

Ecology and biogeochemistry of *Paralvinella sulfincola* at northeast Pacific hydrothermal vents: review and comparison with *Alvinella* spp. of the east Pacific rise

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ABSTRACT

The "sulfide worm" *Paralvinella sulfincola* Desbruyères & Laubier 1993, of northeast Pacific hydrothermal vents, builds a mucous tube on the surface of high temperature chimneys, as does *Alvinella* spp. on the East Pacific Rise. *P. sulfincola* is a deposit feeder and likely grazes on thermophilic chimney bacteria. It is argued that deposit feeding is also the primary source of nutrition for *Alvinella* spp. The influence of both worms on the sulfur cycle and on chimney mineralization processes is discussed. While *Alvinella* appears to be more elaborate in its adaptations to the high temperature chimney environment, the functional significance of some of these apparent adaptations remains unclear. Observed effects of *P. sulfincola* on chimney mineralization suggest that the question of how *Alvinella* spp. influences chimney growth patterns needs to be re-addressed. Two previously proposed roles for the epibiotic bacteria in *Alvinella* spp., nutrition and detoxification, can be accomplished by *P. sulfincola* without the aid of episymbionts. This is a strong argument for a re-evaluation of the nature of the *Alvinella*-bacteria symbiosis.

RÉSUMÉ

Ecologie et biogéochimie du ver *Paralvinella sulfincola* des sources hydrothermales du Pacifique Nord-Est : revue et comparaison avec le genre *Alvinella* de la dorsale du Pacifique oriental

De façon identique aux *Alvinella* spp. présents au niveau de la dorsale du Pacifique oriental, le «ver sulfure», *Paralvinella sulfincola*, des sources hydrothermales situées dans le Pacifique Nord-Est, construit un tube de mucus à la limite des événements des cheminées d'où jaillit le fluide hydrothermal à haute température. Détritivore, *P. sulfincola* broute probablement des bactéries thermophiles présentes sur les cheminées. Pour *Alvinella* spp., l'alimentation détritique pourrait aussi être la source principale de nourriture. L'influence des deux vers sur le cycle du soufre et sur la minéralisation des cheminées est analysée. Bien que les *Alvinella* spp. semblent être mieux adaptés à un environnement de températures extrêmes, la fonction de certaines de ses adaptations apparentes n'est pas encore claire. Les effets observés de *P. sulfincola* sur la minéralisation des cheminées suggè-

rent que toute la question de l'influence d'*Alvinella* spp. sur la croissance des cheminées a besoin d'être reformulée. Ainsi, les deux rôles envisagés pour les bactéries épibiotiques chez *Alvinella* spp., soit la nutrition et la détoxification, peuvent être accomplis par *P. sulfincola* sans l'aide d'épisymbiontes. Ceci est un argument important qui entraîne le réexamen de la nature de la symbiose d'*Alvinella* avec les bactéries.

INTRODUCTION

Since the discovery of hydrothermal vent biological communities in 1977, numerous new vent-specific species have been described, many of which have unusual adaptations for bacterial-invertebrate symbiosis and for life at high temperatures. The intimate association of several species with mineral deposition processes has inspired studies of biomineralization (JUNIPER *et al.*, 1988, 1992). High temperature microorganisms have been the focus for most work on sulfide chimneys. In addition to thermophilic and ultra-thermophilic bacteria that grow within the plumbing system of chimneys and on chimney surfaces, a specialized chimney fauna flourishes in this extreme and rapidly changing environment (TUNNICLIFFE & JUNIPER, 1990). Adaptations of the chimney fauna to its habitat and its influence on mineralization processes are newly emerging areas of research.

Among the first organisms to colonize newly-formed chimney surfaces are the alvinellid worms (JUNIPER *et al.*, 1992). At northeast Pacific vent sites, the "sulfide worm", *Paralvinella sulfincola* Desbruyères and Laubier (1993) [in TUNNICLIFFE *et al.*, 1993], occupies a niche similar to that of *Alvinella pompejana* and *A. caudata* and occasionally *Paralvinella grasslei* on the East Pacific Rise (EPR) (DESBRUYÈRES *et al.*, 1985; DESBRUYÈRES & LAUBIER, 1986; TUNNICLIFFE *et al.*, 1993). The sulfide worm was originally thought to be a form of *Paralvinella palmiformis* that colonized environments where mineral precipitation is heavy, forming loose tube structures with its otherwise amorphous mucous secretions (JUNIPER *et al.*, 1988; TUNNICLIFFE & JUNIPER, 1990). Later morphological, genetic and behavioral studies recognized a separate species, *Paralvinella sulfincola* (TUNNICLIFFE *et al.*, 1993). These tube-building worms colonize large areas of newly-formed portions of high-temperature chimneys (JUNIPER *et al.*, 1988; TUNNICLIFFE & JUNIPER, 1990). Ongoing studies reveal a number of physiological, molecular and behavioral adaptations that allow this organism both to tolerate an extreme environment and to exploit the resources present. Other work indicates that the worm can influence mineralization processes on chimney surfaces. This paper develops an overview of the ecology and biogeochemistry of *P. sulfincola* and compares them with the *Alvinella* species to highlight present understanding and future research directions. Since most previous studies on species of *Alvinella* do not distinguish between *A. pompejana* and *A. caudata*, discussion here will generally refer to them as *Alvinella* spp.

THE HIGH TEMPERATURE CHIMNEY ENVIRONMENT

The smoking chimneys and spires that develop around high temperature vents are the focal points of sulfide mineral precipitation on sediment-starved spreading ridges (HÉKINIAN *et al.*, 1983; HÉKINIAN & FOUQUET, 1985; TIVEY & DELANEY, 1986; HANNINGTON & SCOTT, 1988). Growth of these sulfide edifices passes through two major phases that correspond to changes in the environment of mineral deposition within the chimney structure. HAYMON & KASTNER (1981) and HAYMON (1983) proposed that chimney growth begins when seawater entrained into a jet of high temperature (350 °C) fluid is heated to supersaturation with respect to CaSO_4 . This causes the precipitation of anhydrite and the upward growth of primitive chimney walls in the form of a porous anhydrite shell. Induration of this shell by further precipitation of anhydrite and other minerals eventually begins to isolate hydrothermal fluid within the structure from surrounding seawater to the point where significant physico-chemical gradients develop across the chimney walls. This initiates the second phase of chimney development. While anhydrite continues to accrete on the outer walls and on the distal portion of the growing chimney, hydrothermal fluids migrate outward through the walls, dissolving and replacing anhydrite with sulfide minerals. At the same time, high-temperature, low-pH conditions within the chimney conduit favor the inward growth of Cu-Fe rich sulfides. Chimneys grow in this manner up to several metres in height, accreting new anhydrite material around the vent orifice, and later infilling and replacing it with sulfides. Not all chimneys form in this way. Instead of anhydrite, direct precipitation of barite or sphalerite can form the early shell (PARADIS *et al.*, 1988). The subsequent processes are essentially the same in all cases. Early walls are replaced and sealed by outflowing hydrothermal fluid that is precipitating sulfide.

The zone of early sulfide mineralization on growing chimneys is the preferred habitat of the sulfide worm (JUNIPER *et al.*, 1988; TUNNICLIFFE & JUNIPER, 1990) (Fig. 1). Prior to worm colonization, a thickening of the

anhydrite walls of the chimney appears be necessary to reduce surface temperatures to levels the worms can tolerate (JUNIPER *et al.*, 1992). TIVEY *et al.* (1990) recorded formation and thickening of an anhydrite shell within a thermistor collar fitted around a smoker orifice. An outer wall temperature of 67 °C was recorded at the end of their experiment. No worms had colonized the shell at that point (M. TIVEY, pers. comm.). It is difficult to define

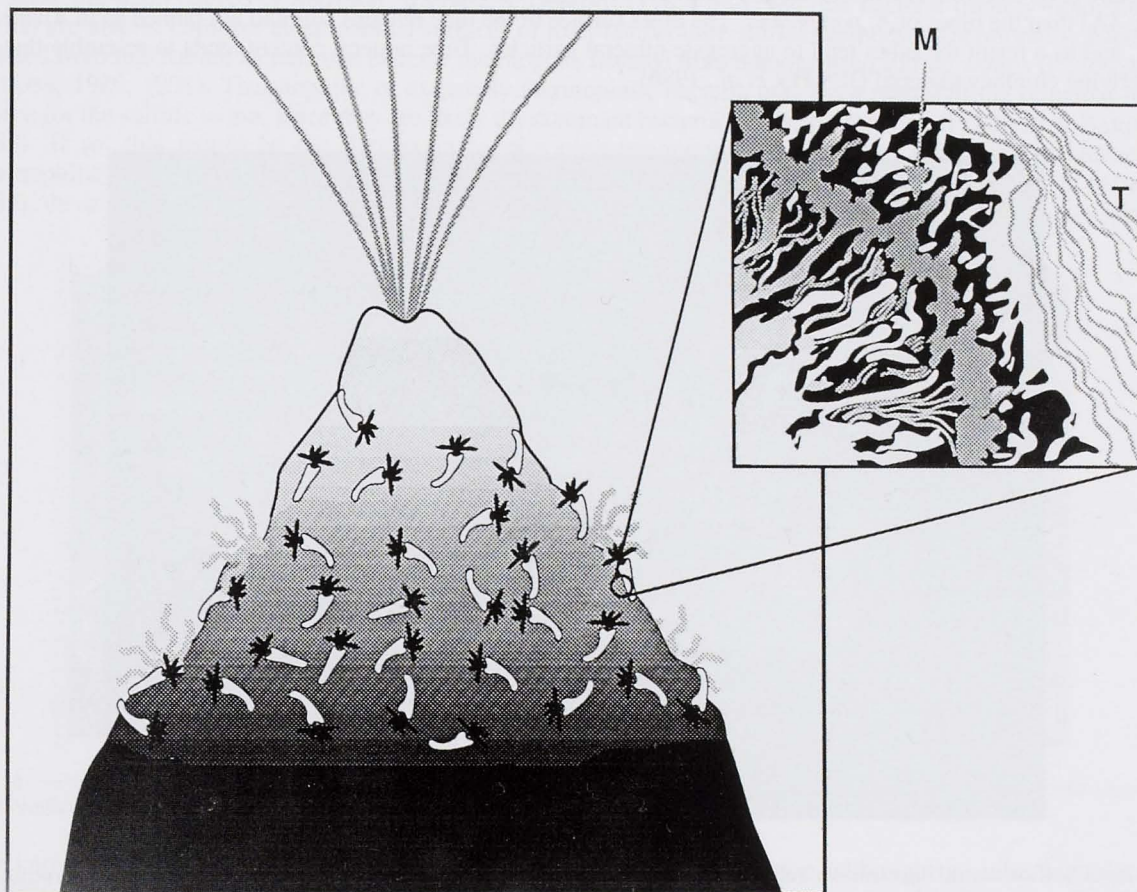


FIG. 1. — Schematic representation of the colonization of high-temperature chimneys by the sulfide worm *Paralvinella sulfincola*. Worms cover extensive surfaces in newly-formed areas of chimney that are undergoing infilling and replacement by sulfide minerals (light shading). Dark shading in lower part of structure represents zone of massive sulfide. Light cap at top indicates a higher temperature zone that is not inhabited by the worms. Insert represents cross-section through chimney wall with location of marcasite crusts (M) indicated beneath worm tubes (T). Right to left in insert is equivalent to moving from the chimney surface toward the interior.

precisely the range of conditions that constitute the worm's habitat. All physico-chemical habitat information must be collected remotely from submersibles, and in this milieu of sharp physico-chemical gradients, remote manipulation of sensors or sampling devices is simply not accurate enough to reliably record conditions within the worm's immediate microenvironment. Temperatures of 20 - 80 °C have been measured on surfaces colonized by sulfide worms (JUNIPER *et al.*, 1992), and it is most likely that the worms regularly experience temperatures within the lower part of this range. *Alvinella* spp. is frequently found at temperatures near 40 °C (FUSTEC *et al.*, 1987) and has recently been reported moving over a 105 °C surface (CHEVALDONNÉ *et al.*, 1992). TUNNICLIFFE *et al.* (1993) emphasize the importance of turbulence and likelihood of occasional blasts of hot water in the upper part of the 20 - 80 °C range.

TUBE BUILDING

Paralvinella sulfincola is one of two northeast Pacific species of *Paralvinella* known to build a tube (Fig. 2). The other species, *P. pandorae*, secretes a thin translucent mucous sheath attached to surfaces such as vestimentiferan tubes (TUNNICLIFFE *et al.*, 1986). The tube of *P. sulfincola* is a more complex multilayered structure (Fig. 3A) that resembles the tube of *Alvinella* spp., although it is less ordered at the ultrastructural level (Fig. 4A) than the tubes of *A. pompejana*. The outer surface of the tube remains soft and not tanned as in *Alvinella* spp., and as a result the tubes tend to aggregate mineral particles. Tube mineral content tends to resemble that of underlying chimney material (JUNIPER *et al.*, 1986).

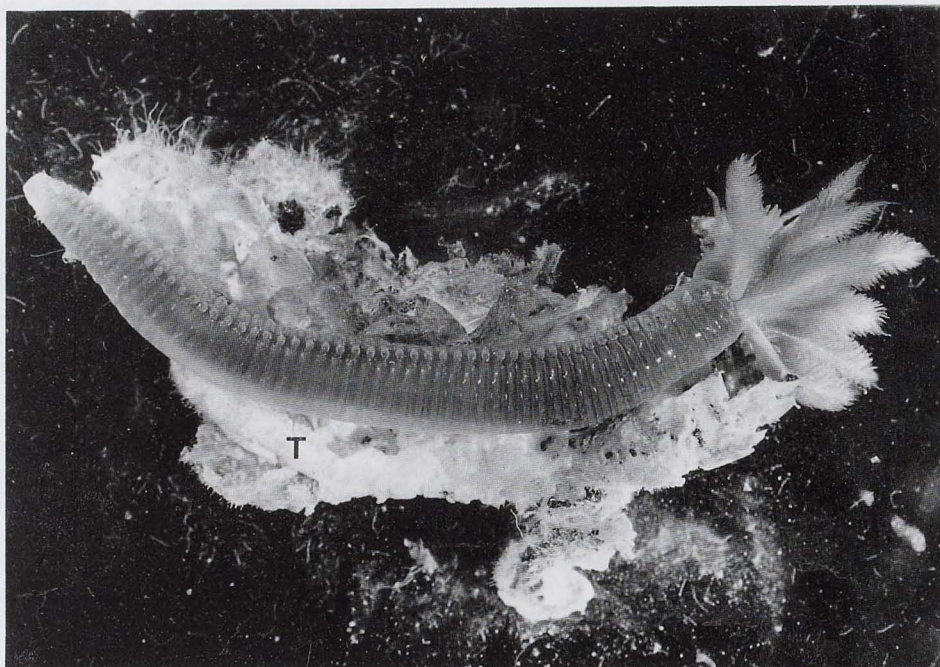


FIG. 2. — Sulfide worm *Paralvinella sulfincola* and its tube (T). In left of photo, bacterial filaments can be seen protruding from edge of tube.

Alvinella spp. has an unusual and abundant epibiotic bacterial flora whose biological relationship with the worms is not fully understood (GAILL & HUNT, 1986; DESBRUYÈRES *et al.*, 1983). Large numbers of filamentous bacteria also occur attached to the inner surface of the tubes of *Alvinella* spp. and enclosed within the organic matrix of the tube wall (GAILL *et al.*, 1988; GAILL & HUNT, 1986; GAILL & HUNT, 1991). *P. sulfincola* has a similar abundance of filamentous bacteria within the tube matrix (Fig. 2), but no equivalent epidermal flora. Scanning electron micrographs reveal that both the inner and outer surfaces of the tubes are colonised by filamentous bacteria, with filaments being most abundant on the inner tube surface (Fig. 3B-C). Transmission electron microscopy shows layers of bacteria between consecutive layers of mucus (Fig. 4B). Assuming that new tube layers are added from the inside, the layers of bacteria likely represent cells that were trapped under successive layers of mucus. Bacterial growth on the inner tube wall must alternate with periods of mucus secretion and tube building, as has been suggested for *A. pompejana* (GAILL & HUNT, 1991).

As chimneys grow upward, surfaces colonized by alvinellid worms cool and eventually lose their supply of fluids. Time lapse camera studies have revealed that adult *P. sulfincola* respond to this change in habitat conditions by abandoning their tubes and migrating upward to colonize newly-formed chimney surfaces (JUNIPER *et al.*, 1992; TUNNICLIFFE *et al.*, 1993). Similar conclusions (for *Alvinella* spp.) were reached by FUSTEC (1985) after comparing colonization patterns and chimney dimensions over a three year interval at 13° N on the East Pacific Rise.

FOOD SOURCES

Paralvinella sulfincola is apparently a deposit feeder, using its oral tentacles to gather particles that are then transferred to the mouth (TUNNICLIFFE *et al.*, 1993). Microscopic examination of gut contents reveals grains of sulfide, globules of elemental sulfur and remains of bacterial cells. Bacteria growing on the chimney surface are probably the main source of nutrition. BAROSS & DEMING (1985) observed that bacteria (mainly filamentous forms) are able to colonize most external surfaces of high-temperature sulfide chimneys. Thermophilic bacteria isolated from this habitat include one extreme thermophile isolated from homogenized sulfide worms (PLEDGER & BAROSS, 1989, 1991). Thermophilic or extremely thermophilic bacteria may even represent the principal food source for the sulfide worm, since they are likely the dominant bacteria in this environment (PLEDGER & BAROSS, 1989). If so, this would be the first example of a high-temperature trophic link. While the influence of thermophilic bacteria on geochemical processes is often discussed (BAROSS *et al.*, 1982; JANNASCH & MOTTIL, 1985), these organisms are rarely, if ever, considered as a possible food source for metazoans. *Alvinella* spp. is

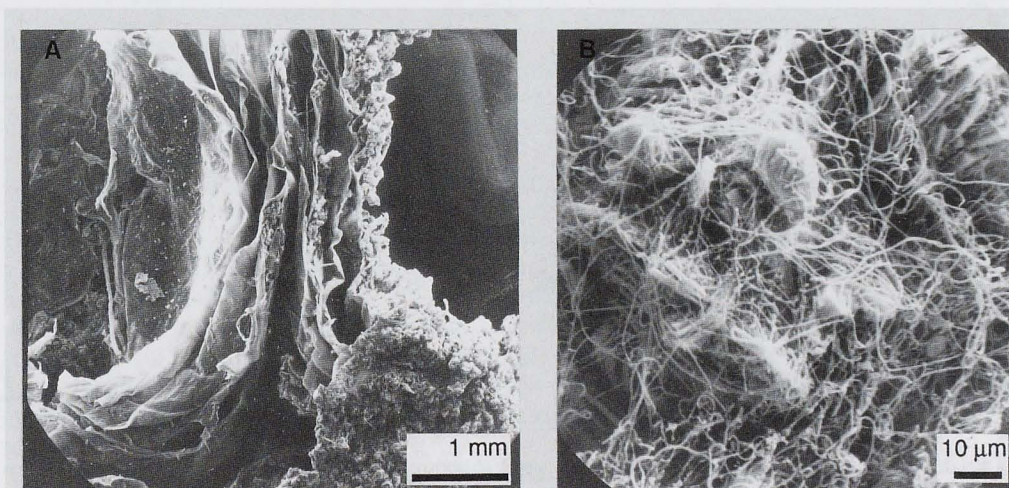


FIG. 3. — Scanning electron micrographs showing layered structure of the tube (end-on view) of *P. sulfincola* (A) and colonization of outer (B) tube surface by bacteria. Outer surface of tube is on right in A.

also known to ingest particles, and this is its most likely mode of nutrition, although the tube bacteria are implicated in a hypothesis concerning a nutrition-related symbiosis with the worm. ALAYSE-DANET *et al.* (1986) proposed that these bacteria secrete dissolved organic matter (DOM) that accumulates within the worm's tube and is subsequently absorbed by *Alvinella* spp. across its epidermal surfaces. They demonstrated incorporation of radioactively labelled compounds by epidermal tissues of *Alvinella* spp. and proposed this as evidence for their hypothesis. However, there are no published data on DOM levels within the tube of *Alvinella* spp. In a study of the digestive tract of *Alvinella pompejana*, SAULNIER-MICHEL *et al.* (1989) note unusual (for polychaetes) evidence for enzymatic breakdown of bacteria in the anterior portion of the digestive tract and suggest that bacterial cells represent an important part of the ingested food. Although they also note an abundance of particulate metals and sulfur in the gut, they do not link this to ingestion of bacteria on chimney particules. Instead, they conclude that the filamentous bacteria inside the alvinellid tubes are the more probable nutritive source (SAULNIER-MICHEL *et al.*, 1989).

ROLE IN SULFUR TRANSFORMATIONS

The principle effect of *P. sulfincola* on the sulfur cycle at vents may be related to the detoxification of H_2S in the tissues of the worm. Hydrogen sulfide has two main toxic effects: it competes with molecular oxygen for binding sites on haemoglobin molecules, leading to asphyxia, and it destroys the porphyrin structure of cytochrome C in the cellular electron transport system, thereby interfering with energy metabolism (SOMERO *et*

al., 1989). Assays of tissues of *P. sulfincola* have revealed the presence of enzymatic sulfide oxidation (JUNIPER *et al.*, 1992), commonly found in polychaete worms from reducing environments, possibly as a detoxifying agent (SOMERO *et al.*, 1989; VISMANN, 1990). Rates of sulfide oxidation by the worms appear to be high enough to lead to accumulations of elemental sulfur in their mucous secretions and tubes. *Alvinella* spp. accumulates elemental sulfur in its tube and epidermal tissue, presumably also as a result of H_2S detoxification. In this case, the epibiotic bacterial flora has been implicated in sulfide oxidation (LAUBIER *et al.*, 1983), although this activity has yet to be quantified. Sulfide oxidation in the tissues of *Alvinella* spp. also remains unmeasured.

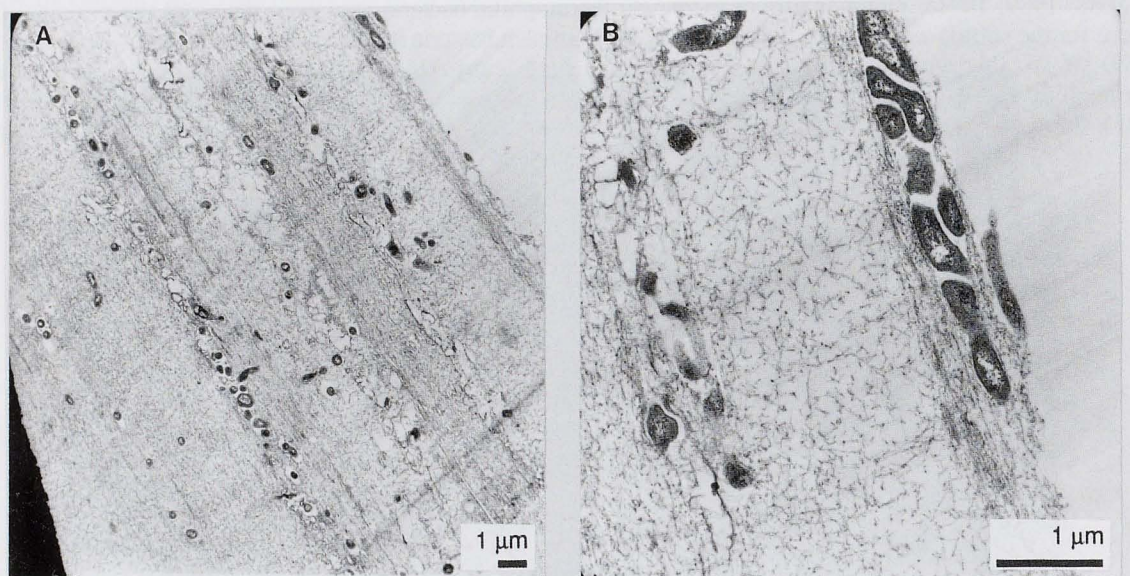


FIG. 4. — Transmission electron micrograph showing layered structure of tube *P. sulfincola* (A) and trapping of bacteria between layers of mucus (B). Tube external surface is on right in both photos.

EFFECTS ON CHIMNEY MINERALIZATION

Essentially all newly-formed chimney surfaces are colonized by migrating sulfide worms within a matter of days (JUNIPER *et al.*, 1992). The effect of worms on chimney mineralogy was studied by examining the texture and composition of chimney material beneath worm tubes. Sections through the outermost layers of older chimneys generally revealed a 2 mm-thick crust of the sulfide mineral marcasite (FeS_2)¹ beneath the mucous tubes (PARADIS *et al.*, 1988; JUNIPER *et al.*, 1992) (Fig. 1). Since the worms generally occur in dense aggregations, the marcasite crust may be extensive enough to affect chimney wall porosity which in turn controls progress of the second stage of chimney mineralization.

The fact that marcasite precipitation is spatially associated with the worm tubes suggests that the worm-bacterial complex alters local geochemistry to favor the precipitation of this mineral. How might this occur? Formation of both marcasite and pyrite usually requires the presence in solution of intermediate sulfur compounds and FeS precursors; at $pH \leq 5$ the precipitation of marcasite is favored over that of pyrite (MUROCHICK & BARNES, 1986). High percentage levels of elemental sulfur have been measured in the tube mucus (JUNIPER *et al.*, 1986; JUNIPER, 1988) and similar sulfur concentrations occur in the tubes of *Alvinella pompejana* (GAILL & HUNT, 1986). PARADIS *et al.* (1988) suggested that interaction of H_2S from hydrothermal fluid with this elemental sulfur could form intermediate sulfur compounds such as polysulfide.

¹ Marcasite and pyrite have the same molar ratio of sulfur to iron (FeS_2), but their crystallographic characteristics are quite different, as are their physico-chemical properties.

Mineralogical and time-lapse camera data studies provide independent lines of evidence linking tube building to crust formation (JUNIPER *et al.*, 1992; TUNNICLIFFE *et al.*, 1993). As well, the proposed role of tube mucus in this process (PARADIS *et al.*, 1988) is supported by recent experimental work on the formation of iron disulfides from solutions. Reaction of elemental sulfur with water generates high concentrations of thiosulfate, polysulfides and polythionates at the sulfur-water interface (SCHOONEN & BARNES, 1991c). This high local concentration of intermediate sulfur species apparently can cause iron disulfides to form directly on elemental sulfur grains (GOLDHABER & STANTON, 1987; SCHOONEN & BARNES, 1991a, b, c). Thus a local source of elemental sulfur in tube mucus can cause marcasite precipitation both by direct reaction with FeS precursors, or indirectly through the generation of intermediate sulfur species.

DISCUSSION

The alvinellid worms (*Alvinella* spp. and *Paralvinella* spp.) probably evolved from a common ancestor that colonized the East Pacific Rise and the Juan de Fuca Ridge when they were contiguous (TUNNICLIFFE *et al.*, 1993). Since the separation of the two ridge systems some 25 million years ago, *Alvinella* spp. and *P. sulfincola* have probably evolved separately. *Alvinella* spp. is the more derived form; epidermal structures that accommodate epibiotic bacteria and organized tube ultrastructure are two examples of the specialized traits that have appeared in this genus. DESBRUYÈRES & LAUBIER (1991) propose an early separation of the genus *Alvinella* from evolutionary lines taken by the *Paralvinella* species.

The fact that *Paralvinella sulfincola* colonizes the same high temperature, high sulfide environment as *Alvinella* spp. raises questions about the importance of the *Alvinella* spp. epibiotic bacteria. *P. sulfincola* is able to enzymatically oxidise sulfide, as are many benthic polychaetes from non-vent environments. *Alvinella* spp. probably does the same, and the example of *P. sulfincola* indicates that this capability should be enough to allow the animal to survive and grow on sulfide chimneys. Then why the symbiosis? The elaborate adaptation of the epidermis to accommodate bacteria indicates that this is more than a simple case of epizooic growth of bacteria. Perhaps the symbiosis reduces the energetic cost of sulfide oxidation to animal. This may explain the larger body size of *Alvinella* spp. compared to *P. sulfincola*. Average wet weights for *A. caudata* and *A. pompejana* are 845 and 783 mg, respectively (TUNNICLIFFE, pers. comm.), whereas wet weights for *P. sulfincola* are around 325 mg (JUNIPER *et al.*, 1992).

The type of nutritional relationship between *Alvinella* spp. and its episymbionts first proposed by ALAYSE-DANET *et al.* (1986) has never been demonstrated in any other organism. Apart from an ability for DOM uptake by the epidermis of *Alvinella* spp., not uncommon among invertebrates, there is little evidence to support any transfer of metabolites from the epibiotic bacteria to the worm. On the other hand, there is good reason to suppose that *Alvinella* spp. and the sulfide worm are deposit feeders. Both worms are anatomically capable of deposit feeding and both are known to ingest particulates from their immediate environment. Without further evidence for symbiosis in *Alvinella* spp., deposit feeding remains its most likely mode nutrition. The fact that *P. sulfincola* is able to nourish itself in the same habitat without episymbionts further supports deposit feeding as the primary mode of *Alvinella* spp. nutrition. A similar grazing/detritivorous mode of nutrition appears to have been adopted by the Bresiliid shrimp on chimneys at Mid-Atlantic Ridge vents. In the absence of vent polychaetes, swarms of shrimp ingest mineral particles and adhering bacteria from the surfaces of black smoker chimneys (VAN DOVER *et al.* 1988; SEGONZAC, 1992).

The influence of *Alvinella* spp. on chimney mineralization has not been examined in the same detail as have the effects of *P. sulfincola*. From descriptions by HAYMON & KASTNER (1981) and DESBRUYÈRES *et al.* (1985), it would appear that *Alvinella* spp. influences chimney morphology to a greater degree than does *P. sulfincola*. In their account of the texture of black smoker chimney samples from East Pacific Rise vents, HAYMON and KASTNER (1981) note an abundance of interconnected cavities in the outer part of the chimney that are clearly remains of *Alvinella* spp. Another type of edifice, the white smokers or snow ball diffusers of EPR vents are referred to as biogenic edifices created by *Alvinella* spp. (FUSTEC *et al.*, 1987). No equivalent structures are known from northeast Pacific vents, even though the chemistry of the source fluids for edifice construction is similar (TUNNICLIFFE *et al.*, 1986; VON DAMM & BISCHOFF, 1988; BUTTERFIELD, 1990). How *Alvinella* spp. shapes chimney morphology is not known. One possible mechanism may involve the effect of convective circulation of cold seawater through the worm's U-shaped tube. *Alvinella* spp. constructs its tube so that the central portion of the tube is cemented against the chimney wall, with the anterior and posterior openings extending into the surrounding seawater. This configuration allows a convective movement of seawater through the tube, that is driven by heat

flow into the tube from the chimney wall. Mineralogical studies of *Alvinella* spp. tubes indicate that convective cooling around the tubes locally reduces chimney wall temperatures enough to saturate metal-bearing fluids and cause mineral precipitation (DESBRUYÈRES *et al.*, 1985). This convectively driven "supercooling" extracts heat from the entire chimney structure. It may occasionally be of great enough magnitude to reduce temperatures deep inside the chimney wall, increasing local precipitation of minerals from high temperature fluids. This could increase outward accretion of chimney material at the expense of upward accretion, and cause some young chimneys to develop into snow ball structures. Whatever the mechanism, it is clear that *Alvinella* spp. is capable of a much greater degree of habitat modification than its counterpart at northeast Pacific vents, *Paralvinella sulfincola*. One notable difference between East Pacific Rise (EPR) and northeast Pacific vents is the relative rarity of vestimentiferans on chimneys at EPR. Is this a result of habitat modification by *Alvinella* spp.?

CONCLUSION

While *P. sulfincola* and *Alvinella* spp. both exploit the high temperature chimney habitat of their respective spreading ridges, *Alvinella* spp. appears to be more elaborate in its adaptations to this environment. The functional significance of some of these adaptations remains to be clarified. *Alvinella* spp. may react to chimney growth by frequently abandoning tubes and migrating to new areas, as has been observed for *P. sulfincola*. Or, the more elaborate tube architecture and greater influence of *Alvinella* spp. on chimney morphology may be indicative of an organism that is better able to control its local microenvironment, and so reduce the frequency (compared to the sulfide worm) of tube abandonment. Time lapse photography was used to study tube building and migration of sulfide worms (JUNIPER *et al.*, 1992; TUNNICLIFFE *et al.*, 1993), and could probably be used to determine whether or not *Alvinella* spp. behaves similarly. In light of recent work on the effects of sulfide worms on chimney mineralization, the entire question of how *Alvinella* spp. influences chimney growth patterns needs reexamining. As well, this comparison has shown that the two roles proposed for the epibiotic bacteria in *Alvinella* spp., nutrition and detoxification, can be accomplished by *P. sulfincola* without the aid of episymbionts. This is a strong argument for a re-examination of the nature of the *Alvinella*-bacteria symbiosis.

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