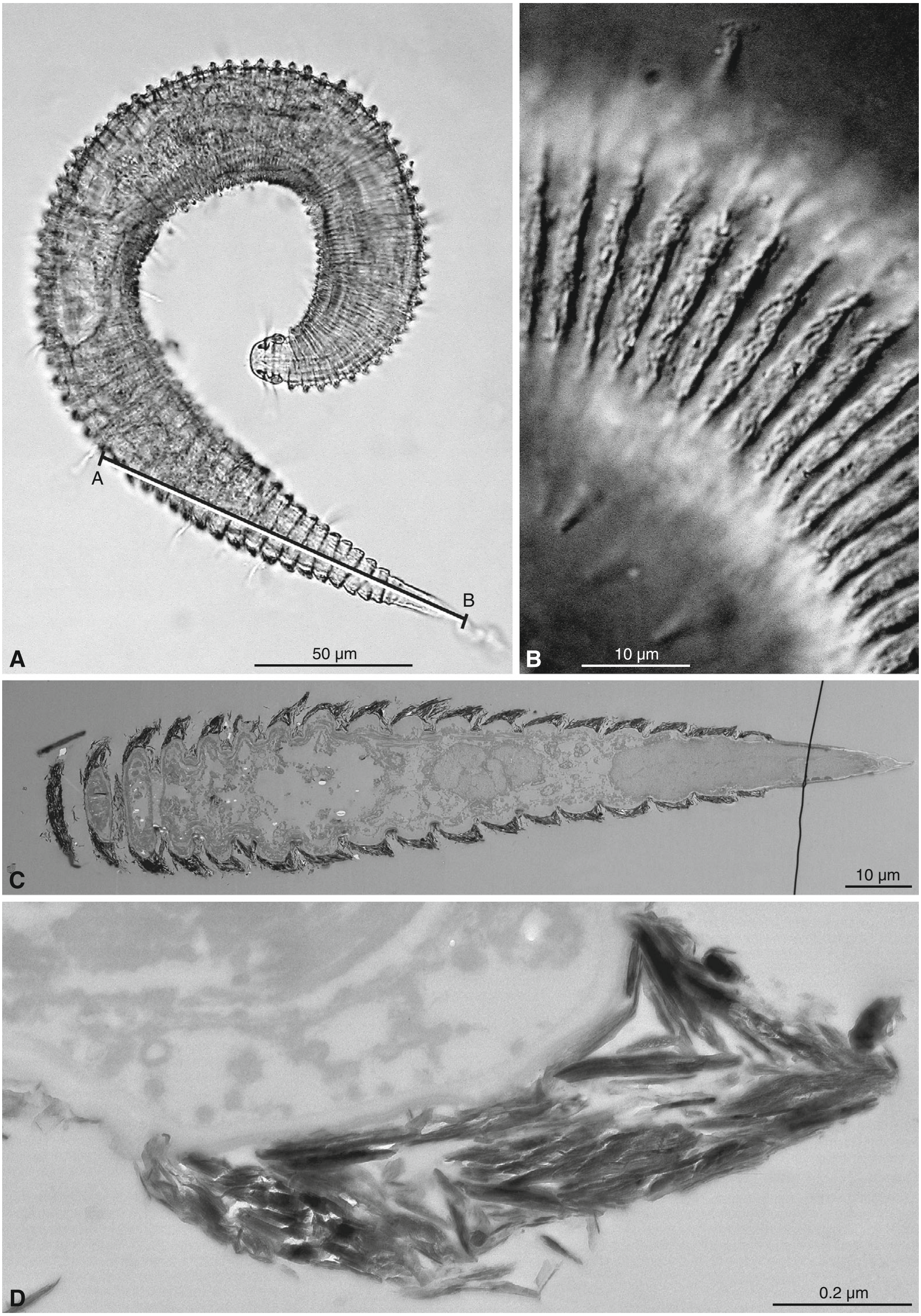
Concretion rings: All concretion rings are closely spaced as is typical of the genus; there are no interzonal rings detectable. The concretion rings are comparatively flat on the tail; between the head and the anus they are more prominent, with distinct ridges. At light-microscopy magnifications the rings appear to be composed of a fine, homogeneously granulated substance with a uniform light refraction; there are no other particles with another light refraction discernible. The same image is offered by the holotype male of *Tricoma lobata* Juario, 1974 (examination in 2004 of the slide NSIMB 521c from the former Nematode Collection of the Institute für Meeresforschung in Bremerhaven, now located at the Zoological Museum, University of Hamburg. The preparation was extremely compressed due to glycerin evaporation). With the Nomarski-microscopy technique using highest contrast and magnification the granulated matter of the Gullmar material appeared to consist of soft, flat, transversely arranged particles that were pinched in the narrow ridges of the concretion rings in the anterior body region (Fig. 1B).

Electron microscopy revealed these particles to be prominent stacks of thin, flat platelets, which are very conspicuous in the uncontrasted preparations (Figs. 1C,D). In the centre of the concretion rings the platelets assume a position more or less perpendicular to the cuticle. We identify the platelet-shaped particles in the submicrometer size range as clay minerals derived from the ambient sediment (see Massalski & Leppard 1979, Leppard 1992).

Iken (personal communication, Second Symposium on Aquatic Nematodes, Bremerhaven, 28-31 May, 1979) demonstrated ultrastructural details of the body wall of North Sea representatives of the genera *Tricoma*, *Quadricoma* and *Desmoscolex*. He observed what he called ‘fine hard needles’ in the covering of the cuticle in all three genera. In the light of the present investigation the needle-like appearance of these structures in longitudinal sections of the worms is due to the direction of sectioning of flat mineral particles, as the stacks of platelets are transversely arranged in the rings. In the concretion rings of one *Desmoscolex* species large, compact electron-dense particles of different sizes and clusters of bacteria were found in addition to the needles. Iken was uncertain about the origin of the fine needles in question, but he related them to the ‘granular component’ mentioned by Timm (1970). We concur with this opinion and consider stacks of clay minerals to be an abundant granular component in the concretion rings of desmoscolecoids. Questionable in this context, however, is the description of fine bands of granulation that are said to occur already in the embryo (Timm 1970. The description appears to be based on an embryo that is enclosed in the egg shell).

Another ultrastructural study on the concretion rings was provided by Tchesunov et al. (1996). They described the main rings of *Desmoscolex* sp. to be covered by cloudy deposits of an amorphous material containing rod-like particles. Although the authors thought the deposits to be secreted by the nematodes, we assume that the rod-like particles are clay minerals from the sediment.

Fig. 1. *Tricoma* sp. **A.** Female, whole mount, lateral view. Line A-B shows plane of section presented in Fig. 1C. ▷ **B.** Male, concretion rings in oesophageal region. **C.** Female, oblique tangential section through posterior end. **D.** Detail of concretion ring in this section series.


A
B
50 µm
A
10 µm
B
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C
0.2 µm
D

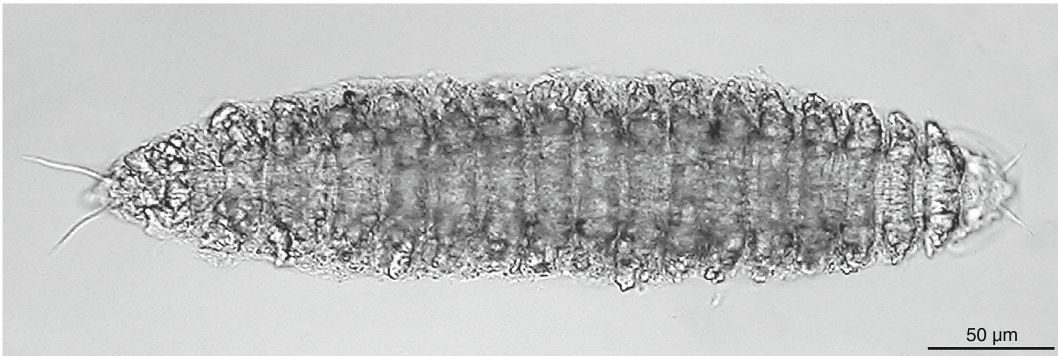


Fig. 2. *Desmoscolex* sp. Male, whole mount, dorsal view.

Desmoscolex sp.
Fig. 2

Taxonomic remarks: The male has 17 main rings, the body length is 371 µm. The species resembles *Desmoscolex laevis* Kreis, 1926 sensu Timm 1970 and *Desmoscolex gerlachi* Timm, 1970. Live observations of specimens rotating around their body axis showed that the species is dorsoventrally flattened. Photographs of preserved specimens made at low magnification suggest the impression of flattening to be caused by lateral protrusions of the conspicuous covering with foreign particles, the body of the worm appears to be round in diameter. – 5 preserved specimens were investigated.

Concretion rings: The 17 concretion rings contain large, massive grains of minerals that determine the outer contours of this species. The spaces around the large grains and the interzones between the concretion rings are filled by a hyaline matrix containing dense masses of fine, round granules with interspersed, strongly light-refractive, small mineral particles. Many of these mineral particles represent flat, transversely arranged platelets that are in a vertical position between the main rings or they are attached to them.

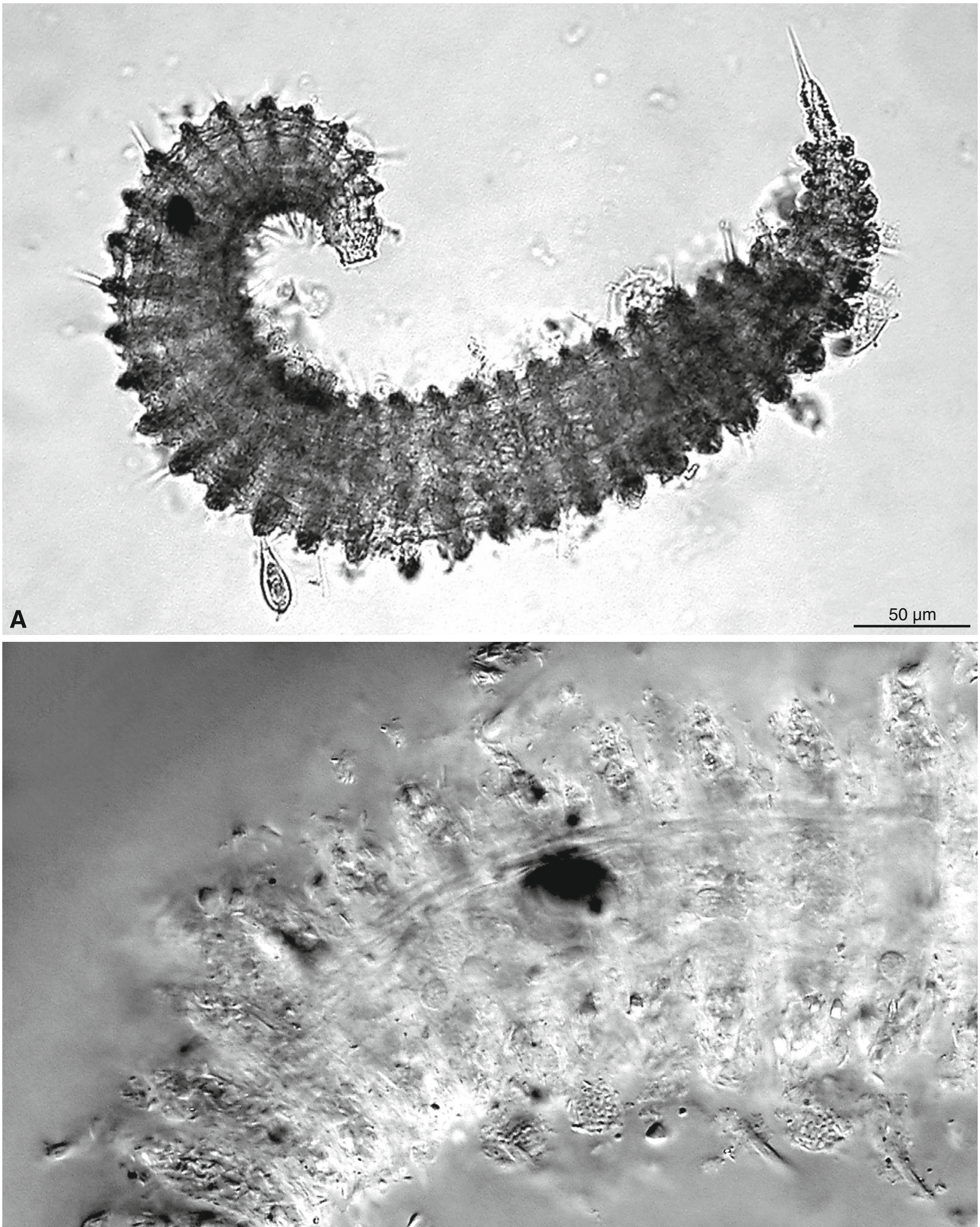
Quadricoma sp.
Figs. 3A-B, 4

Taxonomic remarks: The male has 37 main rings, the body length is 550 µm. The species resembles *Quadricoma noffsingerae* Decraemer, 1977. – 18 preserved specimens were investigated, 4 of them are juveniles, resembling the third juvenile stages described of *Q. noffsingerae* by Decraemer (1977).

Concretion rings: *Quadricoma* sp. has massive dark concretion rings containing strongly light refractive mineral grains of various sizes and shapes. Flat mineral particles are orientated in the transversal position. In the anterior body region, the concretions are concentrated in the middle of each main ring, leaving wide gaps in between. In the posterior region the concretion rings are wider, with narrow gaps. The gaps are filled with merely small amounts of concretion particles. Detrital flocculent aggregates may adhere to the concretion rings or to the body setae. Seven specimens carry several Suctoria (Fig. 3A; at least two different species) on the concretion rings. Additionally, in three specimens compact clusters of microorganisms were observed (Fig. 3B). These were either loosely attached to the body surface, or located in the gaps between the concretion rings, or they are components proper of these rings.

The juveniles are covered by a fine particulate matter with interspersed mineral grains of various sizes (Fig. 4). The covering is thicker in the poste-

Fig. 3. *Quadricoma* sp. **A.** Male, whole mount, lateral view. **B**. Female, anterior end. Clusters of microorganisms ▷ attached to concretion rings.


A
50 µm
B
25 µm

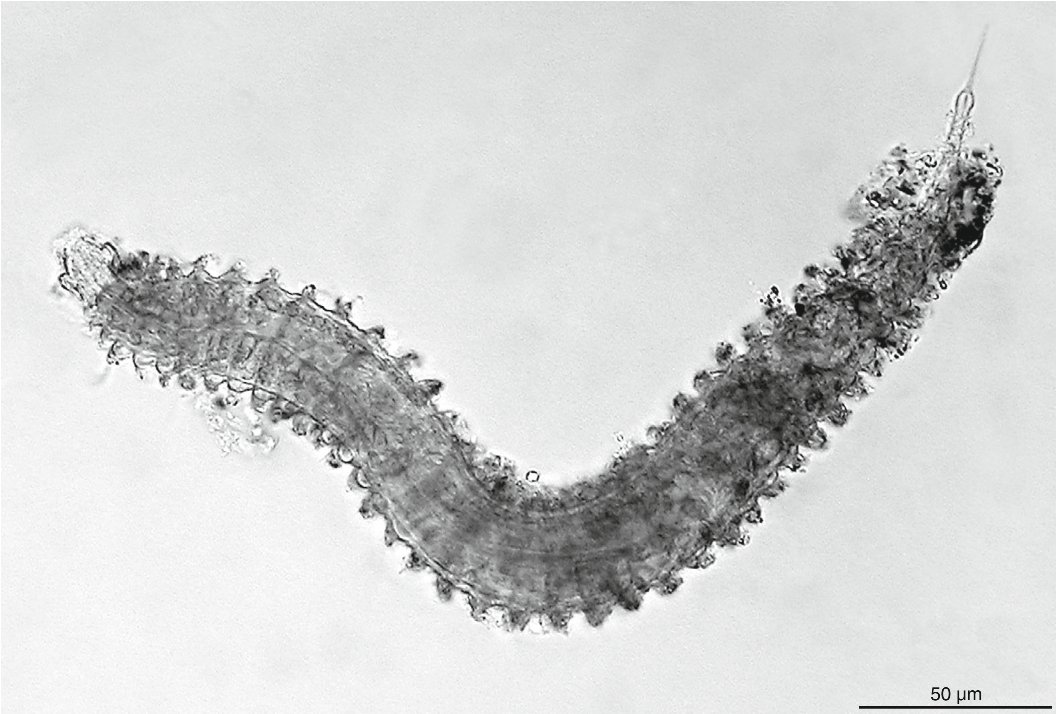


Fig. 4. *Quadricoma* sp. Juvenile, whole mount, lateral view.

rior half of the body than in the anterior region, where merely a thin layer is discernible in two specimens. In another juvenile a comparatively thick covering extends also over the anterior region. The differentiation into concretion rings and interzones is visible, but in juveniles the epicuticular coating appears to be more coherent than in the adults, in which the concretion particles are compressed in the form of distinct rings. In comparison to the description and the drawings presented by Decraemer (1977: *Quadricoma noffsingerae*) the Gullmar juvenile specimens bear a more voluminous covering on the cuticle.

Development of Concretion Rings

Juvenile desmoscolecoids carry a coherent layer on the cuticle consisting of mucoid substances with interspersed small particles. A similar covering with mucus and small particles is known from some adult Microlaimoidea, e. g. *Ixonema sordidum* Lorenzen, 1971 (original description) and *Microlaimus conothelis* Lorenzen, 1973 (personal observation made in 1999 at the type material from Helgoland, slide NSIMB 321b from the former Nematode Collection of the Institute für Meeresforschung in Bremerhaven, now located at the Zoological Museum, University of Hamburg).

The relevant question is how in the adult desmoscolecoids the transition takes place from a coherent mucus layer to the formation of the characteristic main rings separated by more or less broad naked interzones. Members of the genus *Desmoscolex* Claparède, 1863, in particular, show a distinct articulation (Decraemer 1976). In our opinion, the following factors are operative in the development of concretion rings. (1) The initial presence of a coherent mucoid cover containing particles. (2) The peculiar vigorous undulations of the body as were mentioned in the chapter on live observations. (3) Differences in the rigidity of successive cuticular rings. As a consequence, the accretion of particles takes place predominantly on comparatively rigid rings, because during the undulating movements any adhering deposits will be pushed from the soft, pliable sections of the cuticle (soft rings or hinges between rings) to the stiffer sections. Indicative of the transportation forces acting against the anterior and posterior margins of the concretion rings are the transverse arrangement of flat mineral particles and the formation of transverse ridges on these rings. Decraemer (1976) observed that in most *Desmoscolex* species the cuticle is elevated at the region of the main ring as compared with the interzone. In our opinion, such structural differentiation may cause a local stiffening of the cuticle that is effective in the deposition of concretion particles.

Our concept of the formation of concretion rings describes a dynamic process. Consequently, there are transitional stages known in some species, where more or less distinct amounts of particles are distributed between the main rings. Examples are the descriptions of *Desmoscolex balticus* Lorenzen, 1971, *D. laevis* Kreis, 1926, sensu Timm, 1970 and *D. gerlachi* Timm, 1970. An adult male of *D. membranosus* Decraemer, 1974, drawn by Decraemer (1996) shows a coherent layer of particulate matter reminiscent of juvenile conditions. Of the present Gullmar material, the specimens of *Desmoscolex* sp. and *Quadricoma* sp. contain particulate fillings between the main rings.

Functional Aspects

The functional significance of the mineral accretions on the cuticle of desmoscolecoids is unknown. Older speculations (cited by Timm 1970, p. 5) referred to a presumed thick cuticle as a possible protection against pressure or action of surf. However, contrary to this assumption the cuticle of *Desmoscolex* sp. is thin in comparison to other nematode groups (Tchesunov et al. 1996).

In our opinion both the formation and the functional significance of the concretion rings could be pertinent to the observed stationary undulations of the desmoscolecoids. According to this idea the prominent concretion rings increase mechanical effects of the undulations on ubiquitous microbial populations residing on ambient sediment particles. Evidently, any object that stays on or close to the cuticle of desmoscolecoids experiences strong mechanical effects of the undulatory body movements of desmoscolecoids, as the gaps between concretion rings are sequentially widened and closed (compare Fig. 3A). When the gaps are closed on the concave section of the body curvature, objects such as detrital bacterial aggregates in reach of the concretion rings will be pinched. This kind of bioturbation may be important for the microbial productivity. In general, mechanical disturbance of sediments may boost values of microbial activities by an order of magnitude compared to undisturbed sediments as the microbial cells are optimally supplied with substrate and inhibitory reaction products may be removed (Meyer-Reil 1986). Along these lines of argument we assume a nutritional benefit for the desmoscolecoids derived from increased microbial production.

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