

face that separates Pleistocene cross-strata from Holocene unit D is a 4-km-wide marine terrace that dips about 0.1° across most of its width. The inner edge of the terrace is defined by a shoreline angle at 58 m below present sea level and the outer edge is defined by the shelf break. Although the terrace angle has not been dated, it is inferred from the terrace's configuration that it formed during a slow rise of sea level relative to the rate of sedimentation, perhaps followed by a stillstand near 58 m below present sea level (15). Landward of the shoreline angle, the dip of the Pleistocene/Holocene unconformity increases to as much as 10° and is truncated by a younger erosional surface at 24 m below present sea level. The presence of sigmoidal onlapping cross-strata in unit D suggests a rapid rise in sea level relative to the rate of sedimentation. The truncation of upper Pleistocene strata and unit D indicates a subsequent lowering of sea level. The erosional surface extends to 56 m below present sea level, which implies that sea level fell to at least 46 m below present sea level, thus allowing an additional 10 m for wave erosion (16). The final rise of sea level to its present position appears to have occurred without major interruption. Changes in the slope of the transgressive unconformity may reflect changes in the rate of sea-level rise. During this most recent transgression, the parallel onlapping beds of Holocene unit E were deposited.

The amplitudes and chronological sequence of Flandrian sea-level fluctuations are largely constrained by the seismic reflection data. Radiocarbon dating of Holocene shell material (Table 1) (17) from the coarse basal transgressive deposit of unit E and from lagoonal mud has permitted the partial calibration of a Flandrian sea-level curve (Fig. 2). All of the samples dated at less than 11,000 years and, with the exception of sample V-52, reveal that the sea-level fluctuations associated with the erosion of the 58-m terrace as well as the deposition of unit D and its subsequent truncation occurred before that time. Subsequently, sea level rose more slowly from 20 m below present sea level to its present position. Assuming that the dates for samples V-17 and V-43b are correct, sample V-52 yields an anomalously young age that is inconsistent with the seismic stratigraphy; thus contamination, reworking, or misidentification of the Pleistocene/Holocene boundary in the core is suspected (18).

An inspection of published late Quaternary sea-level curves shows that no single curve can be applied worldwide

(5). However, the curve constructed from these data (Fig. 2) is similar in shape, although not necessarily in phase or amplitude, to those presented in other studies (2, 5, 14, 19). For example, a comparison with Curray's (14) Texas shelf curve shows similarities in shape for the last 18,000 years, but a second sea-level lowering in Curray's curve at 9000 years was not recognized in our study area. Differences in phase and amplitude can reflect local tectonic or isostatic conditions (1-4, 6). Relative to the Texas shelf, the inner Santa Monica shelf appears to have experienced uplift before 10,000 years ago and subsidence thereafter.

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18. In the less likely event that both samples V-17 and V-43b are in error and V-52 is correct, the curve would indicate that sea level was about 50 m below present sea level 8600 years ago (rather than 11,000 years ago), rose rapidly to 15 m below present sea level 5000 years ago, and rose more slowly thereafter.
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## *Riftia pachyptila* Jones: Observations on the Vestimentiferan Worm from the Galápagos Rift

**Abstract.** *The obturacular plume, composed of numerous tentacles, is suggested as a site for the uptake of molecular "food" by Riftia pachyptila (Pogonophora) from the Galápagos Rift; symbiotic bacteria are another possible source of nutrition. Differing organizations of the linings of the five major body cavities of Riftia demonstrate the inadequacy of "coelom" as a descriptive term.*

During investigations of the geothermal vents of the Galápagos Rift region and the East Pacific Rise at 21°N, large worms were observed to form a major element of unique biological communities (1, 2).

A total of 63 worms collected at Dandelions, Garden of Eden, and Rose Garden geothermal vents in the Galápagos Rift area and from the East Pacific Rise have been deposited in the collections of the National Museum of Natural History (USNM), and these have formed the basis for a description of *Riftia pachyptila* Jones (3).

*Riftia pachyptila* is the only species in the family Riftiidae; the other two known vestimentiferan worms, *Lamellibrachia barhami* Webb and *L. luymesii* van der Land and Nørrevang are of the family Lamellibrachiidae. Together, the three species are the sole members of the order Vestimentifera Webb, the class Afrenulata Webb, and subphylum Obturata Jones. The trio, with the subphylum Perviatia Jones (comprised of all pogonophoran worms with a bridle and lacking an obturaculum), are considered, at present, to make up the phylum Pogonophora.

*Riftia pachyptila* has four body regions: (i) an anterior tentacular plume on a central supporting obturaculum, (ii) a "winged" vestimentum, (iii) a trunk, and (iv) a segmented posterior opisthosome (Fig. 1). There is neither mouth nor gut present in any specimens from the largest (1.5 m long) to the smallest (0.75 mm).

The anterior plumed region, with a longitudinal dorsal groove (4) and a ventral ridge along the length of the obturaculum, bears tentacular lamellae oriented perpendicularly to the axis (Fig. 1, *OB* and *TL*) and these extend nearly to the tip of the obturaculum.

In life, the dorsolateral regions of the vestimentum overlap one another within the tube in which the worm lives, and a dorsal chamber is so formed (Fig. 1, *VW*). The genital apertures of both males and females open into this vestimental chamber at the posterior third of the dorsal vestimental surface. On the ventral vestimental surface a ciliated field is bounded by paired ventral nerves and neurular tubes (Fig. 1, *CF* and *BN*). In the trunk region a now-united, single ventral nerve (and neurular tube) extends posteriorly to the end of the trunk (Fig. 1, *VN*). The opisthosome is comprised of a variable number of setigerous segments and terminates in a rounded posterior tip. Setae in this most posterior region are identical to those found in the girdle of the more anterior trunk region of other pogonophorans.

Tubes are white, flexible, extremely sturdy, and essentially cylindrical. Basally they are blind-ending and approximately conform to the shape of the opisthosome.

The gelatinous matrix of the obturaculum is penetrated by paired obturacular blood vessels that are blind-ending near the split anterior end of the obturaculum (Figs. 2 and 3, *OV*); these originate from two anterior branches of the dorsal vessel in the vestimental region and lie in a perivascular cavity that lacks any connection to any other body cavity.

Tentacles of the lamellae of the obturacular plume are covered with a layer of cuticle of varying thickness throughout their length. They are fused basally for from 50 to 75 percent of their length to form lamellae; the tips of the tentacles are free (Fig. 2). Each tentacle has a central cavity lined with longitudinal muscle cells and containing two blood vessels (Fig. 5, *TC*); more peripherally is the basement membrane of a single layer of epithelial cells. The tentacular blood vessels are connected along the length of the tentacle by transverse intraepithelial vascular loops which also communicate

with the central cavities of pinnules; the latter are arranged in two rows on the posterior face of each tentacle, along the distal 45 percent of the tentacular length. In the holotype of *Riftia pachyptila* (USNM 59951), there are about 340 tentacles per lamella and 335 lamellae on each side of the obturaculum, making a total of approximately  $2.28 \times 10^5$  tentacles in the plume.

In the basal region of the lamellae, the cuticle of fused tentacular lamellar bases becomes thickened, and successive lamellae are fused to one another serially for a short distance (Fig. 5, *I* to *5*). Basally the blood vessels of all tentacles of a given lamella join single transverse blood vessels (Fig. 5, *LV*); the latter, in turn, join anterior axial branches of either the dorsal or the ventral vessels of the main body (Fig. 5, *DB* and *VB*). The remaining residue of the tentacular bases moves ventromedially and forms a thin bandlike structure that proceeds posteriorly in company with similar bandlike structures derived from more apical lamellae (Fig. 5, *CTI* and *CT2*); in cross section, the aggregate gives the impression of narrow compartments (Fig. 5, *CT*); at the base of the obturaculum this compartmented tissue is continuous with the tissue of the brain [figure 4, C to F, in (3)].

The vestimental region is quite solid and is composed of a mass of intermixed muscles and connective tissue elements. Close-packed pyriform glands are present in a discrete layer, and these open to the external surface of the overlapped wings (dorsolateral) and of the vestimentum proper. The brain is anteroventral, internal to the ventral overlapping of the anterior margins of the vestimental wings (Fig. 1, *AF*). The presumed excretory organ is just posterior to the brain. Its tubules have no obvious orientation and have no apparent internal openings; they unite, successively, with other tubules and ultimately open into nonciliated (under light microscopy) cavities, which lead to paired nonciliated canals which move anterolaterally, then dorsally, and, at the level of the anterior margin of the vestimentum, open into the basal area of the dorsal groove of the obturaculum by paired excretory pores.

The sexes of *Riftia pachyptila* are separate, and there is a single external difference between males and females; that is, paired anterior ciliated grooves and ridges, associated with the genital apertures of the males, are lacking in females. Eggs from just inside the female genital aperture are at the germinal vesicle stage and are about 78  $\mu$ m in diameter. Sperm from just inside the male

aperture have elongate, corkscrew-shaped bodies about 9  $\mu$ m long and 0.6  $\mu$ m in diameter; tails are about 9  $\mu$ m in length. No spermatophores have been observed.

The internal surface of the body wall of the trunk bears numerous longitudinal "feather" muscles, internal to a thin layer of bundles of more conventional longitudinal muscles (Fig. 4, *FM*). One pair of cavities extends throughout the entire length of the trunk; these are separated by medial dorsoventral mesenteries which contain the dorsal and ventral blood vessels (Fig. 4, *DM* and *VM*) and are attached to the centrally located gonad and trophosome.

In the trunk, the dorsal vessel is thin-walled, with a thin layer of connective tissue, covered with what appear to be circular muscles; vascular branches, the mesenterial and other vessels running to the trophosome, traverse the medial mesentery (Fig. 4, *DV*, *MV*, and *DM*). Anteriorly, the dorsal vessel has a thin muscular lining, with a succeeding thick layer of connective tissue, surrounded by a layer of striated, circular, ring muscles. The whole is supported in a perivascular cavity, and the entire complex is supported by a second set of dorsoventral mesenteries in an anterior extension of the trunk cavity. Just posterior to the level of the brain, the dorsal vessel branches, and each branch moves anteriorly to run the length of the obturaculum, ventromedially (Fig. 3, *DB*); here, the dorsal vessel also gives rise to the paired obturacular vessels. Anterior branches of the ventral vessel extend the length of the obturaculum, ventrolaterally, in company with the two branches of the dorsal vessel and receive branches from each transverse tentacular lamellar vessel (Fig. 3, *VB*). At the base of the obturaculum, posterior to the level of the brain, these branches unite and proceed posteriorly as a single ventral vessel. The fate of the anterior branches of the dorsal and ventral vessels is unknown.

Blood taken directly from the dorsal vessel of living animals, 2 hours after collection, was of the dark red color and the viscosity of port wine. Fluid from the cavities of the trunk and the opisthosome had a similar color and viscosity (5).

The trophosome, the structure that with the gonad and gonoducts occupies the trunk cavity, is made up of many lobules, each with a central lumen, and is well vascularized (Fig. 4, *TP*). The lumina are actually blood vessels which give rise to capillaries and ramify throughout the lobular masses. The "tissue" of the trophosome, in reality, is great numbers of close-packed bacteria (6). The surface

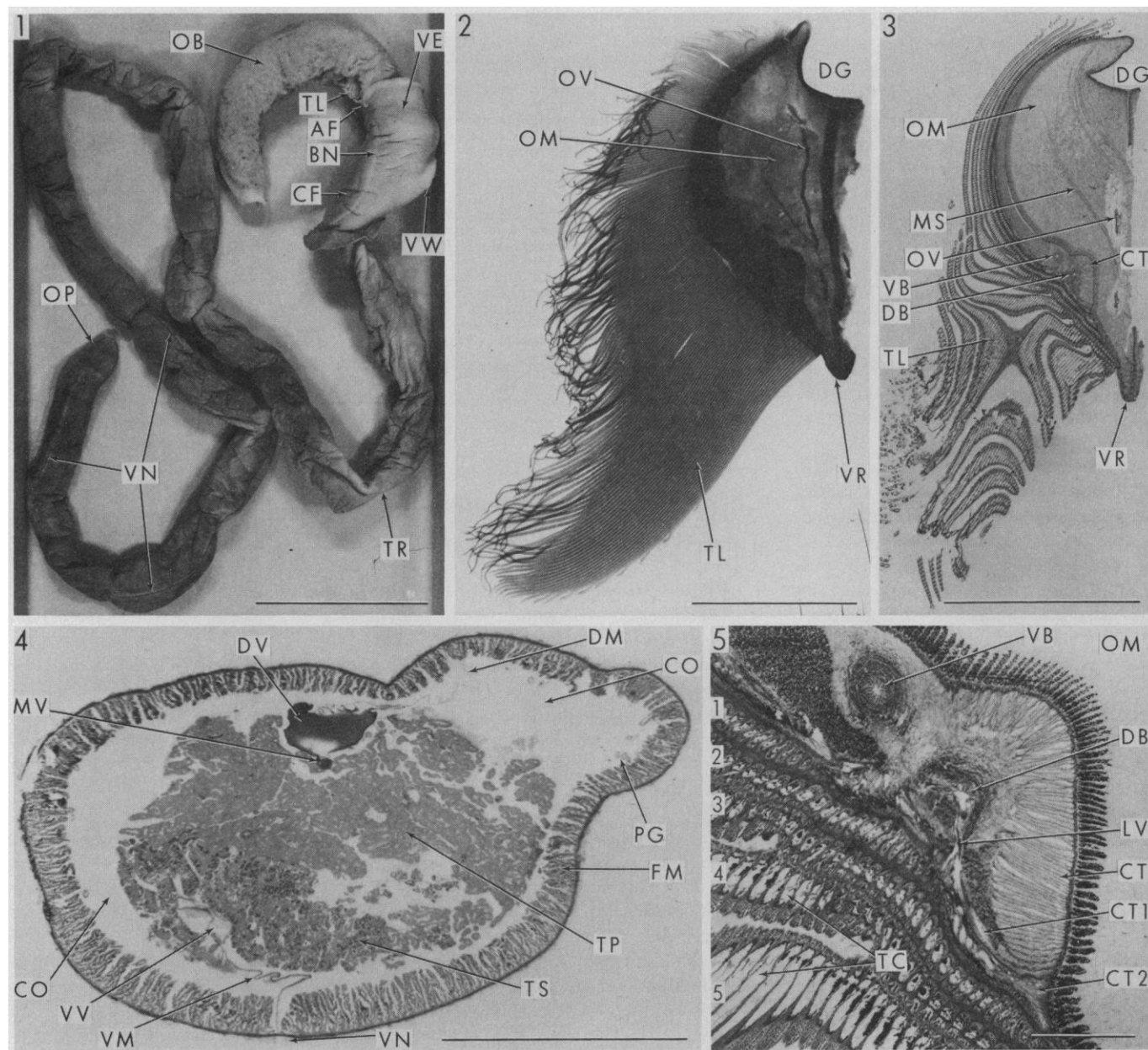
of the trophosomal lobes is provided with numerous fine pigment granules and spots, and is in intimate association with the gonads and gonoducts (Fig. 4, *TP* and *TS*). In the trophosomal "tissue" of most specimens of *Riftia*, there are crystals of elemental sulfur.

Opisthosomal segments are separated internally by septa with muscle fibers on the anterior and posterior faces. Individual segmental cavities are paired and

separated medially by a dorsoventral mesentery. The ventral nerve, here, lacks a neurular tube.

Concerning the five different types of cavities in *Riftia*, the following observations can be made. The cavities of the tentacles are lined with a layer of muscle fibers one cell thick. The perivascular cavities of the obturacular vessels are lined with a thin epithelial layer. The perivascular cavity of the dorsal vessel

in the anterior trunk region has a thin cellular layer on its peripheral surface, but the muscles associated with the dorsal vessel proper lack any covering. The paired trunk cavities have dorsal and ventral mesenteries, each with a thick central layer of connective tissue and a superficial thin layer of muscle cells; the dorsal and ventral blood vessels are covered with connective tissue, with a succeeding layer of muscle cells in the for-



Figs. 1 to 5. *Riftia pachyptila* Jones. Fig. 1. Overall view of holotype. Fig. 2. Complete tentacular lamella, with half of obturaculum, from mid-region of obturacular plume; Mallory's Triple stain. Fig. 3. Section of tentacular lamellae and obturaculum (5  $\mu$ m thick); Chlorazol Black. Fig. 4. Transverse section of trunk (5  $\mu$ m); Mallory's Triple. Fig. 5. Transverse section of compartmented tissue adjacent to obturacular matrix and the basal origins of five consecutive tentacular lamellae (5  $\mu$ m); Mallory's Triple. Abbreviations: AF, anterior flaps of vestimental wing; BN, bifurcated ventral nerve; CF, ventral ciliated field; CO, coelom; CT, compartmented tissue; CT1 and CT2, "compartments" of lamella "1" and "2," respectively; DB, anterior branch of dorsal vessel; DG, dorsal groove of obturaculum; DM, dorsal mesentery; DV, dorsal vessel; FM, "feather" longitudinal muscles; LV, vessel from tentacular lamella "2"; MS, muscle strands inserting on "mesentery" of obturacular vessel; MV, mesenterial vessel; OB, obturaculum; OM, obturacular matrix; OP, opisthosome; OV, obturacular vessel; PG, pyriform glands; TC, tentacular "coeloms"; TL, tentacular lamella; TP, trophosome; TR, trunk; TS, testes; VB, anterior branch of ventral vessel; VE, vestimentum; VM, ventral mesentery; VN, ventral nerve; VR, ventral ridge; VV, ventral vessel; VW, vestimental wing; and numerals 1 through 5, serially more proximal tentacular lamellae. The scale bar (lower right) for Fig. 1 is 10 cm; for Figs. 2 to 4, it is 5 mm; and for Fig. 5, it is 0.5 mm. [Fig. 1, USNM 59951; Figs. 2 to 5, USNM 59953]

mer and of epithelium in the latter. There is a thin epithelial covering over the bacteria which comprise the mass of the trophosome and over the gonads and gonoducts as well; there is no covering layer over the peripheral feather muscles. The paired cavities of each opisthosomal segment are separated by septa, which bear muscle fibers on both the anterior and posterior faces, as well as long glandular structures situated in blood vessels or sinuses on the anterior septal face; the internal layer of the body wall of each segment is made up of bundles of normal longitudinal muscles in a connective tissue matrix; within each segment, between septa, there are thin circular bands of muscles which form partial, incomplete septa. In addition, there are transverse segmental blood vessels running just internal to the body wall. All of these morphological features appear to lack a covering of epithelial cells.

Considering the most widely accepted definition of a coelom as provided by Hyman (7), only the perivascular cavity of the obturacular vessels would appear to qualify as a coelomic cavity; the status of the other cavities is equivocal because they lack to a greater or lesser extent a complete peritoneal lining. Fransen (8) has found a similar perplexing series of linings in her examination of the coelomic cavities of a number of species of polychaetes and archiannelids. Previously Southward commented, in passing, on the equivocal nature of the coelomic lining of pogonophorans (9). In light of the present findings, use of the term "coelom" by previous workers in reference to the differing cavities of pogonophorans (in the strict sense) and vestimentiferans (10), as well as for other taxonomic groups, now requires a reexamination.

In the case of a marine animal as massive as *Riftia* (the largest specimen is 1.5 m long, with an average diameter of about 35 to 40 mm) the problem of nutrition is of more than passing interest because the worms lack a mouth and gut. The most obvious method of food uptake would appear to involve a direct pathway across the body wall, and the obturacular plume, in life extending from the opening of a thick-walled tube, would seem to be the obvious site for such food transport. With the large numbers of tentacles, each with more than 200 pairs of intraepidermal vascular loops and the large additional surface of up to 200 pairs of vascularized pinnules on each tentacle, the plume is an exceptional organ for the uptake of organic molecules (11). The trophosomal bacteria may also play

a role in the nutrition of *Riftia*. The similarity of ratios of  $^{13}\text{C}$  to  $^{12}\text{C}$  in the trophosome (bacteria) and in the vestimental musculature found by Rau (6) suggests that *Riftia* may utilize the bacteria or their metabolites (or both) as a source of organic carbon.

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12. I thank J. B. Corliss, Oregon State University, for placing the first specimens of *Riftia* at my disposal; J. F. Grassle, Woods Hole Oceanographic Institution, for further specimens; R. Rieger, M. Fransen, and S. Gardiner, University of North Carolina, and K. Fauchald, National Museum of Natural History, for stimulating discussions, and the latter two for reviewing this manuscript; L. Cullen, of J. Harshbarger's Registry of Tumors of Lower Animals, National Museum of Natural History, for assistance in histological procedures; and E. Jarosewich and P. Dunn, National Museum of Natural History, for determination of sulfur crystals. Travel support, which allowed me the opportunity of making personal observations of living *Riftia*, was from the Research Fund of the Secretary, Smithsonian Institution. *Alvin* dive time was made available through D. Cohen, National Marine Fisheries Service, National Oceanic and Atmospheric Administration. This is contribution No. 19 of the Galápagos Rift Biology Expedition, supported by the National Science Foundation.

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## Chemoautotrophic Potential of the Hydrothermal Vent Tube Worm, *Riftia pachyptila* Jones (Vestimentifera)

**Abstract.** *Trophosome tissue of the hydrothermal vent tube worm, Riftia pachyptila (Vestimentifera), contains high activities of several enzymes associated with chemoautotrophic existence. Enzymes catalyzing synthesis of adenosine triphosphate using energy contained in sulfur compounds such as hydrogen sulfide, and two diagnostic enzymes of the Calvin-Benson cycle of carbon dioxide fixation, ribulose-bisphosphate carboxylase and ribulose 5-phosphate kinase, are present at high levels in trophosome, but are absent in muscle. These data are consistent with an autotrophic mode of nutrition for this worm, which lives in hydrogen sulfide-rich waters and lacks a mouth and digestive system.*

The sparse food supply of the deep sea has been thought to preclude a high biomass in this environment (1). Biomass decreases rapidly with increasing distance from the surface zone of primary productivity, and the metabolic rates of deep-living organisms are often vastly lower than those of shallow-living species (1, 2). The discovery of dense animal communities at hydrothermal vents near the Galápagos Islands (3, 4) and off the coast of Mexico (5) at depths of approximately 2500 m has led to a major reevaluation of our concepts of trophic interactions and biomass densities in the deep sea. The ultimate source of nutrition for the vent community animals, which include clams, mussels, crabs, anemones, fishes, and, particularly, large tube worms of the class Vesti-

mentifera, is still in question (3-5). According to the main theory (6) the vent communities have chemosynthetic bacteria as the ultimate food source; food reaching these deep vent communities from surface productivity is quantitatively unimportant. Thus, the vent communities would differ from all known food chains in not depending on photosynthetic carbon fixation. The energy and reducing power needed by the vent bacteria for carbon fixation are thought to be generated by the oxidation of sulfur compounds, especially hydrogen sulfide ( $\text{H}_2\text{S}$ ), which is dissolved in high concentrations (millimolar) in the hot effluent waters of the vents (4, 7).

Whereas a food chain based on chemoautotrophic bacteria appears probable in the case of filter-feeding animals