The Giant Tubeworms

by

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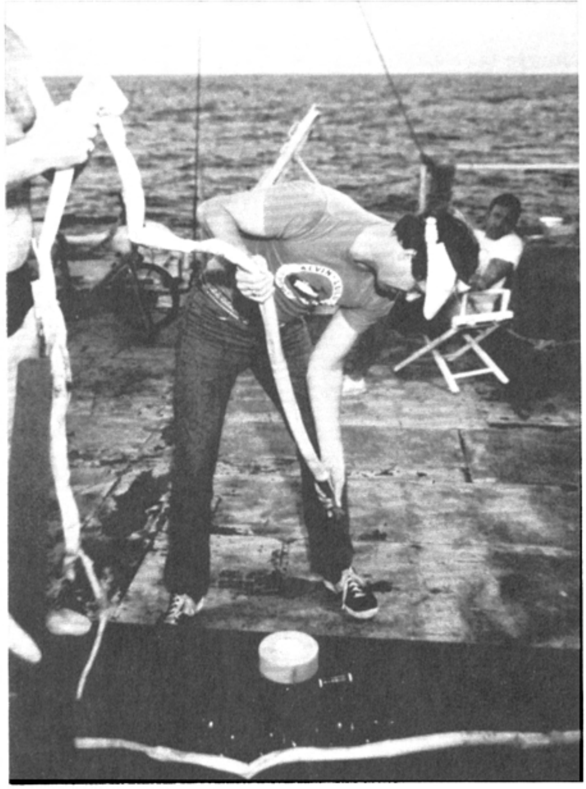
When John Corliss and John Edmond took *Alvin* down 2,500 meters to the Galápagos Rift in 1977, they truly opened a can of worms for biologists. The collections made by these and other geologists on that particular expedition have been a source of amazement for and conjecture by biologists for the succeeding seven years. From my standpoint, the most impressive and interesting of the animals brought back are the so-called "giant tube worms."

Looking like something dreamed up for the latest sci-fi spectacular, the worms for a time defied classification; we referred to them simply as "tube worms" until their anatomy and ultimately their taxonomic relationships could be worked out. The first clue to the tube worms' taxonomy was their lack of mouth and gut structures. This strongly suggested a relationship to the Pogonophora, a group of worms mostly found in the deep sea and likewise lacking mouth and gut structures (accepted in other animals as being of more than passing import). This phylum, the name of which means "beard bearers," was unknown until the 20th century.

Of the several external differences between the Rift tube worms and the pogonophorans, size was most striking. The largest pogonophorans previously reported were 450 millimeters long, and perhaps 1.5 millimeters in diameter. The largest of the Rift tube worms collected in 1977 was 320 millimeters long and 25 millimeters in diameter; subsequent collections have yielded one specimen with a length of 1.5 meters and a diameter of 37 millimeters.



When scientists first encountered the giant tube worms, they were surprised by their length and by other characteristics. For example, the tube worms lacked any visible means of support, as they did not have either a mouth or gut. (Photo by Jack Donnelly, WHOI)

A thicket of tube worms on the floor of the Galápagos Rift in 1979. Initially the relationship of the tube worms to other animals was unclear. (Photo by Jack Donnelly, WHOI)

The New Species

In 1969, Michael Webb of the University of Stellenbosch, South Africa, described a pogonophoran worm collected off the California coast near San Diego. The sea bottom there was unremarkable—silt with some rocky outcrops. The specimens of the new species, *Lamellibrachia barhami*, were something in excess of 650 millimeters long and from 7 to 9 millimeters in diameter at their anterior ends. Throughout his description of these worms, Webb referred to various of their morphological characteristics as "aberrant," "unique," and "unusual" in comparison to roughly similar structures in the other Pogonophora.

Among other things, *L. barhami* differs from other pogonophorans in the structure of the plume of tentacles (gill filaments) that protrudes from the open end of its tube. Another difference is in the portion of the worm that supports the plume region and anchors the worm's body at the tube opening. It has the aspect of a long collar with flaps that meet over the worm's dorsal surface, forming a canal-like passage. Webb called this region the "vestimentum."

On the basis of the unique structure of his new worm, Webb proposed a new class, order, family, genus, and species for it in the phylum Pogonophora. The class name, Afrenulata, refers to a structure, present in the other Pogonophora, lacking in the new species; the ordinal name, Vestimentifera, refers to the vestimentum, a morphological feature not found in the other pogonophores; and the familial name, Lamellibrachiidae, is based on the name of the new genus.

In 1975, Jaap van der Land of the Leiden Museum (The Netherlands) and Arne Nørrevang of the University of Copenhagen, Denmark, described a second species of the genus, *Lamellibrachia luymesi*, found off the coast of Guayana in the western Atlantic. *L. barhami* had been collected by the submersible *Deepstar 400* at 1,125 meters depth in the Pacific; the new Atlantic species (represented by a single specimen) was taken by bottom trawl at a depth of only 500 meters. In the course of their extensive monograph on *L. luymesi*, van der Land and Nørrevang refer to the anterior plume-like area as the obturacular region. They note, as did Webb, that the plume filaments are borne on a central support structure, the obturaculum.

Both species of *Lamellibrachia*, in common with all other known Pogonophora, have a long, relatively undifferentiated third region, the trunk. However, several other pogonophores have a fourth segmented region, the opisthosome. This structure was not found in either species of *Lamellibrachia*—not necessarily because they lack such a region, but probably because of the method of collection and the thinness of that portion of trunk.

Anatomy

Further collections of giant tube worms from the Galápagos Rift in 1979, made available a large number of specimens for examination, allowing some general observations to be made. The body of the giant tube worm comprises four discrete regions. At the head end, protruding from the tube, is a red plume, colored by the hemoglobin carried in the tube worm's blood. The second region was a collar-like, double flap structure, comparable to the vestimentum of *Lamellibrachia*. The third region, the trunk, makes up about 70 to 80 percent of the total body length. In contrast to *Lamellibrachia*, there was, indeed, a fourth multisegmented region comparable to the opisthosomes of the other known Pogonophora (Figure 1).

The sub-structure of the obturacular plume merits further comment, for subsequent examination and research has shown it to be crucial to the life of the vestimentiferan worms. Although a glance at the obturacular plume mat suggests that it is a hodge-podge of filaments oriented in all directions, actually it has a rather rigorous pattern of organization.

The plume (Figure 2) has an axial support (the obturaculum of van der Land and Nørrevang). The plume's feather-like aspect is due to the numerous branchial lamellae (gill layers) projecting at right angles to the obturaculum. Each of the lamellae is composed of numerous gill filaments fused together at their bases. In the largest specimen available, we estimated that the plume had 228,000 individual filaments. Each filament is provided with a pair of blood vessels, one carrying blood to the tip of the filament and the other bringing blood back to the body. Along the length of the filament, capillaries connect the two vessels and pass immediately below the outer cuticle of the filaments. Thus the plume forms a most remarkable exchange organ for the uptake of life necessities and the elimination of wastes.

Another structural character of vast importance to the worms is the so-called trophosome (Figure 3). Looking superficially like

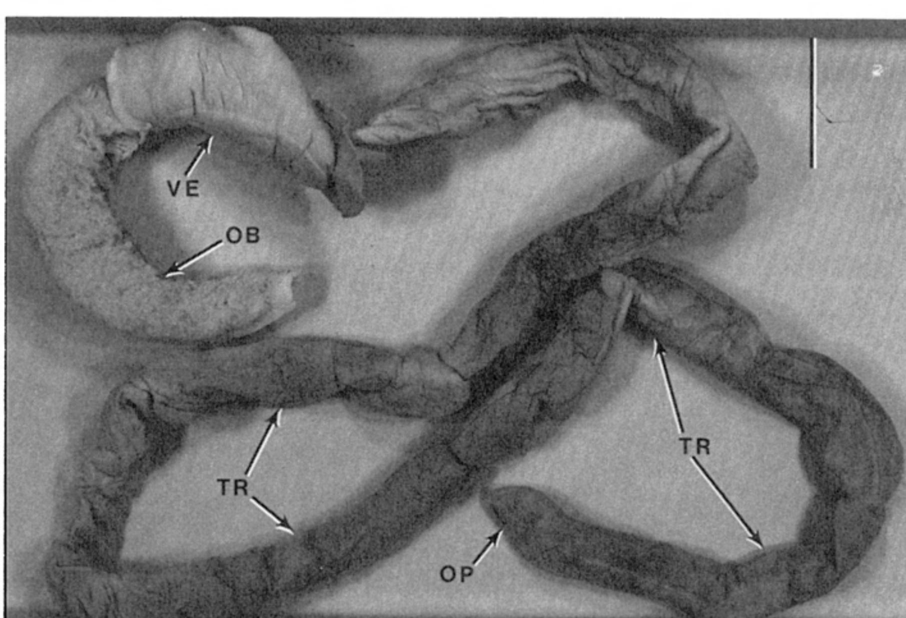


Figure 1. The largest specimen of Riftia pachyptila, *1.5 meters long, from the Rose Garden hydrothermal vent on the Galápagos Rift. When the animal is alive, the most anterior region, the plume or obturaculum (OB) extends from the tube; the vestimentum (VE) holds the worm at the tube opening; the long trunk (TR) contains the trophosome, gonads, and other organs; the posteriormost region, the opisthosome (OP) anchors the base of the tube (scale bar is 5 centimeters).*

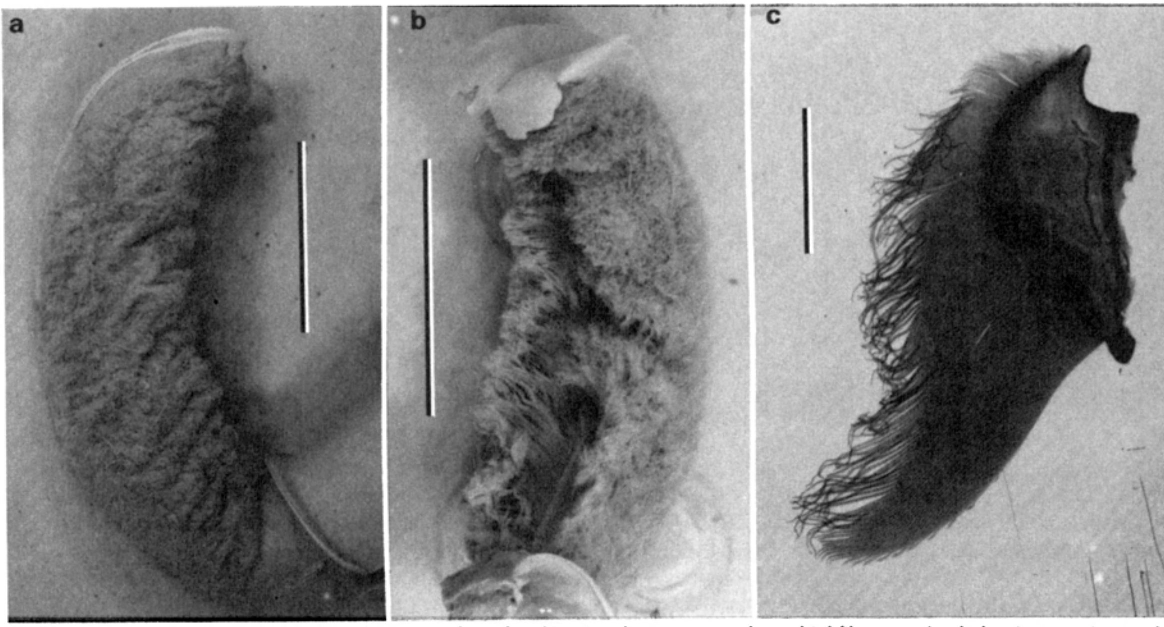


Figure 2. a) Lateral view of the plume of Riftia pachyptila, *showing the numerous branchial filaments (scale bar is 5 centimeters); b) ventral view of the* Riftia *plume showing the relationship of the branchial lamellae to the ventral ridge of the obturaculum (scale bar is 5 centimeters); c) an isolated single lamella of* Riftia *with half of the obturaculum to the right and more than 100 branchial filaments to the left (scale bar is 5 millimeters).*

proper worm tissue, the trophosome is actually composed of large numbers of symbiotic bacteria. Certain of these "lodgers" within the worms' bodies obtain energy from a biochemical "treatment" of sulfide brought to them by the blood system of the worm. Utilizing carbon dioxide and the energy drived from the sulfide, the bacteria form organic carbon, primarily for themselves (see page 79). Some of this organic carbon finds its way into the worms' tissues, strongly suggesting that the mouthless, gutless worms obtain much, if not most, of their nutrition from their "guests."

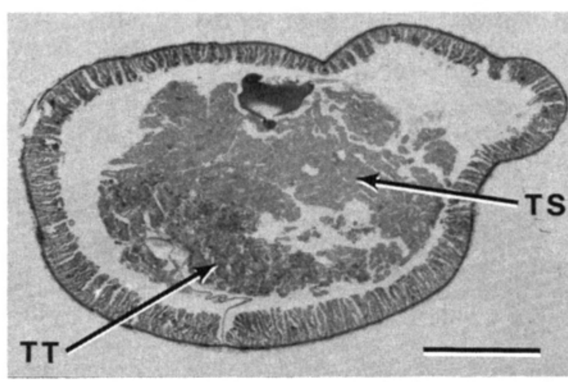


Figure 3. A transverse section of the trunk of a male Riftia, *showing the extent of testicular tissue (TT) and trophosome (TS) (scale bar is 3 millimeters).*

Another New Species

Extensive morphological and histological comparisons of the Galápagos Rift tube worms with written descriptions of both species of *Lamellibrachia* and with museum specimens of *L. barhami* revealed several things. The tube worms from the Galápagos Rift are, indeed, related to the two species of *Lamellibrachia*. In fact, these three worms are more closely related to one another than to any of the other pogonophorans, but certain structural features set the Galápagos Rift tube worms apart from their new-found relatives.

The end result of all of this comparing back and forth was that the Rift tube worms were declared a new genus and species, *Riftia pachyptila*. They have a new family, the Riftiidae, whereas the two previously described species made up the family Lamellibrachiidae. Finally, the structure and cellular make-up of these three species are so much at variance with the remainder of the phylum Pogonophora that two separate subphyla are needed to accommodate both groups.

Thus it was, subsequent to the collections from the Galápagos Rift and prior to the collecting of biological material from more recently discovered hydrothermal vent and related sites, that there were three formally recognized vestimentiferan species. In later collections *Riftia* has been found at hydrothermal localities on the East Pacific Rise at 11 to 13 degrees North and at 21 degrees North, as well as on the muddy bottom of the Guaymas Basin in the Gulf of California. At least two other species of vestimentiferans were taken by the French submersible *Cyana* at the 11 to 13 degrees North site, in about 2,600 meters of water in March 1982; yet another species was recovered by *Alvin* at 21 degrees North, also at about 2,600 meters, in May 1982. More recently, in August 1983, the Canadian submersible *Pisces IV* collected at least one other new species of vestimentiferan from a hydrothermal site at about 1,600 meters depth on the Juan de Fuca

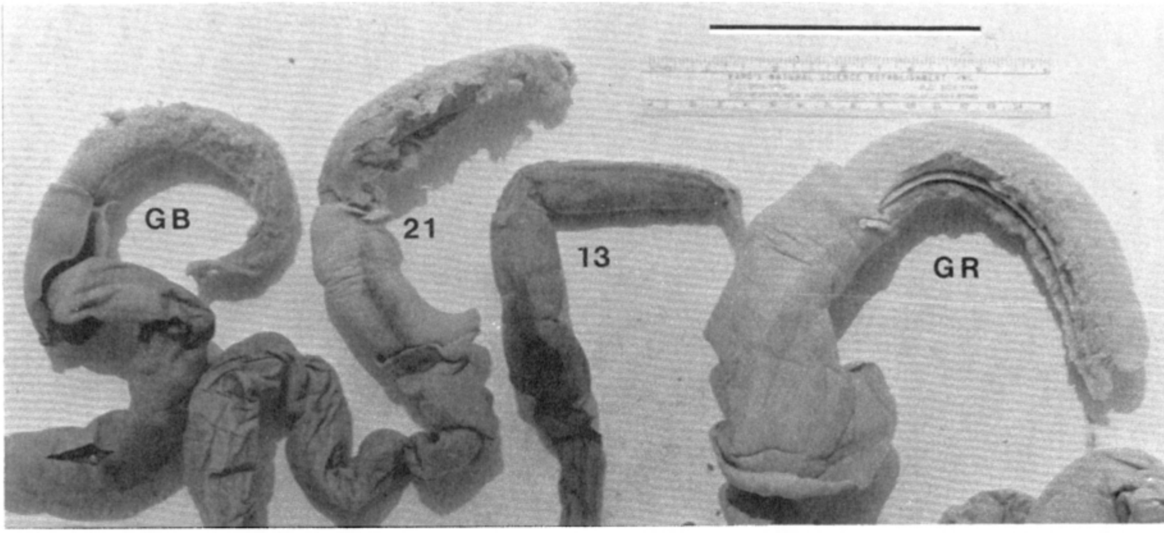


Figure 4. Anterior regions of the specimens of four populations of Riftia*—Guaymas Basin (GB), 21 degrees North (21), 11 to 13 degrees North (13) and the Galápagos Rift (GR). Note differences in relative lengths of obturacula and vestimenta (scale bar is 10 centimeters).*

Ridge off the coasts of British Columbia and Washington. And, while recollecting *Lamellibrachia barhami* off San Diego in 1980, the U.S. Navy submersible *Seacliff* brought up still another new vestimentiferan species from about 1,800 meters depth. Most recently, in March 1984, *Alvin*, working at approximately 3,200 meters in the eastern Gulf of Mexico, collected an undescribed vestimentiferan.

Comparing *Riftia* Populations

In considering the relationships among the four populations of *Riftia* (Guaymas Basin, 21 degrees North, 11 to 13 degrees North, and Galápagos Rift—see map, page 9) the most obvious morphological difference is the comparative lengths of the obturacular and vestimental regions. The specimens of *Riftia* pictured here were chosen as being nearest to the average of all specimens available from each of the various sites (Figure 4). The ratios of the vestimentum length to obturaculum length are: Guaymas Basin (northern most site), 2.32; 21 degrees North, 1.50; 11 to 13 degrees North, 1.32; and Galápagos (southern most site), 1.10. These differences may merely reflect a gradual north-to-south change in relative length of body regions or they may demonstrate a real taxonomic difference among the four populations. A firm decision in this case must await further study of present and future collections of *Riftia*.

Whereas an adult *Lamellibrachia* or *Riftia* has an unadorned anterior face of its obturacula, such is not the case in the three undescribed vestimentiferans from the sites on the East Pacific Rise (Figure 5). Of the two species from 11 to 13 degrees North, the larger has a thin, fin-like structure emerging between the two obturacular halves. The smaller new species has, arising from the obturacular face, a central axial rod provided with a variable number of cup-like structures that appear to have been secreted by the anterior face of the obturaculum; the whole structure, rod and cups, is brown-orange in color and opaque. The new vestimentiferan species from 21 degrees North also possesses a rod-and-cups structure on the anterior obturacular surface, but it is consistently whitish—nearly transparent—and would seem to be composed of a quite different material than that of the species from 11 to 13 degrees North. There are other structural differences that allow a discrimination between the two.

In 1981, I received a small collection of vestimentiferans from Paul Johnson and John DeLaney of the University of Washington, which they obtained by dredging on the Juan de Fuca Ridge. These specimens were provided with an obturacular rod-and-cups structure similar to that of the species from 11 to 13 degrees North, but different in their relatively longer obturaculum. In 1983, using *Pisces IV*, Verena Tunnicliffe (University of Victoria, British Columbia) made more extensive collections of vestimentiferans at a site approximately 75 kilometers southeast of the Johnson-DeLaney site. Although some small specimens from a single site (the Lamphere Chimney) were similar, if not identical, to the Johnson-DeLaney specimens, most of the specimens in the Tunnicliffe collection were larger and lacked the opaque rod-and-cups ornamentation, having instead a single transparent cup on the obturacular face (Figure 6). These two forms from the Juan de Fuca Ridge are presently under study; hopefully histological and other comparisons will soon confirm whether there are one or two species present at this most northerly of the hydrothermal vents.

Cold-Water Vestimentiferans

Thus far I have considered new vestimentiferan material from hydrothermal vents where the environment is characterized by elevated water temperatures and sulfide-rich vent waters. However, the first known vestimentiferan, *Lamellibrachia barhami*, was collected off San Diego at an unremarkable site (not the home of a hydrothermal vent) differing rather little from any sea bottom of

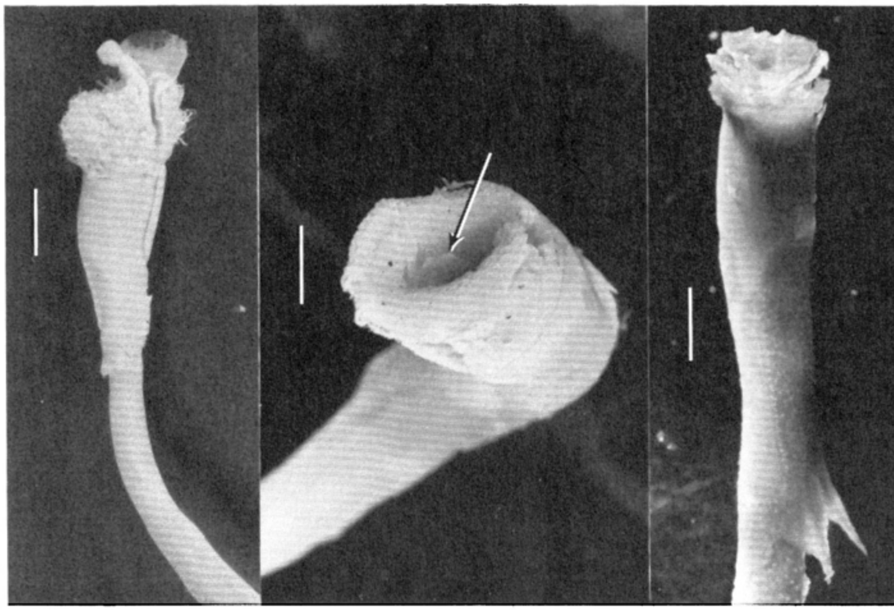


Figure 5. Undescribed vestimentiferan from the 11 to 13 degrees North site. The larger, "finned" species is on the left (scale bar is 5 millimeters), with a closer view (middle) of its fin-like ornament (arrow; scale bar is 1 millimeter); on the right, a smaller species with rod-and-cups obturacular ornament (scale bar is 1 millimeter).

similar depth. No sulfide analyses have been carried out on the waters of the San Diego site, but curiously enough, deposits of barite (barium sulfate) are present in the area; this would suggest that the site might be a cold-water sulfide habitat. When *Seacliff* dove there in 1980, we anticipated that new collections of *L. barhami* would be obtained. With mixed feelings, I found that *L. barhami* was outnumbered, about four to one, by yet another new vestimentiferan. *Lamellibrachia barhami* has a smooth and unadorned obturacular face, and its branchial plume comprises branchial filaments of uniformly small size protected by several lamellar sheaths. The new vestimentiferan possesses a rather thick crust over the obturacular face, from the center of which projects a stout spike-like structure; it has branchial filaments of two sizes and lacks any kind of protective lamellar sheath.

Finally, when biological material from the *Alvin* collecting expedition on the Florida Escarpment in the eastern Gulf of Mexico came to our laboratory for examination, we discovered still another new vestimentiferan (Figure 7). The Florida Escarpment habitat is similar to the cold-water environment off San Diego, so it is not too surprising that the new worm bears a thick crust over the anterior face of the obturaculum, has plume filaments of two different sizes, and lacks lamellar

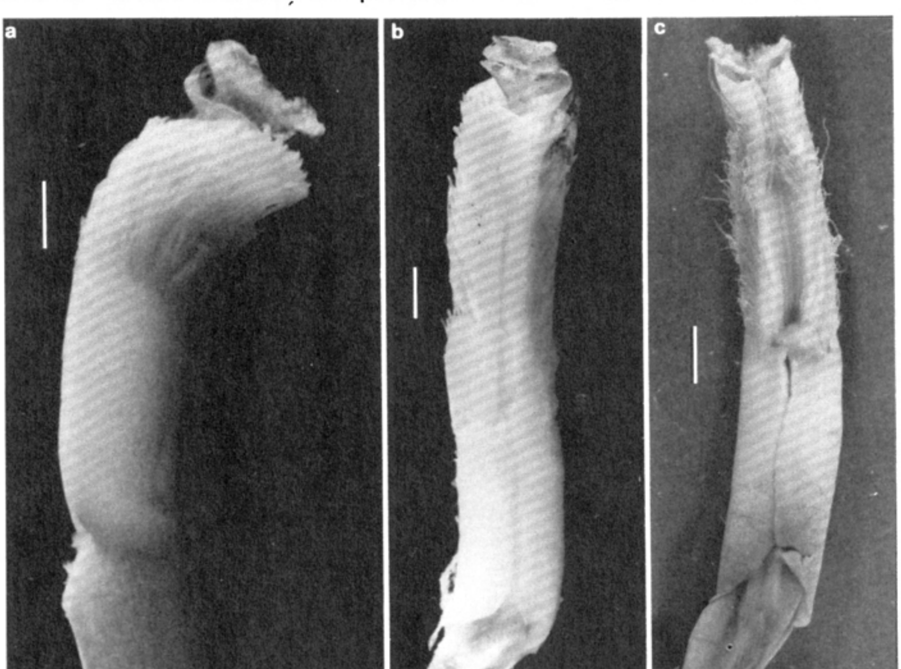


Figure 6. a) Undescribed rod-and-cups species of vestimentiferan from 21 degrees North (scale bar is 1 millimeter); b) undescribed rod-and-cups form from the northern Juan de Fuca Ridge (scale bar is 1 millimeter); c) undescribed species with a single transparent cup from the southern Juan de Fuca Ridge (scale bar is 5 millimeters).

Fossilized Worm Tubes Found in Oman

According to a recent report in Science, geologists working in the Sultanate of Oman have discovered what appear to be fossilized worm tubes dating from the Upper Cretaceous period. The mineralized remains of the tubes typically have sinuous shapes and are randomly oriented, two features that would suggest that they were not formed by physical processes, but are indeed of biological origin. They are preserved in a matrix of zinc and iron sulfide minerals in an ophiolite deposit that was formed at a ridge crest spreading center some 95 million years ago. The patterns of mineralization, the scale, and the orientation of the fossils are all strongly suggestive of recent fossilized worm tubes found near hydrothermal vents.*

The resemblence of the fossilized organisms to modern worms found at deep-sea hot springs and sulfide seeps seems quite strong, but the authors note that it is impossible at this point to say whether the Cretaceous worms were ancestors of the present-day species, or whether the modern worms evolved independently, adopting a similar form in response to similar evolutionary pressures or by chance. The existence of these fossils, however, does suggest that hydrothermal vent communities have existed for some time.

Another piece of evidence for the existence of hydrothermal vent communities in the Cretaceous period comes from the existence at hydrothermal vents of two species (the limpet Neomphalus fretterae *and the stalked barnacle* Neolepas zevinae*) that apparently survived the Late Cretaceous extinctions only at hydrothermal vents. Scientists postulate that these two organisms took refuge in hot spring communities at relatively shallow spreading centers near continents or around islands, and eventually migrated to other spreading centers to escape predation pressures.*

—FLL

* Haymon, R. M., R. A. Koski, and C. Sinclair. 1984. Fossils of hydrothermal vent worms from Cretaceous sulfide ores of the Samail ophiolite, Oman. *Science*. Vol. 223: 1407–9.

sheaths surrounding the plume. However, it differs from the San Diego specimens in that it lacks the central spike-like structure. Instead, a thin fin-like ornament arises from between the obturacular halves, much the same as with one of the species from the 11 to 13 degrees North site.

So, what can we say about the plethora of Vestimentifera from various habitats in the eastern Pacific, the Gulf of Mexico, and the western Atlantic off northern South America? For now, I can only acknowledge one valid species of *Riftia*, with the possibility that at least one more species may be justified. At least six more vestimentiferan species are undescribed. How all of the various species, "new" and "old," will fall into families, orders, and classes remains to be seen. I am confident that the presence or absence of obturacular ornamentation, the presence or absence of lamellar sheaths, the relative lengths of the obturaculum and the vestimentum, the presence of different size plume filaments, as well as a number of morphological characteristics beyond the purview of the present discussion, will all help in the ultimate resolution of the enigma of the Vestimentifera.

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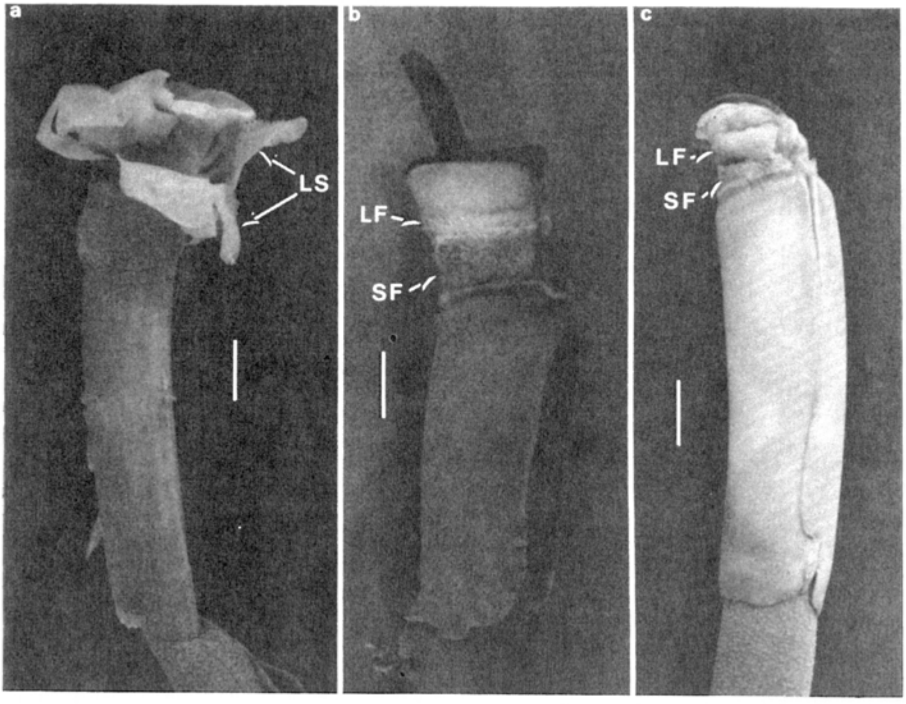

Figure 7. a) Lamellibrachia barhami, *the first described vestimentiferan species, found off San Diego, showing lamellar sheaths (LS) surrounding the branchial filaments; b) the spiked form, an undescribed species, also found off San Diego; c) undescribed species from the Florida Escarpment in the Gulf of Mexico. For the latter two specimens, the region of larger (LF) and smaller branchial filaments (SF) are indicated (scale bar for all three pictures is 5 millimeters).*