

Bacterial endosymbioses in marine littoral worms

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Abstract: Symbioses with sulfur bacteria are not restricted to the deep sea. Littoral sediments with hydrogen sulfide underneath an oxic surface layer are often populated by gutless marine Oligochaeta living in obligate symbiosis with "sulfur bacteria". Representatives of about 100 interstitial whitish species occur preferably around the oxic/sulfidic chemocline in calcareous sediments of warmer regions. A thick layer of endosymbiotic bacteria is extracellularly located between extensions of the epidermal cells underneath the cuticle. As chemoautotrophs, the prokaryotic symbionts gain metabolic energy by oxidizing reduced sulfur compounds, but can also store inert sulfur. They are regularly enclosed and lysed by the worm's epidermal cytoplasm. Transcuticular uptake of dissolved organic compounds at considerable rates has been shown. Transmittance of the bacteria to the next generation of annelid hosts is probably vertical by "infection" of the freshly deposited eggs. A recent approach by molecular genetic methods attempts to characterize the symbiotic prokaryotes and relate their genetic distance to the taxonomic and zoogeographical pattern of their hosts. The structure of the symbiosis in gutless oligochaetes is compared to that in various other bacteria-symbiotic "worms", most of them with a modified digestive system. They fall into five structural categories, from an endocuticular to an endointestinal position. Two putative pathways of symbiotic establishment, via the outer surface and the gut lumen, are outlined.

Introduction

Symbioses of animals with chemoautotrophic bacteria are not restricted to the deep sea. Shallow-water sediments harbor interesting parallels to deep-sea symbioses in several groups of invertebrate worms. Like the deep-sea representatives, they are also associated with gram-negative bacteria oxidizing reduced sulfur compounds. In fact, endosymbiotic marine Oligochaeta (as well as interstitial ectosymbiotic nematodes) have been discovered prior to the hydrothermal vents and their symbiotic fauna. But, since the discovery of new meiobenthic worms is not unusual, since their affiliation to known families did not seem problematical, and since their habitat is by no means as spectacular as the deep sea vents, no detailed studies on either the marine oligochaetes or nematodes were immediately performed. Their bacterial symbiosis was therefore not revealed (GIERE 1981) before that of *Riftia* and cohabitants from the deep sea.

The systematically vague term "worms" allows focussing on our annelid studies, putting these in context to some nematode work (OTT et al. 1982), as well as relating these to the situation in pogonophores and to some little-studied "worms" which maintain an internal association with bacteria.

Material and Methods

Worms were fixed in Trump's fixative (MCDOWELL 1978), a buffered mixture of formaldehyde and glutaraldehyde solution (buffer: cacodylate). The numerous preparations for electron microscopy followed routine procedures (embedding in Spurr's resin, copper grids, contrasting in aqueous uranyl acetate and lead citrate). In order to directly record sulfide and oxygen in the sediment column, combined needle electrodes (VISSCHER et al. 1991) were modified and specially adapted for use with a micromanipulator.

Results

The habitat of the gutless oligochaetes is an important clue for understanding their symbiosis. In the light of the fascinating world of hydrothermal vents, it is sometimes overlooked that the "marine sulfide system" is ubiquitous and quite common. It occurs world-wide underneath a few millimeters of surface sediment in most soft-bottom areas (Fig. 1). Rich in detritus and bacteria, these subsurface layers around the oxic/anoxic interface are inhabited by a specially adapted fauna taking advantage of the rich food supply and the reduced interspecific competition. One of the most favourable biotopes are calcareous or coralline sands in warm-water areas. Here, oligochaete annelids of the family Tubificidae can attain high population abundance. They often also co-occur syntopically in several species, all of them with a shiny white appearance.

While their white colour is already unusual (Fig. 2), microscopical examination reveals the complete absence of a gut (Fig. 3), mouth, and anus (as well as excretory nephridia). But the most striking feature, a thick layer of endobacteria, is clearly visible only in the electron microscope (Fig. 4).

Two morphotypes of extracellular, gram-negative bacteria fill the space between cuticle and epidermis along most, but not the entire length of the worm's body. They diverge significantly in both size and fine structure (GIERE et al. 1995a, Fig. 5). Their characteristic arrangement in the worm's body as well as the fact that the smaller, rod-shaped type is typically positioned more peripherally than the bigger, oval type points to a highly organized and distributionally controlled association in this obligate symbiosis.

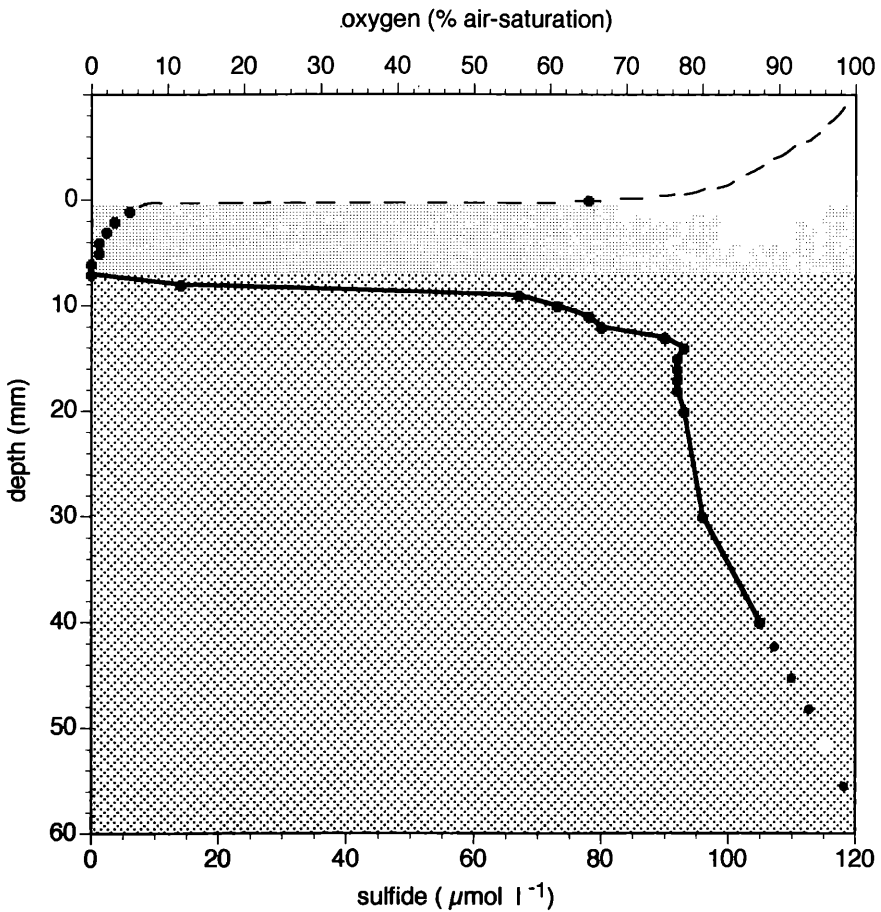


Fig. 1: Vertical profiles of oxygen and hydrogen sulfide in the habitat of *Inanidrilus leukodermatus*, calcareous sand from Bermuda; note shallow depth of oxic layer: bright gray; sulfidic layer: dark gray; needle electrode recordings.

This characterization is underlined by our studies on the transmittance of the bacteria: Although based on a few cases only, we can assume vertical transmittance of the prokaryotes to the next host generation. The eggs of the worm are apparently infected at oviposition by bacteria released from a "bacterial pad" adjoining the ovipore. After intrusion into the egg, a balanced relation of division and digestion of bacteria is established. Bacterial cell division takes place in the more peripheral zone underneath the cuticle, phagocytotic enclosure into the host's epidermal cells and gradual lysis of the prokaryotes in a deeper, more central zone (GIERE and LANGHELD 1987). The completely reduced digestive tract and excretory organs in these tubificid annelids underline the high degree of integration in the symbiotic relation and the dependence on the worms' internalized bacterial food source.

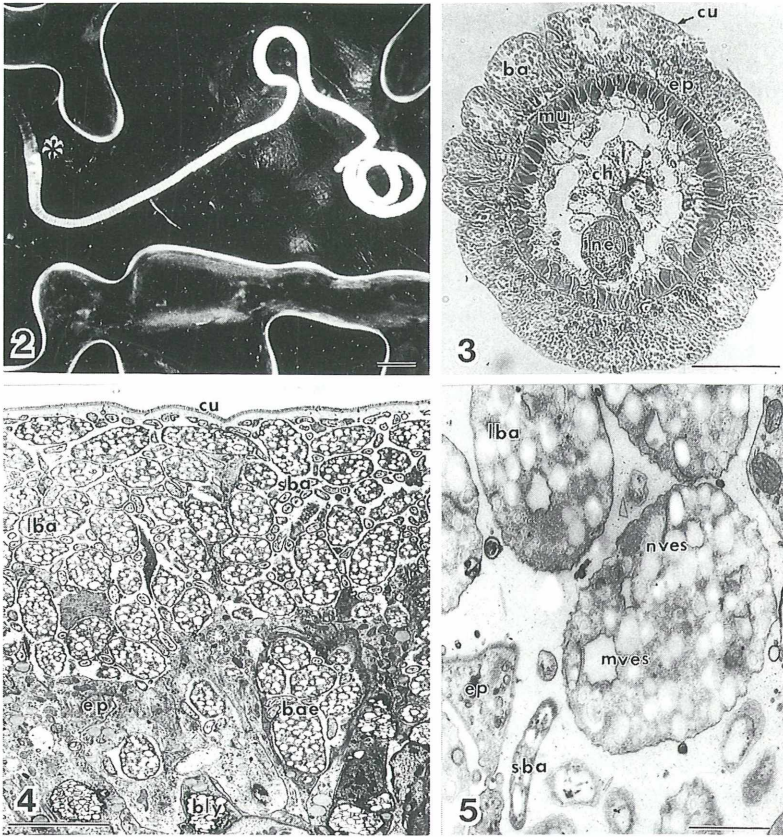


Fig. 2: *Inanidrilus leukodermatus* (Annelida, Oligochaeta, Tubificidae), anterior end to the left; asterisk: clitellar region; live photograph, stereomicroscope with microflash; scale bar: 1 mm.

Fig. 3: *Inanidrilus leukodermatus*, cross section; ba: extracellular bacteria; ch: chloragocytes; cu: cuticle; ep: epidermal cells; mu: body musculature; ne: nerve cord; light micrograph; scale bar: 50 μ m.

Fig. 4: *Inanidrilus leukodermatus*, cross section through epidermis and cuticle showing two morphotypes of bacteria and their gradual enclosure and phagocytosis; bae: bacteria enclosed by epidermal cytoplasm; by: bacteria in phagocytotic lysis; cu: cuticle with epicuticular projections; ep: epidermal cytoplasm; lba: large bacterial morphotype; sba: small bacterial morphotype; transmission electron micrograph; scale bar: 5 μ m.

Fig. 5: *Inanidrilus leukodermatus*, cross section; two morphotypes of subcuticular bacteria, the large one with some membrane-bound and numerous non-membrane-bound vesicles; mves: membrane-bound vesicle; nves: non membrane-bound vesicles; for further abbreviations see Fig. 4; transmission electron micrograph; scale bar: 1 μ m.

The bacteria have been calculated to make up about 25 % of the host's body volume (GIERE et al. 1995a). This is much more than calculated for obturate Pogonophora (1 %, Southward 1982) and comparable to Vestimentifera (FISHER 1990). The light carbon stable isotope ratio of the worms (-26 ‰), signifies a substantial, if not dominant bacterial contribution to the nutrition of their hosts (GIERE et al. 1991). If well fed, the bacterial cytoplasm is filled with globules containing rich amounts (10 % of the worm's weight) of polyhydroxybutyrate, a common bacterial reserve substance. In addition, sulfur is stored in membrane-bound vacuoles (Fig. 5, GIERE 1985), apparently in the viscid form of polythionates or other long-chained hydrophilic sulfur compounds which can be easily metabolized (STEUDEL 1989).

This mobilization of reserves apparently takes place when the worms are exposed to oxic sediment conditions. Then, the animals' shiny white colour, caused by the light refraction of the bacterial reserves, turns into a pale gray; the original color is quickly restored after incubation in H₂S-containing sediments. Contrary to the initial assumption, the chemoautotrophic bacteria in the worms assimilate thiosulfate at a high rate more than they take up hydrogen sulfide. Energy is gained by oxidation into either inert sulfur, stored in membrane-bound vesicles (see above, Fig. 5), or into sulfate; the latter was found to increase in the ambient medium after maintenance under oxic conditions (GIERE et al. 1988). The oxygen required is taken up by diffusion through the cuticle while the worms invade oxic layers. Whether the blood in the large vessels of the worms has an oxygen-storing function remains to be investigated.

The prokaryotes' physiological requirement for an alternating uptake of oxygen and sulfide or thiosulfate has an ecological consequence: The most efficient zone to gain access to both of these compounds is the oxycline, usually a rather narrow boundary layer requiring only short migrations to reach oxic or sulfidic horizons. Thus, the worms orientate themselves according to the needs of their bacteria, preferring and following the chemocline. In a fluctuating environment the host is the vehicle for the immobile bacteria, keeping them in their optimal geochemical microhabitat (GIERE et al. 1991).

The obligate symbiosis between chemoautotrophic sulfur bacteria and annelid worms outlined here appears to have developed in principally the same pattern in perhaps 100 species of gutless oligochaetes belonging to two widely distributed genera. In many respects this association parallels the bacteria symbioses of animals from deep sea hot vents and cold seeps. The host diversity in oligochaetes is especially intriguing, enabling studies on the genetic aspects and possible phylogenetical pathways of this association.

Initial gene sequences of the prokaryotic symbionts in *Inanidrilus leukoder-matus* from Bermuda pointed to the existence of just one bacterial phylotype despite the presence of two morphotypes (DUBILIER et al. 1995). They indicated a close relationship to the ectosymbiotic bacteria in the nematode *Laxus* within the γ -subdivision of proteobacteria (POLZ et al. 1994). However, new data on *Inanidrilus leukoder-matus* from Belize as well as on other, related species do not rule out the existence of more than one symbiotic bacterium, with one major, dominating, and another "minor" bacterial type which is rarely well expressed. Further studies are needed to reach safer ground in this field.

Discussion and Conclusions

The pathways along which symbiotic bacteria have been incorporated into the hosts' body apparently proceeded along different lines. None the less, modification and functional reduction of the digestive tract seems a common morphological feature in bacteria-symbiotic marine animals (LE PENNEC et al. 1995). This is related to a common ecological feature, life in microoxic habitats with steep oxic/sulfidic gradients, regardless whether they originate from geothermal processes or normal microbial activity.

Taxonomically divergent bacteria-symbiotic worm taxa, mostly with a modified digestive tract, can be grouped into five categories (Fig. 6 a-f)

Intracuticular endobacteria (Fig. 6a)

Examples for this rare group are species of the aberrant polychaete family Questidae (GIERE, unpubl., Fig. 7) and the enigmatic worm *Jennaria pulchra* (RIEGER 1991, RIEGER and RIEGER 1991). The echiurid *Urechis caupo* also harbours numerous endobacteria in the deeper layers of its cuticle, but also in its epidermis (MENON and ARP 1993). Within this category, the nature and role of the symbiotic bacteria is unknown. Aberrant structures in the general anatomy of the Questidae do not seem to be related to the bacterial association.

Subcuticular extracellular symbionts (Fig. 6b)

The gutless tubificid oligochaetes described above exemplify that, despite the peripheral and extracellular position of bacteria, the hosts fully depend on the obligate symbiosis, having completely reduced all digestive and excretory structures.

Intraepidermal, intracellular symbionts (Fig. 6c)

Knowledge of this group is restricted to a few structural descriptions. The nematode *Siphonolaimus tubicen*, investigated by OTT et al. (1982), is a good representative. *Urechis caupo* (Echiurida) has also been reported to bear numerous endobacteria in the peripheral layers of its epidermis (MENON and ARP 1993). The nature of the symbiotic bacteria is unknown, but their abundance in the epidermis indicates a considerable role.

Extracellular gut bacteria in a vestigial and functionally modified intestine (Fig. 6d)

This group is represented by another siphonolaimid nematode, *Astomonema southwardorum*, found in the North Sea bottom in characteristic, pock mark-like methane seeps with reducing conditions. As indicated by the generic name, the animal is mouthless, lacking pharynx and anus. Huge bacteria (one type only) were shown to fill the lumen of the intestinal tube (GIERE et al. 1995b). The intestinal cells are large yet degenerated, sometimes forming only a thin cover around the bacterial mass (Fig. 8). The geochemical data of the surrounding sediment suggest a function of these bacteria as sulfide oxidizers.

Intracellular bacteria in intestinal cells, intestine non-functional and much modified (Figs. 6e, f)

This category can be exemplified by two different worms. The nematode *Astomonema jenneri* was found in detritus-rich \pm sulfidic marine sands (OTT et al. 1982). Again, a functional pharynx is not developed. But here, the intestinal rudiment is a massive string of large cells harbouring two morphotypes of numerous intracellular bacteria which may occupy 25 to 50 % of the host's body volume (Fig. 6e). Judging from the habitat, these bacteria, similar to the oligochaete symbionts, are thought to be chemoautotrophic sulfide oxidizers. Also the mouthless turbellarian *Paracatenula* sp. (Retronectidae) from reducing sediments was described (OTT et al. 1982) to harbour in its solid, non-functional gut intracellular bacteria, a structural situation closely resembling that in *Astomonema jenneri*. The "classical" examples of symbiotic animals from the deep sea are doubtlessly the "vent worms", the Vestimentifera, and their relatives from deep-water muds, the smaller Perviata (Pogonophora) (Fig. 6f). Although morphologically much different from the above small invertebrates, they display a symbiotic arrangement allowing them to be grouped in the last-mentioned category. Since these endosymbioses are well documented, only some structural details need to be mentioned here.

SOUTHWARD(1988) has shown that the conspicuously brownish central strand of tissue, the trophosome - a dominant structure in the posterior part of the body, particularly in the Vestimentifera - represents modified intestinal tissue. In the larvae the trophosome still has a narrow lumen, which in some species is maintained even in the adults. The intestinal cells contain abundant chemoautotrophic intracellular bacteria. Divergent in size and structure in the various species, they usually lie intracellularly in vacuoles (most Perviate) or directly in the trophosomal cytoplasm (Obturata or Vestimentifera).

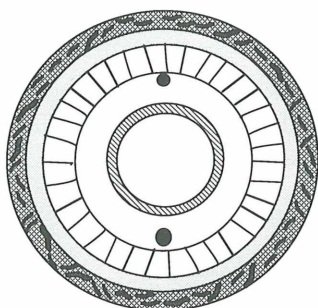
The above categories give rise to questions about the evolutionary pathways in these symbioses. The prevalent hypothesis is that the association originated with bacteria from the environment (SMITH 1979) and that it subsequently evolved into an interactive dependence of symbiotic partners following two principal progressive lines.

The first line begins with a transformation of an occasional aufwuchs-type association of bacteria on animal surfaces into a regular, regulated, and interactive symbiosis of cuticular epibacteria (OTT et al. 1991, POLZ et al. 1994). The next step would be incorporation of the bacteria into the cuticle (e.g., in Questidae). A wide interface between cuticle and epidermis offers spatially more possibilities for establishing an extracellular symbiosis of enhanced mutual importance, as exemplified in the group of gutless oligochaetes.

A parallel aspect might be intrusion of bacteria directly into the epidermal cells. This is common in molluscs (FISHER 1990, PRIEUR et al. 1990), but unusual in worms like annelids and nematodes. The existence of bacteria both in the inner cuticle and outer epidermis in the echiurid *Urechis caupo* (MENON and ARP 1993) underlines the possibility of a bacterial transition from cuticle to epidermis. In worms, the relevance of these cuticular or epidermal endosymbiotic patterns is poorly studied and remains to be clarified.

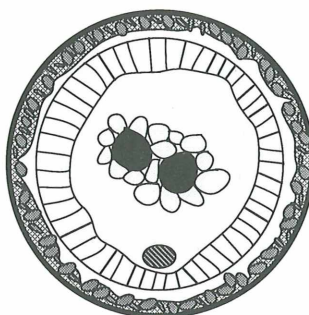
Fig. 6a-f: Categories of endobacterial symbioses in various "worm" taxa; schematic cross sections; bacteria and bacteria-bearing layer differently hatched.

a. Intracuticular symbionts



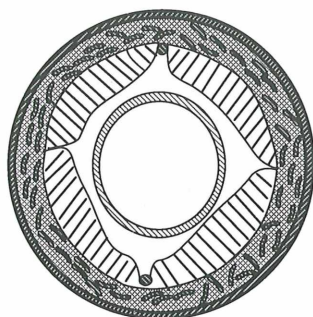
Polychaeta: *Questa* sp.
Annelida ?: *Jennaria pulchra*
Echiurida: *Urechis caupo* (partim)

b. Subcuticular extracellular symbionts



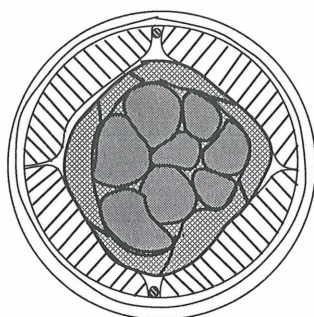
Oligochaeta:
Inanidrilus spp.
Olavius spp.

c. Intraepidermal symbionts



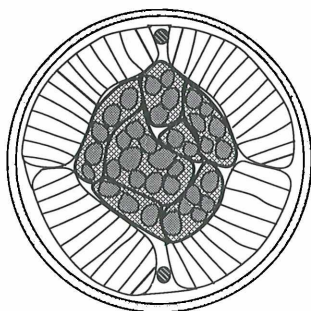
Nematodes: *Siphonolaimus tubicen*
Echiurida: *Urechis caupo* (partim)

d. Extracellular gut symbionts



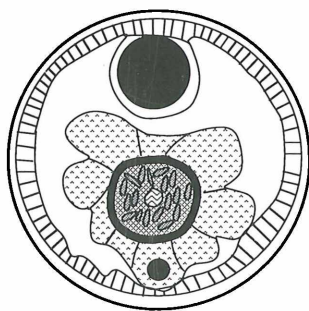
Nematodes: *Astomonema southwardorum*

e. Intestinal intracellular symbionts



Nematodes:
Astomonema jenneri

f. Intestinal intracellular symbionts



Pogonophora:
Vestimentifera, *Perviatia*

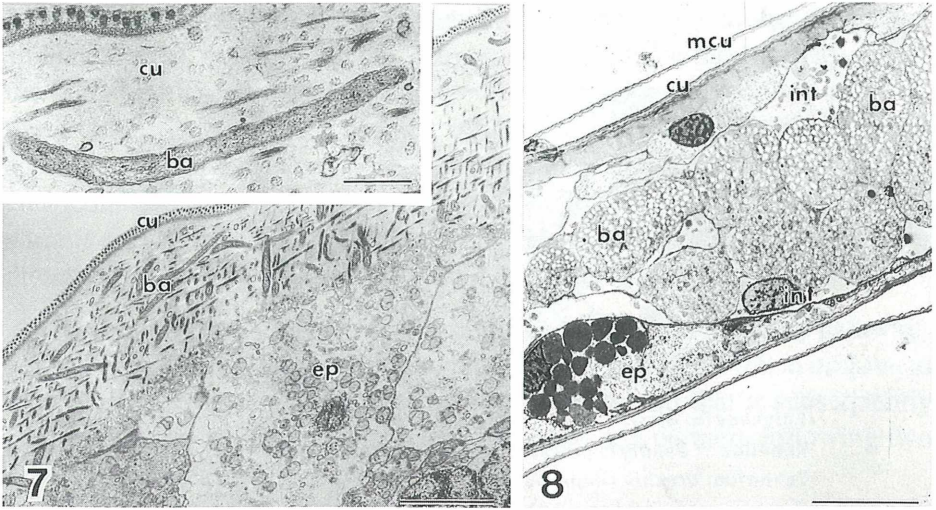


Fig. 7: *Questa* sp. (Annelida, Polychaeta), Belize; cross section, with intracuticular bacteria; ba: bacteria; cu: cuticle; ep: epidermis; scale bar: 2 µm; inset: one longitudinal sectioned bacterium in cuticle, transmission electron micrograph, scale bar: 0.5 µm.

Fig. 8: *Astomonema southwardorum* (Nematoda, Siphonolaimida), longitudinal section through moulting animal, median region of body; ba: extracellular bacteria filling intestinal lumen; cu: cuticle, ep: epidermal cell; int: intestinal cell; mcu: moulted cuticle; transmission electron micrograph, scale bar: 5 µm.

The second line may have started with bacterivorous deposit feeders (many meiofauna) or from a regular intestinal bacterial biota. A shift from bacteria-mediated nutrition to a fully bacteria-based metabolism would benefit from packing as many bacteria as possible into the gut lumen. Completely filling the intestinal lumen, the prokaryotes could then gradually take over most nutritional tasks of the host, allowing for rudimentation of the gut with closure of mouth and anus (example: *Astomonema southwardorum*). The alternative solution in this scenario would be invasion of the intestinal cells themselves by the symbiotic bacteria. This often results in a voluminous and complex organ, as in the vestimentiferan Pogonophora, i.e., the step from extra- to intracellular intestinal bacteria-symbiosis.

Abandoning the mouth and functional gut clearly requires uptake of metabolic substances by diffusion through the animals' body. This is facilitated in microscopically small animals (see POWELL 1989) and is therefore frequent in meiofauna, which may even lack a blood or other distributive system (nematodes and plathelminths, OTT et al. 1982). Animals with larger bodies or surrounded by tubes (e.g., Vestimentifera) require a well-developed vascu-

lar system to supply their endobacteria with reduced, energy-rich compounds, as exemplified in the trophosome of the giant tube worms (similarly in many symbiotic bivalves; FISHER 1990). Hence, in intestinal symbioses of large animals, a reduction of digestive structures will probably occur only in parallel with the maintenance or even aromorphosis of distributive systems like blood vascularisation. Reliance solely on the diffusive potential of metabolites is functionally unfavourable or impossible in macroscopic animals.

LE PENNEC et al. (1995) postulated for symbiotic bivalves a progressive modification and reduction of the digestive tract in relation to sulfide exposure. No similar ecological connection can be established for the worms considered here. More small-scale sulfide measurements are needed to test this hypothesis. This survey also revealed no corresponding relation between gut reduction and the host's trophic reliance on the bacterial symbionts.

Other structural systems like annelid genital organs and nephridia have also been found to regularly harbour bacteria (GIERE, unpubl. data), but the nature of this association remains to be assessed. Only muscular layers have not been reported to be regularly colonized by non-pathogenic prokaryotes (see review by SAFFO 1992).

In conclusion, endosymbioses with bacteria have developed several times independently in the marine realm, both in the deep sea and - along similar lines - in shallow-water habitats. The structural aspects emphasized here are usually much better known than the ecological background or the physiological mechanisms involved. In all cases, symbiotic bacteria seem to gain energy autotrophically by oxidation of reduced substances, mainly the ubiquitous sulfide, but probably also thiosulfate (NELSON and FISHER 1995), present wherever sulfide develops (HOWARTH and TEAL 1980, JØRGENSEN and BAK 1991). Another energy source is methane, often concurrently present with sulfide. The pogonophoran tube worm *Siboglinum poseidoni* is known to harbour methanotrophs in its trophosome (SCHMALJOHANN and FLÜGEL 1987). One can even speculate on the discovery of animal symbioses with ammonium-oxidizing bacteria (for details see NELSON and FISHER 1995).

The genetic variety of endosymbiotic bacteria in worms is large. LAW's (1985) predictions concerning the evolution of organisms involved in endosymbioses are apparently invalid for these bacterial associations: There is no reduced rate of speciation recognizable in the inhabitant compared to the exhabitant (the host). Also, a reduced speciation among the partners joined in an endosymbiotic complex is not recognizable versus antagonistic associations (e.g., based on predation). Several genetically and perhaps also functionally little related types can occur in the same or closely related host. This would

correspond to the diversity of zooxanthellae in many marine animals (ROWAN and POWERS 1991). On the other hand, the genetic distance of the various gutless tubificid host species also needs to be clarified in order to assess the evolutionary and distributional steps of the intimate symbiosis with bacteria occurring in geographically disjunct areas in the absence of any propagatory stages like planktonic larvae. At any rate, speciation in the mutualistic complex "sulfur bacteria with gutless tubificids" seems very intense (ERSÉUS 1984, 1990); at present, however, a congruence in speciation between hosts and prokaryotes, as suggested by HAYGOOD and DISTEL (1993) for certain bacteria-luminescent fish and by DISTEL et al. (1994) for thiobiotic bivalves, is not recognizable.

This complicated scenario will no doubt stimulate further studies on the phylogenetic development of these intricate associations. Flocks of morphologically closely related host species, such as the gutless oligochaetes, represent especially promising material for further research in this fascinating field. Beyond the evolutionary aspects, these studies also offer opportunities to trace the distributional pathways of these symbioses which occur both along Atlantic and Pacific shores. At present, however, any zoogeographical conclusions drawn from this pattern are premature.

The chemoautotrophic endosymbioses show many similarities between worms living in such different habitats as the deep sea and shallow reaches. This is similar to the situation in bivalves (LE PENNEC et al. 1995). Our future studies on hydrothermal fauna will address this interesting parallel perspective between such highly contrasting biotopes, combining results from the shallow tidal bottoms with data from mid-water depths and deep-sea environments. Within this frame, shallow-water sites are clearly favoured by their easier access and simpler logistics.

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