

Sulphide ectosymbioses in shallow marine habitats

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Abstract: Ectosymbioses are of interest in understanding the evolution of mutualistic relationships between organisms, because in general both partners are similar to their closest non-symbiotic relatives in morphology, physiology, and behaviour. This allows the reconstruction of the scenario in which the relationship evolved. The Stilbonematinae are free-living nematodes occurring in reduced marine sands. They are covered by films of regularly arranged bacteria of characteristic shape. The nematodes feed on the micro-organisms, which they supply with reduced sulphur compounds and oxygen as an electron acceptor by migrating through the chemocline. The bacteria belong to the γ -subgroup of the Proteobacteria and are related to the symbionts of shallow-water bivalves and deep-sea Vestimentifera. The worms probably infect themselves with members of the free-living bacterial community and subsequently control the shape, size and arrangement of the microbes. A second ectosymbiosis involves the colonial ciliate *Zoothamnium niveum*, which lives on mangrove peat. It is covered by a continuous layer of ectosymbiotic chemoautotrophic bacteria which utilise a sharp, microscopic sulphide/oxygen gradient developed in the boundary layer on the surface of the peat. Extension and retraction of the ciliate host transports the bacteria through the chemocline within fractions of a second.

Introduction

Numerous symbioses between invertebrates and sulphur-oxidising chemo-lithoautotrophic bacteria have been described from deep-sea hot vents, continental-slope cold seeps, and shallow-water sulphidic habitats (CAVANAUGH 1985, GIERE 1992, FISHER 1990, NELSON and FISHER 1995). In most of these symbioses the micro-organisms are contained in the invertebrate host's body. The position of the symbionts ranges from subcuticular or intercellular to intracellular in special organs of the host (see the contributions of FISHER and GIERE in this volume). Only in a few cases - the holotrich ciliate *Kentrophoros* and the peritrich *Zoothamnium*, the stilbonematid nematodes, the alvinellid polychaetes, the priapulid *Halycrpytus spinulosus*, the bresiliid shrimps, and the echinoid *Echinocardium cordatum* - the symbiotic bacteria are found on the surface of their hosts (RAIKOV 1974, FENCHEL and FINLAY 1989, BAUER-NEBELSICK et al. 1996, DESBRUYERES et al. 1983, OTT and NOVAK 1989, OTT et al. 1992, OESCHGER and SCHMALJOHANN 1988, POLZ and CAVANAUGH 1995, this volume, TEMARA et al. 1993). These ectosymbioses, however, are of interest because the symbionts constitute the interface be-

tween the host organisms and their environment, and this condition may represent the initial stage of the formation of the more intimate association found in endosymbioses. Studies of ectosymbioses thus may serve as models for the development of symbioses in general and may help us to understand the highly evolved endosymbioses in which the morphology and physiology of at least the invertebrate host is highly altered compared with non-symbiotic relatives. Moreover, some of the ectosymbiotic systems may be taken apart and the partners studied separately (SCHIEMER et al. 1992).

Recent studies (POLZ and CAVANAUGH 1995, this volume) suggest that the symbiotic bacteria are at the same time members of the free-living community, where they may even dominate numerically. Symbiotic bacteria are probably recruited from those members of the free-living community which had been part of more diverse microbial mats fouling the surface of the ancestors of today's hosts. Such fouling communities can be found on close relatives of the symbiotic species in both *Zoothamnium* and the Stilbonematinae. Traits in the biology of the host - such as movement through the oxic/sulphidic chemocline - must have given a selective advantage to certain bacterial species (e.g., sulphur-oxidising chemoautotrophs) which benefited from these traits and thus attained competitive dominance on the host. The host in turn seems to control the position and arrangement of the bacteria on certain regions of its body and probably also influences growth form and division rate (POLZ et al. 1992). Ultimately, it may provide a positive feedback to the free-living community by constantly re-inoculating it (POLZ and CAVANAUGH, this volume).

Here, evidence is provided on the sequence from occasional bacterial epigrowth, over frequent or even obligatory fouling by a diverse microbial and protistan community, to a species-specific obligatory symbiotic bacterial coat in marine free-living nematodes and among members of the peritrichous ciliate genus *Zoothamnium*.

Associations between micro-organisms or protists and marine nematodes

Approximately 4000 species of free-living marine nematodes have been described thus far. With few exceptions they belong to the Subclass Adenophorea and may be classified into 6 orders (Enoplida, Areolaimida, Desmoscolecida, Monhysterida, Chromadorida, and Desmodorida). The body of nematodes is covered by a highly complex cuticle (BIRD and BIRD 1991, WRIGHT 1991, URBANCIK et al. in press) which is moulted 4 times during development from larva to adult. Although the life span of marine free-living nematodes - much of which is spent in the adult stage - may exceed one year (GERLACH and SCHRAGE 1972), the cuticle of most animals is remarkably

free of microbial fouling. In contrast, the surface of other objects in the sea, living or non-living, is rapidly fouled by a diverse consortium of bacteria, diatoms, fungi, and protozoans (SIEBURTH 1975, NOVAK 1984) which may not only completely cover the surface, but even form several layers by different species overgrowing each other. Keeping the cuticle clean must be an active process involving substances secreted by the nematodes as long as they are alive and healthy, because moribund and dead individuals are rapidly colonised by a varied and abundant microbial assemblage (TIETJEN 1967, RIEMANN pers. comm., OTT unpubl. observ.).

The occasional occurrence of bacterial patches has been observed in a variety of nematode species from systematically diverse groups such as the *Syringolaimidae*, the *Oncholaimidae*, and the *Monhysteridae*. In all these cases only a small area of the body shows fouling and not all individuals in a sample are infected (the tip of the tail in *Syringolaimus* sp., the praeanal area in *Paroncholaimus* sp., and the cephalic setae in *Steineria sterreri*) (Fig. 1).

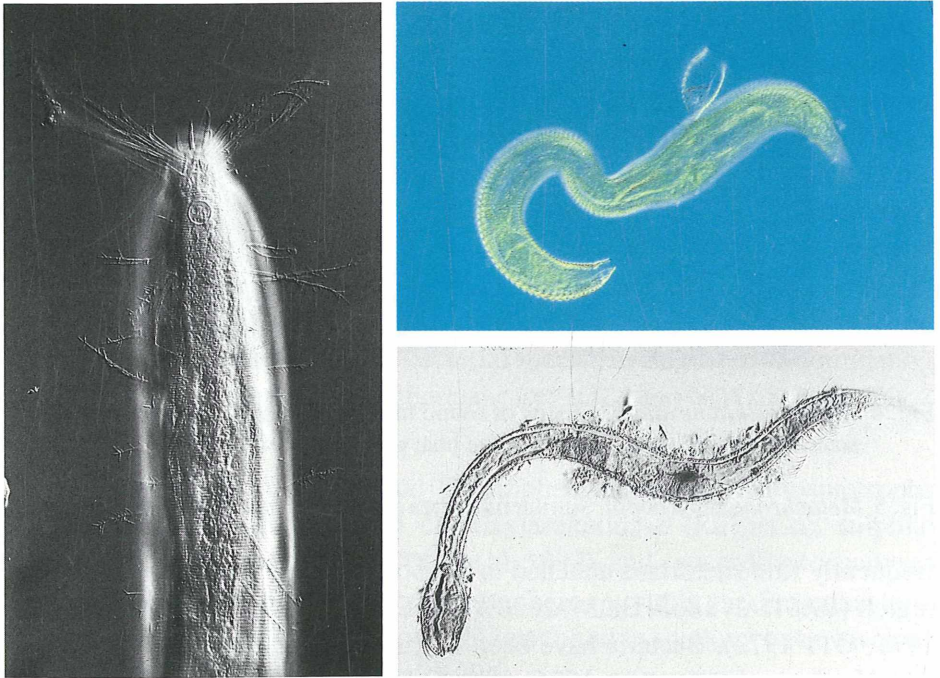


Fig. 1. *Steineria sterreri*. Anterior end with rod-shaped bacteria attached to cephalic setae.

Fig. 2. Epsilonematid with a suctorium attached to its body (Photo R. NOVAK).

Fig. 3. Draconematid covered by a diverse microbial consortium embedded in fluffy detritus.

In the Desmoscolecida, which incorporate foreign particles in special, ring-shaped zones of their cuticle colonies of microbes have been found attached to the cuticle (BLOME and RIEMANN 1987), and suctorians have been reported from several species (KREIS 1934, ALLGÉN 1951, TIMM 1970).

Only in the Desmodorida, however, has a larger number of cases of fouling of the cuticle by microbes and protists been reported. Suctorians are found in the family Epsilonematidae (Fig. 2), and the Draconematidae are rarely found without a detritus cover on their cuticle containing numerous bacteria (Fig. 3). Within the Monoposthiidae, filiform micro-organisms are attached to the anterior body region in *Monoposthia duodecimalata* (CHITWOOD 1936, as "fungal spores") and *M. hexalata* (Fig. 4). In the family Desmodoridae we

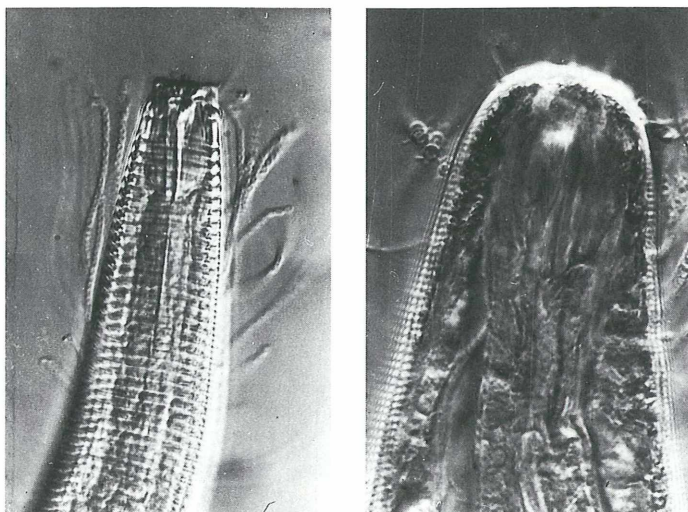


Fig. 4. *Monoposthia hexalata*. Chains of round micro-organisms (bacteria or cyanobacteria) attached to the cuticle in the pharyngeal region.

Fig. 5. *Metachromadora obesa*. Similar microbes as in Fig. 4 attached to anterior region.

frequently find suctorians attached to the body, mainly in the posterior body region (BASTIAN 1865, DE MAN 1890, ALLGÉN 1949, TIMM 1952, TIETJEN 1971, OTT 1972). Bacteria have been noted on *Metachromadora onyxoides* and *M. obesa* (CHITWOOD 1936) (Fig. 5), on *Spirinia gnaigeri* (own unpublished observation) and *S. parasitifera* (BASTIAN 1965), as well as on several species of the genus *Desmodora* (BLOME and RIEMANN 1987, own observations). In fact, in almost all specimens belonging to the genera *Desmodora*, *Spirinia*, and *Chromaspirina* in the author's collection a more or less well-developed and sometimes almost regular bacterial epigrowth is evident (Fig. 6). TIETJEN (1971) describes diatoms growing on the cuticle of *Chro-*

maspirina pontica and *Metachomadora onyxoides*. Certain species of the genus *Desmodora* carry veritable "microgardens" on their bodies (Figs 7-9) which may change in intensity seasonally (OTT unpubl. observ.) or may be connected with reproductive status (BLOME and RIEMANN 1987). It is unclear whether the worms suffer or even benefit from this microbial epigrowth. The microbes probably take advantage of the association with a vagile host, which ensures a defined position with respect to the surface or the chemocline in the sediment, gives them access to constantly new resources in the environment, and which even may secrete substances of immediate use to the microbes and protists.

In the Stilbonematinae, a subfamily within the Desmodoridae, we find an obligatory, species-(or at least genus-)specific cover of chemolithoautotrophic sulphur-oxidising bacteria on the cuticle. This coat covers the entire body, leaving only the tip of the tail and the anterior end (in some cases an anterior portion several hundred microns long) free of microbes (Figs 10-11). Within one animal (and also within one species of worm) the bacteria appear uniform in shape and are arranged regularly on the cuticle, forming striking patterns. In the highly structured bacterial coats typical for the genus *Eubostrichus*, several types of bacteria are present. The dominating morphotype consists of large nonseptate filaments containing multiple nucleoids (POLZ et al. 1992). They are either crescent-shaped and arranged in a spiral pattern around the worm's body (*E. parasitiferus*, *E. topiarius*, and related forms). Alternatively, the microbes are up to 100 µm long, attached with one end, and arranged parallel, thus forming a well-groomed fur covering the worm's body (*E. diana*) (Figs 12-13). Whether the abundant and diverse cocci and rods found among the fur represent different bacterial species or stages of the dominating morphotype is not clear in the individual cases (OTT and NOVAK 1989, POLZ et al. 1992, OTT 1994).

The bacteria are sulphide- and thiosulphate-oxidising chemoautotrophs containing ribulose biphosphate carboxylase/oxidase (RuBisCo), sulphite oxidase and APS-sulphurylase (POLZ et al. 1992), and - according to analyses of the 16s rRNA gene - belong to the γ -subgroup within the Proteobacteria and are closely related to the endosymbionts found in shallow-water bivalves and the Vestimentifera (POLZ et al. 1994).

The stilbonematids feed on these microbes. Stable isotope ratios ($\delta^{13}\text{C}$) of bacteria and worms suggest that the bacteria are their preferred (if not exclusive) food. The worms, in turn, provide the bacteria alternately with sulphide and oxygen by migrating through the chemocline (OTT et al. 1991).

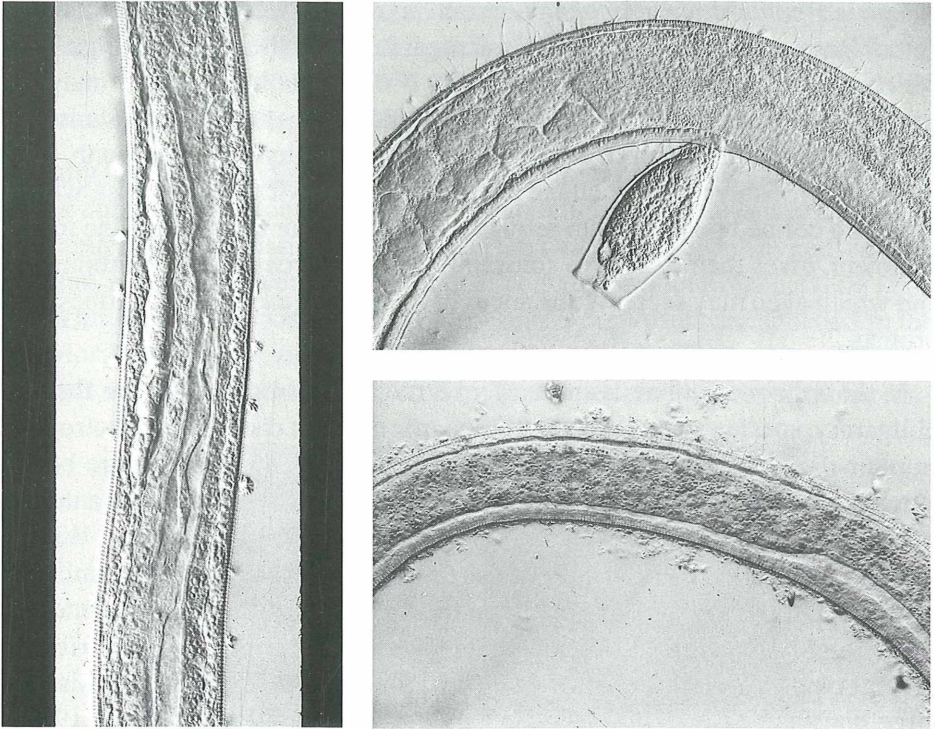


Fig. 6. *Chromaspirina* sp. Tufts of bacteria regularly arranged along the body of the worm.

Fig. 7. *Desmodora* sp. Suctorians and bacteria on cuticle of midbody region.

Fig. 8. *Desmodora ovigera*. Diatoms and bacteria covering cuticle.

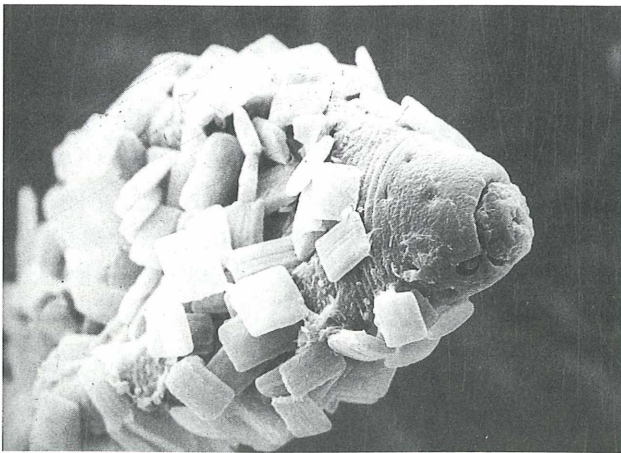


Fig. 9. *Desmodora ovigera*. Stalked diatoms (*Grammatophora* sp.) almost completely covering the cuticle of the worm. SEM (Photo R. NOVAK)

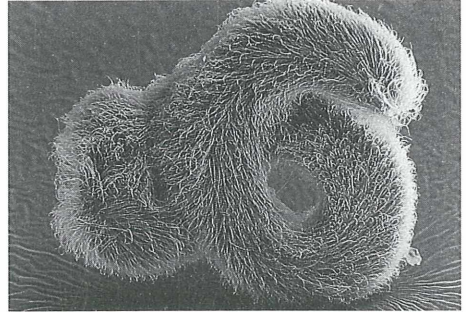
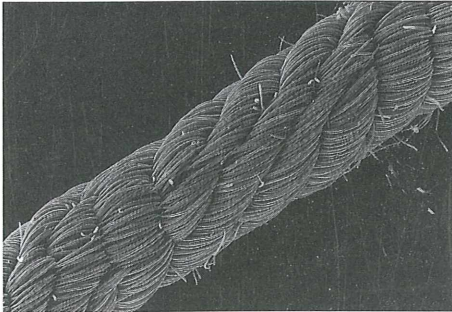
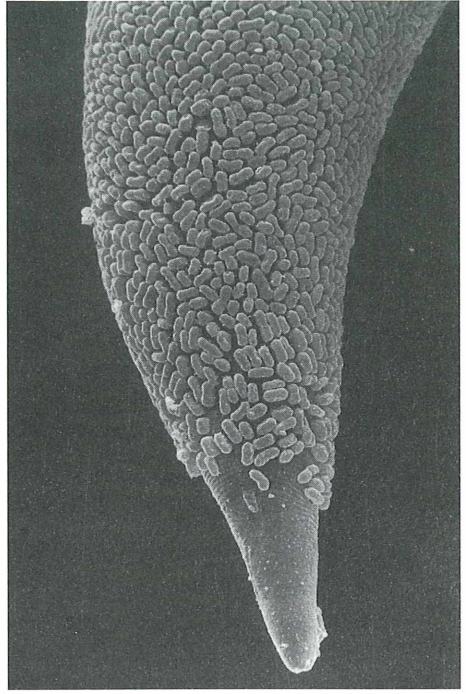
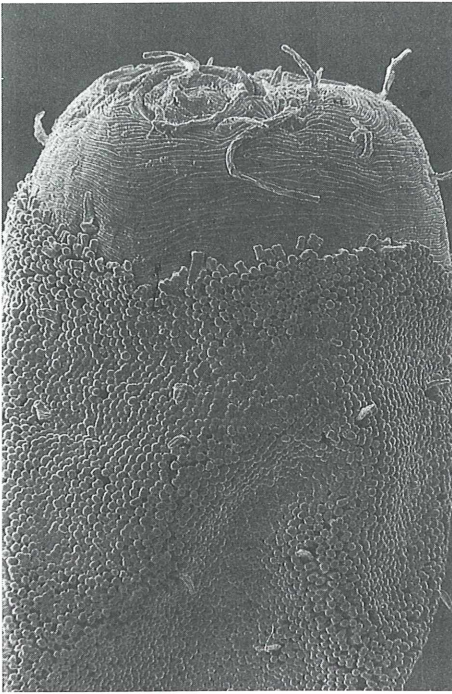


Fig. 10. *Laxus cosmopolitus*. Anterior end showing begin of bacterial coat shortly behind amphids. SEM (Photo R. NOVAK and M. POLZ).

Fig. 11. *Laxus cosmopolitus*. Posterior end. Only the tip of the tail is free of bacteria. SEM (Photo R. NOVAK and M. POLZ).

Fig. 12. *Eubostrichus* sp. Midbody region with crescent-shaped microbes arranged spirally around the body (Photo R. NOVAK and M. POLZ)

Fig. 13. *Eubostrichus diana*. Total view of a specimen covered by long, nonseptate filaments. SEM (Photo W. URBANCIK)

Associations between peritrichous ciliates and micro-organisms

In the colonial ciliate genus *Zoothamnium* (Peritrichida) (Fig. 14) - which comprises many sessile and a few free-swimming species - microbial epigrowth has been reported in a number of species (see BAUER-NEBELSICK et al. 1995 for a review). *Zoothamnium niveum* was described by HEMPRICH and EHRENBURG (1831) more than hundred years ago from the Red Sea. The authors already remarked on the white colour of the colonies and the species name, in fact, means "snowy". This species is abundant on vertical or overhanging peat walls bordering mangrove channels in the Belize Barrier Reef system (BAUER-NEBELSICK et al. 1995). The mangrove peat - consisting mainly of the roots of the Red mangrove, *Rhizophora mangle* - contains high concentrations of sulphide (up to 1 mM) in its pore water, whereas the water in the channels is oxygen-saturated most of the time. *Zoothamnium niveum* is probably widespread in tropical and warm-temperate waters along sharp interfaces between sulphidic and oxic water. White *Zoothamnium* colonies have been observed in Mediterranean *Caulerpa* and *Posidonia* meadows, occurring close to accumulations of dead organic matter and sulphide formation (T. PILLEN, A. SVOBODA pers. comm.), and around submarine sulphur springs at Madeira (P. WIRTZ pers. comm.).



Fig. 14. Group of *Zoothamnium niveum* colonies on mangrove peat. Twin Cayes, Belize, 0.5 m depth.

Zoothamnium niveum is completely covered by a bacterial microfilm (Fig. 15) consisting of oblong cocci on the microzooids (feeding zooids) and rods on the stalk, the branches, and the macrozooids (swarmers). From the branches towards the distal portions of the microzooids these two morphological types of bacteria intergrade into each other.

Ecological (occurrence at the sulphide/oxygen interface), biochemical (presence of RuBisCo), and ultrastructural evidence (fine structure of bacteria and their presence in food vacuoles) points to a chemolithoautotrophic sulphur-oxidising nature of the bacteria and to their dominant role as food for the ciliates. They are most probably taken up from suspension in the vicinity of the oral ciliature. SEM pictures show that bacteria tend to be liberated in the distal portion of the microzooids (Fig. 16). The spontaneous contraction and expansion behaviour of the ciliate colonies exposes the bacteria to high sulphide concentrations in the boundary layer just above the peat surface and - upon expansion to the total height of the colony of 10-12 mm - gives them access to oxygen in the ambient water.

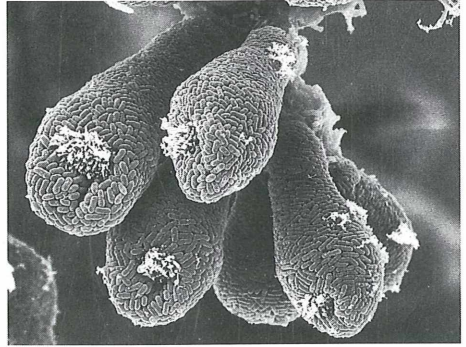
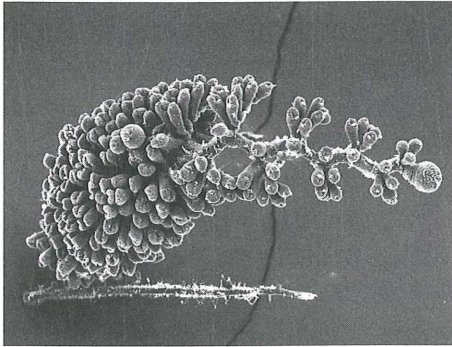


Fig. 15. *Zoothamnium niveum*. Contracted colony covered by symbiotic bacteria attached to a plant fibre. SEM (Photo M. BAUER-NEBELSICK)

Fig. 16. *Zoothamnium niveum*. Several microzooids showing detachment of bacteria on distal part. SEM (Photo M. BAUER-NEBELSICK)

The evolution of bacterial symbioses

Both the nematodes and the ciliates with their associated epigrowth may serve as a model for the evolution of more intimate, species-specific and obligatory symbioses. In the nematodes, the Stilbonematinae represent a case in which several genera which have developed such a symbiosis (whether only once or several times is still unclear) belong to a family where a mixed,

occasional microbial epigrowth is frequently found. In the case of the ciliates, *Zoothamnium niveum* is the sole species which is a partner in an obligatory symbiosis within a large genus with a record of microbial fouling. This points to a very early stage in the development of such a symbiosis and contrasts with most endosymbioses, which are characteristic for families (Lucinidae and Thyasiridae among the bivalves) or even phyla (Vestimentifera, Pogonophora).

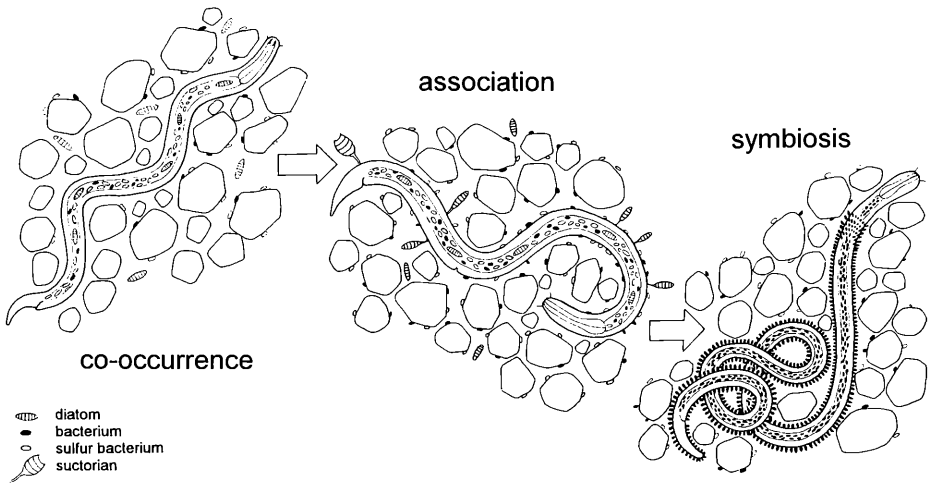


Fig. 17: Model of the evolution of bacterial extosymbioses in nematodes. Diatoms and bacteria co-occur with a microvorous nematode in a marine sand (left); a variety of microorganisms form an association with a worm by fouling its cuticle (center); the preference of the worm for life in the chemokline selects sulfur bacteria, which coat the cuticle of the nematode and serve as food for their partner in a symbiosis (right).

A prerequisite for establishing a relationship between two species is their co-occurrence in the same habitat (Fig. 17). The reason for this may be the same factor or different but coupled factors. In the case of the Stilbonematinae we may assume that it is the tolerance to low oxygen concentrations and low metabolic rates (HEIP et al. 1985, SCHIEMER et al. 1991) on the side of the nematodes and the requirement for reduced sulphur compounds in the bacteria that brought the ancestors of both together in the RPD layer (redox potential discontinuity layer, chemocline). The limited capability of the worms to prevent fouling of the cuticle facilitated attachment of the bacteria. Migrations of the worms between the surficial oxic layers and deep sulphidic layers - probably to exploit anaerobic bacterial mats or deeper pools of DOM produced through bacterial fermentation - selected sulphur bacteria from the mixed epigrowth because they not only tolerated but also benefited from the change

between oxic and sulphidic conditions. This benefit and the concomitant selection force is especially pronounced in situations with weak or changing chemoclines where the association with a vagile host pays off even considering the cost of being eaten. Such weak and unstable chemoclines are the typical habitat of the Stilbonematinae, whereas they are rare or absent in stable sharp gradients where bacterial mats (e.g., *Beggiatoa*, *Thioploca*) are more efficient in using sulphide in the absence of an invertebrate consumer.

Although the symbiosis is obligatory for the worms, it is still unclear whether this is also the case for the bacteria. There are indications that the bacteria may be members of the free-living community which infect (or are actively picked up by) the nematodes. In the deep-sea hot vent shrimp *Rimicaris exoculata*, the species of ectosymbiotic bacteria covering parts of the body probably makes up almost half of the free-living bacterial population covering the vent chimneys on the outside (POLZ and CAVANAUGH 1995). Although both the shrimp and the nematodes probably exclusively feed on their symbionts, the primary association was through fouling of the host's surface. A similar route to symbiosis may be assumed in *Zoothamnium niveum* and its ectosymbiotic bacteria. In this case the mobile stage (macrozooid) may be instrumental in finding areas of high sulphide flux suitable for the bacteria.

An alternative path to symbioses in nematodes may have been directly through the worms feeding on bacteria or accumulations of organic matter containing bacteria. Certain bacteria may have resisted digestion. Nematodes have difficulties to digest bacteria that have not been broken up mechanically. The bacteria found in the gut rudiments of species of the mouthless genus *Astomonema* and the turbellarian *Paracatenula* sp. (OTT et al 1981, GIERE et al. 1995, GIERE this volume) may have been food items of the ancestors of these worms. Similarly, the ancestors of Pogonophora and Vestimentifera were probably bacterivorous suspension feeders.

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