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The Vestimentifera, their biology, systematic and evolutionary patterns

Vestimentifera
Trophosome
Riftia pachyptila
Bacteria
Symbiosis

Vestimentifères
Trophosome
Riftia pachyptila
Bactéries
Symbiose

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ABSTRACT

The taxonomy of the vestimentiferan worms is reviewed, covering nine described species in six genera. The morphology and anatomy of the vestimentiferans are reviewed, with emphasis on the vascularization of the branchial complex and the trophosome. A recently discovered ciliated duct, functional only in juvenile vestimentiferans, is hypothesized as the means of entry of bacteria into the trophosome. The external opening of this duct is at the distal end of a ciliated, ventral medial process, which arises from the base of the obturacular region ; internally the duct appears to open into an anteroventral expansion of the trophosome. Morphological criteria are presented supporting the designation of five families, three orders and two classes, as well as the separation of the vestimentiferans in their own phylum, Vestimentifera; the latter judgment is based on the morphology of the opisthosome and the arrangement of anterior coelomic segments.

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RÉSUMÉ

Vestimentifères : biologie, systématique et évolution

La taxonomie des vers vestimentifères est récapitulée sur neuf espèces décrites en six genres. La morphologie et l'anatomie des vers vestimentifères sont examinées en soulignant la vascularisation du complexe branchial et le trophosome. Un canal cilié, récemment découvert, et présent seulement dans les vestimentifères juvéniles, est supposé être le moyen d'entrée des bactéries dans le trophosome. L'ouverture extérieure de ce canal est une région ciliée sur la face externe, à l'extrémité d'une structure ventromédiale issue de la base de la région obturaculaire ; à l'intérieur, le canal paraît s'ouvrir dans une extension antéro-ventrale du trophosome. Les critères morphologiques présentés corroborent la désignation de cinq familles, trois ordres et deux classes, aussi bien que la séparation des vestimentifères en leur phylum vestimentifère ; cette dernière conclusion est fondée sur la morphologie de l'opisthosome et l'arrangement des segments coelomiques antérieurs.

Oceanol. Acta., **1988**. Actes du Colloque Hydrothermalisme, Biologie et Écologie, Paris. 4-7 novembre 1985, 69-82.

INTRODUCTION

The first vestimentiferan, *Lamellibrachia barhami* was described by Webb (1969) from material collected in 1966 at a site off the southern California coast at a depth of 1125 m. Based on the morphology and histology of the new species, Webb assigned it to the phylum Pogonophora, but found so many unique characters in *Lamellibrachia barhami* that he established a new class (Afrenulata) and a new order (Vestimentifera) for it. In common with the pogono-phorans, *Lamellibrachia barhami* possesses a proteinaceous tube and four body regions (of which the third is a very long trunk) and lacks a mouth, gut and anus. Webb noted that *Lamellibrachia barhami* lacked a bridle (= frenulum); in additional contrast, it is provided with : 1) excretory ducts not connected to the "tentacular coelom"; 2) a first region comprised of a branchial plume (= tentacular crown) surrounding a central support structure, and the plume, in turn, surrounded by a series of lamellar sheaths ; 3) a second (vestimental) region bearing lateral wing-like folds; 4) genital apertures of both males and females that open at the anterior end of the third (trunk) region.

In 1970 a single vestimentiferan specimen was trawled from a depth of 500 m off the coast of Guyana in the western Atlantic; this formed the basis for the description of a second species of *Lamellibrachia, Lamellibrachia luymesi* (van der Land, Nørrevang, 1975). In addition to documenting species differences, relative to *Lamellibrachia barhami*, van der Land and Nørrevang presented a number of general anatomical observations that were amplified in a later, account (van der Land, Nørrevang, 1977). One particular structure noted in the trunk of *Lamellibrachia luymesi* was the so-called trophosome, considered by van der Land and Nørrevang to serve a nutritive function for developing spermatozoa ; these authors considered the Pogonophora and the Vestimentifera to be separate classes in the phylum Annelida.

In the course of a series of dives by DSRV Alvin on the Galapagos Rift, a number of vestimentiferans were collected from hydrothermal vents at a depth of about 2500 m. These specimens were described (Jones, 1981 *a*) as a new species, *Riftia pachyptila.* Among other features noted were the fourth, most posterior, region, the opisthosome, and that crystals of elemental sulfur were present in the trophosome. Further, in considering the unique morphological characters of the vestimentiferans relative to those of other pogonophorans, it was suggested that the two taxonomic groups were best separated at the subphylum level, the vestimentiferans being relegated to the subphylum Obturata and the remaining pogonophores to the subphylum Perviata.

Subsequent expeditions to hydrothermal vents by Alvin, the French submersible Cyana and the Canadian submersible Pisces IV, as well as those to cold sites by Alvin and her US Navy sister ships, Sea Cliff and Turtle, have yielded other vestimentiferans ; from these collections six additional species have been described ; at present, six genera in five families are recognized (Jones, 1985 *b*).

MATERIALS AND METHODS

All but one of the specimens in Figure 1 are in the collections of the National Museum of Natural History, Smithsonian Institution ; the exception is the holotype of *Tevnia jerichonana* (Fig. 1*f*), which is in the collections of the Muséum National d'Histoire Naturelle, Paris. Paraffin-embedded histological material from the Galapagos Rift was sectioned at 5 µm; specific histological stains are noted in the appropriate figure legend. Specimens examined by scanning electron microscopy (SEM) were processed according to methods outlined by Jones and Gardiner (1985). Samples of trophosome of *Riftia pachyptila*, from Clam Acres at 21° N on the East Pacific Rise, were treated in two ways : some were macerated for several months in 30 % ethanol, then agitated for extended periods in a vortex mixer; others were sonicated, for as long as an hour, in order to free small blood vessels of their associated bacteria.

THE DESCRIBED VESTIMENTIFERANS

Although the first described vestimentiferan was *Lamellibrachia barhami* Webb (Fig. 1*a*), a short discussion of the external morphology of vestimentiferans will be based *Riftia pachyptila* Jones (Fig. 1*b*, *c*). With but a few exceptions the structure of *Riftia pachyptila* is similar to that of all other vestimentiferans.

All vestimentiferans are composed of four body regions :

- the obturacular region (Fig. 1*b*: OB) : there are two distinct components in this region. A central supporting structure, the obturaculum (van der Land, Nørrevang, 1975; 1977) (=lophophoral organ, Webb, 1969), is actually comprised of paired obturacular halves, fused medially (Fig. 1*b*: OB). Immediately inside the outer epithelial layer of each half is a system of rings of muscles, oriented in either parasagittal or frontal planes (Jones, 1985 *b*); these surround what appears to be a connective tissue matrix that is penetrated by a blind-ending blood vessel, the obturacular vessel, suspended in a perivascular cavity by a mesentery-like structure (Jones, 1985 *b*). The second component of the obturacular region is the branchial plume that consists of a series of paired branchial lamellae, each of which is comprised of fused branchial filaments (= tentacles, Webb, 1969; van der Land, Nørrevang, 1975; 1977; Fig. 1*b* : BF). There is a system of perivascular cavities associated with all blood vessels leading to and returning from the branchial plume, from the dorsal vessel to the ventral vessel, including the blood vessels of the branchial filaments (Jones, 1985 *a*). Although the branchial complex and the obturaculum appear to be a single entity, they are separated from one another by independently secreted cuticular material. There are no extensive cavities in the obturacular region. Primary functions of the obturacular region are to act as an exchange organ and to close off the tube when the animal is withdrawn ;
- the vestimentum (Fig. 1*b*: VS) : the second region of the vestimentiferan body is, for the most part, of solid construction, comprised of muscle and connective tissue, and lacking any obvious cavities, apart from a second, posterior perivascular cavity associated with the dorsal

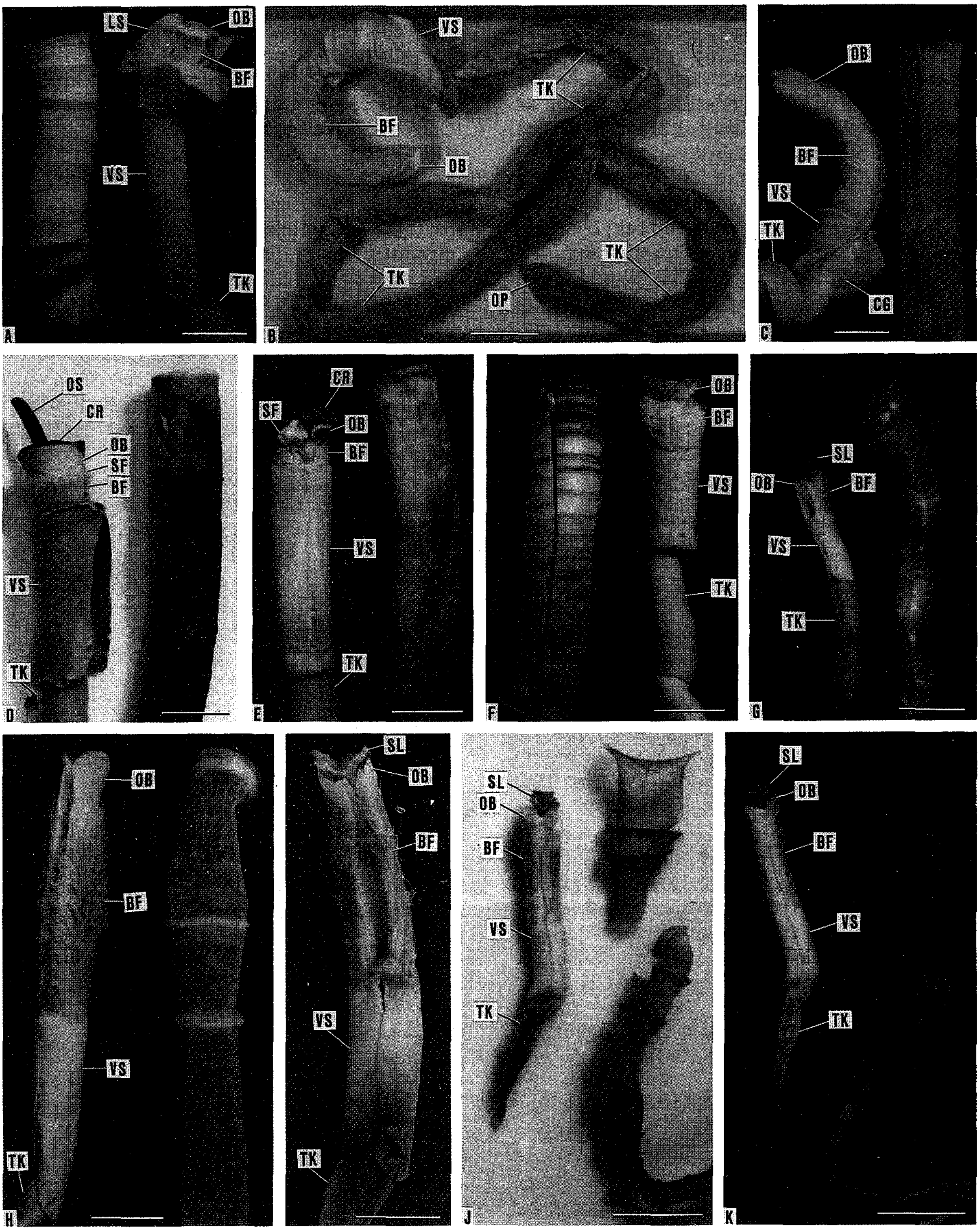


Figure 1

Vestimentiferan worms from hydrothermal (H) and non-hydrothermal (N) sites : A) Lamellibrachia barhami *Webb (USNM 98023), N, off San Diego, California, 1818 m depth, right ventrolateral view, with tube ; scale bar : 10 mm. B)* Riftia pachyptila *Jones (holotype, USNM 59951), H, Rose Garden, Galapagos Rift, 2450 m depth, left lateral view; scale bar 5 cm. C) Same, young specimen (paratype, USNM 59959), H, Rose Garden, Galapagos Rift, 2450 m depth, lateral (branchial region) and dorsal (vestimentum) view, with tube ; scale bar : 10 mm. D)* Escarpia spicata *Jones (paratype, USNM 98006), N, off San Diego, California, 1818 m depth, lateral view, with tube; scale bar : 10 mm. E)* Escarpia laminata *Jones (paratype, USNM 97993), N, Florida Escarpment, Gulf of Mexico, 3268 m depth, ventral view, with tube ; right side of anterior region damaged; scale bar : 10 mm. F)* Tevnia jerichonana *Jones (holotype, MNHNP), H, 11°27'N on the East Pacific Rise, about 2600 m depth, ventral view, with tube; scale bar : 10 mm. G)* Oasisia alvinae *Jones (paratype, USNM 98013), H, 20°50'N on the East Pacific Rise, 2600 m depth, right dorsolateral view, with tube; scale bar : 5 mm. H)* Ridgeia piscesae *Jones (paratype, USNM, 98108), H, Axial Seamount, Juan de Fuca Ridge, 1599 m depth, right dorsolateral view, with tube; scale bar : 10 mm. I) Same (holotype, USNM 98105), H, Axial Seamount, Juan de Fuca Ridge, 1599 m depth, dorsal view; scale bar : 10 mm. J) Ridgeia phaeophiale Jones (holotype, USNM 98111), H, Endeavour Segment, Juan de Fuca Ridge, about 2100 m depth, dorsal view, with tube; scale bar : 5 mm. K) Same specimen, dark background; scale bar : 5 mm. BF : branchial filaments; CG : ciliated groove; CR: obturacular crust; LS: lamellar sheath; OB: obturaculum; OP : opisthosome; OS : obturacular spine; SF : sensory filaments; SL : saucer-like obturacular structure; TK : trunk; VS : vestimentum.*

vessel (Jones, 1985 *a*). The brain is situated in the anteroventral region of the vestimentum (this is a reevaluation of an earlier conclusion that the brain is part of the obturacular region; Jones, 1985 *a*) and gives rise to paired intraepidermal nerve cords that diverge on the anteroventral surface of the vestimentum and unite in its posterior portion; the ventral ciliated field is a somewhat pear-shaped area between the paired nerve cords and is densely ciliated. From the dorsolateral areas of the vestimentum arise paired wing-like structures that overlap dorsally when the worms are within their tubes ; by means of the overlap, there is formed a vestimental canal. The paired genital pores of both males and females open posteriorly in this passage, on the dorsal body surface. In certain vestimentiferans, a ciliated ridge/groove leads anteriorly from each genital pore (Fig. 1*c* : CG) ; these appear to be restricted to males. The outer surface, not including the vestimental canal and ventral ciliated field, is richly provided with plaque papillae and papillated openings of pyriform glands; the pyriform glands appear to secrete tube material. Primary functions of the vestimentum are to act as temporary holdfast at the distal end of the tube when the plume is extended and to lay down tube material for distal extension of the tube ;

- the trunk (Fig. 1*b* ; TK) : the longest of the vestimentiferan body regions is the third, the trunk. Externally, it appears to be an undifferentiated cylinder in *Riftia*, in contrast to other vestimentiferans, all of which have noticeably tapered trunk regions; its surface bears both plaque papillae and the papillated openings of pyriform glands. Internally, the trunk consists of a single pair of coelomic cavities, separated by a medial mesentery in which is found the major longitudinal blood vessels ; in the case of *Riftia* (Fig. 2 *a*), both the dorsal and the ventral mesenteries (Fig. 2*a* : DM, VM) are separated by a central structure composed of gonad and the trophosome (Fig. 2 *a* : TT, TR). The anterior end of the trunk, with its anterior extensions of the trunk coelom, overlies the dorsal surface of the posterior one-third to one-quarter of the vestimentum and, near its anterior end, the genital ducts move laterally form the trunk coelom to open as genital pores at the vestimentum-trunk boundary. Primary functions of the trunk are to house the trophosome and gonads and to thicken the tube wall proximal to the tube opening;
- the opisthosome (Fig. 1 *b* ; OP) : the fourth and terminal region of the vestimentiferan body is the shortest and bears a number of nearly circumferential rows of setae on its anterior surface. The setae reflect an internal segmentation of the opisthosome, which extends past the setal rows to the posterior end of the animal. The opisthosome has not yet been observed in *Lamellibrachia* and *Escarpia*. Primary functions of the opisthosome are to act as a holdfast when the animal withdraws into the tube and, in *Riftia*, to secrete basal partitions that isolate more basal, unused portions of the tube.

Of the six vestimentiferan genera so far described, four are known only from hydrothermal vent localities. The following is derived from a recent account of the vestimentiferans (Jones, 1985 *b*).

Lamellibrachia is characterized by the presence of a series of lamellar sheaths surrounding the branchial filaments of the obturaculum (Fig. 1*a* : LS); there are no ornamental structures on the anterior face of the obturaculum ; the tube of *Lamellibrachia barhami* is quite rigid, up to 1.5 m in length, and bears indistinct collars and irregularly spaced, pigmented bands (Fig. 1*a*). *Lamellibrachia barhami* is known only from the eastern Pacific, in the southern San Clemente Basin off southern California and from the Oregon subduction zone, from non-hydrothermal sites at 1125-2050 m depth. *Lamellibrachia luymesi* differs from *Lamellibrachia barhami* mainly in the different relative lengths of the obturacular and vestimental regions and in having a smooth tube with inconspicuous collars and no pigmented bands. The species is known from a single specimen trawled off the coast of Guyana at a depth of 500 m.

Riftia pachyptila is remarkable for its size, the largest specimen being 1.5 m in length and approximately 40 mm in diameter (Fig. 1 *b*). The species lacks lamellar sheaths and, in the adult, lacks obturacular ornamentation (Fig. 1 *b, c*) ; in the case of small juveniles of *Riftia* there may be a central obturacular spine and lateral expansions of this spine have been observed occasionally (pers. observ.). The tube of *Riftia* may bear very reduced collars and is flexible, except where thickened (> 3mm) ; the living space of individual animals may be restricted to the apical portion of tubes due to the formation of basal partitions, apparently secreted by glands in the opisthosome; thus a tube of 2.5 m length has a living space of only the apical 1.2 m (Jones, 1981 *a*). *Riftia* is known only from hydrothermal sites in the eastern Pacific, on the Galapagos Rift, at about 21° N, 13° N and 18° S on the East Pacific Rise, and in the Guaymas Basin, at depths of 1957-2655 m.

The two species of *Escarpia* are known only from non-hydrothermal localities; they secrete rigid tubes, up to about 0.9 m in length, which lack collars; their anterior obturacular faces bear a thick crust (Fig. 1 *d, e* : CR) and a medial structure; branchial filaments are confined to the proximal region of the obturaculum (Fig. 1*d, e* : BF) and a series of sensory filaments are more distal (Fig. 1 *d, e* : SF). *Escarpia spicata* is characterized by a prominent medial obturacular spine (Fig. 1 *d* : OS) and is known from a single site, in the southern San Clemente Basin off the southern California coast, where it occurs with *Lamellibrachia barhami* at a depth of 1818-1847 m. *Escarpia laminata* (Fig. 1 *e*) bears a small medial laminate obturacular structure and is known from a single site at the base of the Florida Escarpment in the Gulf of Mexico, at a depth of 3268-3270 m.

Tevnia jerichonana has a somewhat rigid tube of moderate length, up to 0.3 m, and bears numerous closely set, prominent collars (Fig. 1 *f*). The anterior obturacular face of *Tevnia jerichonana* bears a medial laminate structure, similar to that of *Escarpia laminata*. *Tevnia jerichonana* is known only from hydrothermal localities on the East Pacific Rise at about 12° and 13° N, at depths of 2630-2635 m.

Oasisia alvinae is a small species with a transparent/translucent tube, up to 123 mm in length, with irregularly placed collars (Fig. 1 *g*) ; its obturaculum bears a medial rod, with saucer-like lateral structures, on the anterior face (Fig. 1 *g* : SL). This species is known only from Clam Acres, a hydrothermal site at 2600 m depth, on the East Pacific Rise at about 21° N.

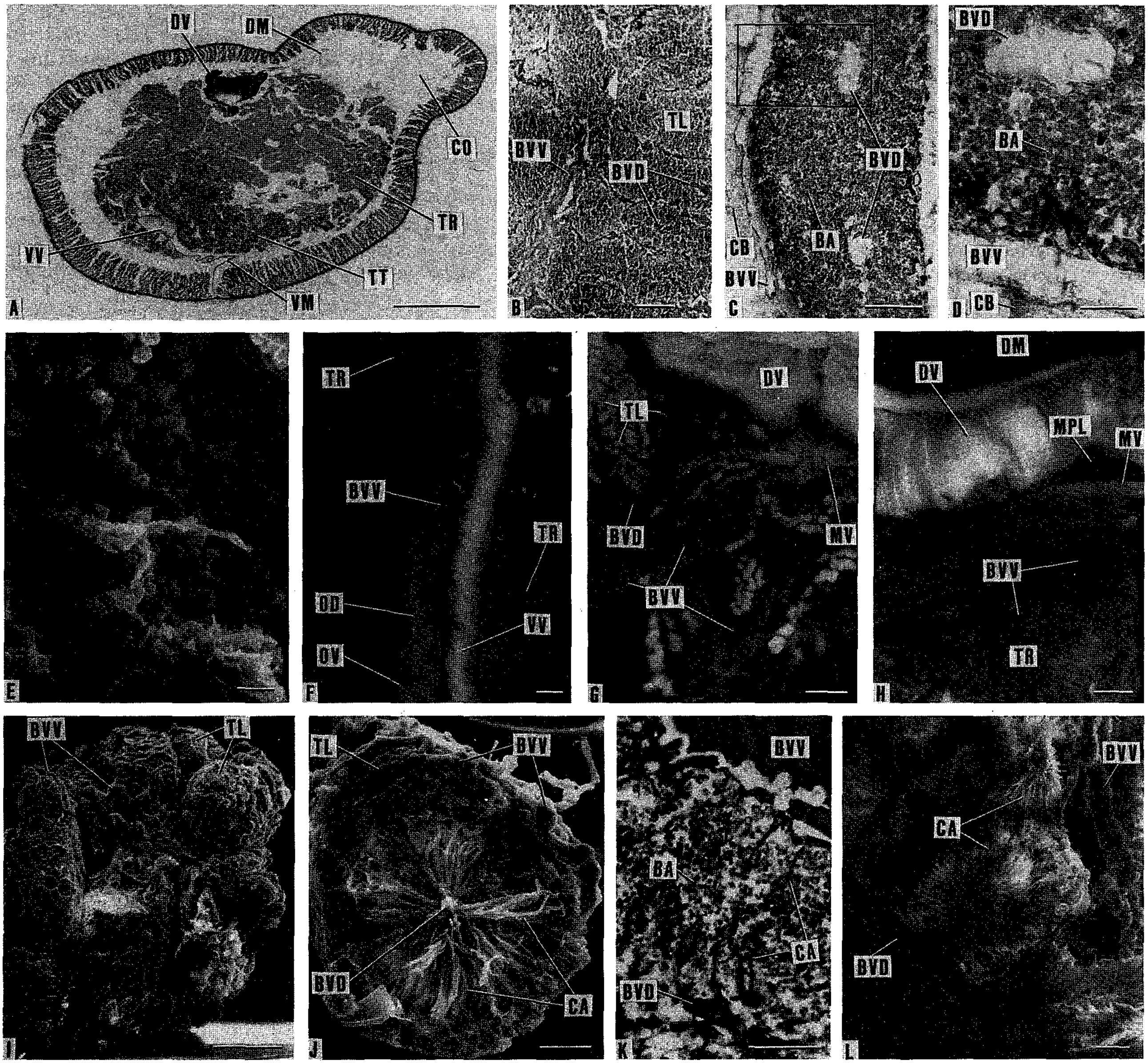


Figure 2

Trophosome of Riftia pachyptila *and its vascularization; A : Mallory's trichrome; B-D, K : Masson's trichrome : A) Transverse section through trunk of male showing relationship of trophosome, testicular tissue and dorsal and ventral blood vessels; scale bar : 5 mm. B) Overview of transverse section of trophosome showing organization of lobular substructure; scale bar : 100 µm. C) Detail of trophosomal lobule showing main vascular elements; scale bar : 50 µm. D) Enlargement of boxed area of C; scale bar : 20 µm. E) SEM micrograph of bacteria of trophosome; scale bar : 5 µm. F) Arrangement of blood vessels arising from ventral vessel of female; scale bar : 1 mm. G) Vascular elements of trophosome, macerated to free smaller blood vessels from trophosomal lobules; scale bar : 1 mm. H) Arrangement of blood vessels associated with dorsal vessel, macerated; scale bar: 1 mm. I) SEM micrograph of cluster of trophosomal lobules showing superficial vascularization derived from ventral vessel; scale bar : 200 µm. J) SEM micrograph of sonicated transverse face of trophosomal lobule, freed of bacteria, showing peripheral vessels (derived from ventral vessel), central vessel (derived from mesenterial/dorsal vessel) and intervening, radiating, capillary bed; scale bar : 50 µm. K) Section showing relationship of vascular elements of trophosomal lobule; scale bar : 30 µm. L) SEM micrograph of sonicated trophosomal lobules, devoid of bacteria; scale bar : 50 µm. BA : bacteria; BVD : blood vessel derived from dorsal vessel = efferent trophosomal vessel; BVV : blood vessel derived from ventral vessel = afferent trophosomal vessel; CA : capillaries; CB: coelomic blood; CO : coelom; DM : dorsal mesentery; DV : dorsal vessel; MPL : mesenterial blood plexus; MV : mesenterial vessel; OD : oviduct; OV : ovary; TL : trophosomal lobule; TR : trophosome; TT : testicular tissue; VM : ventral mesentery; VV : ventral vessel.*

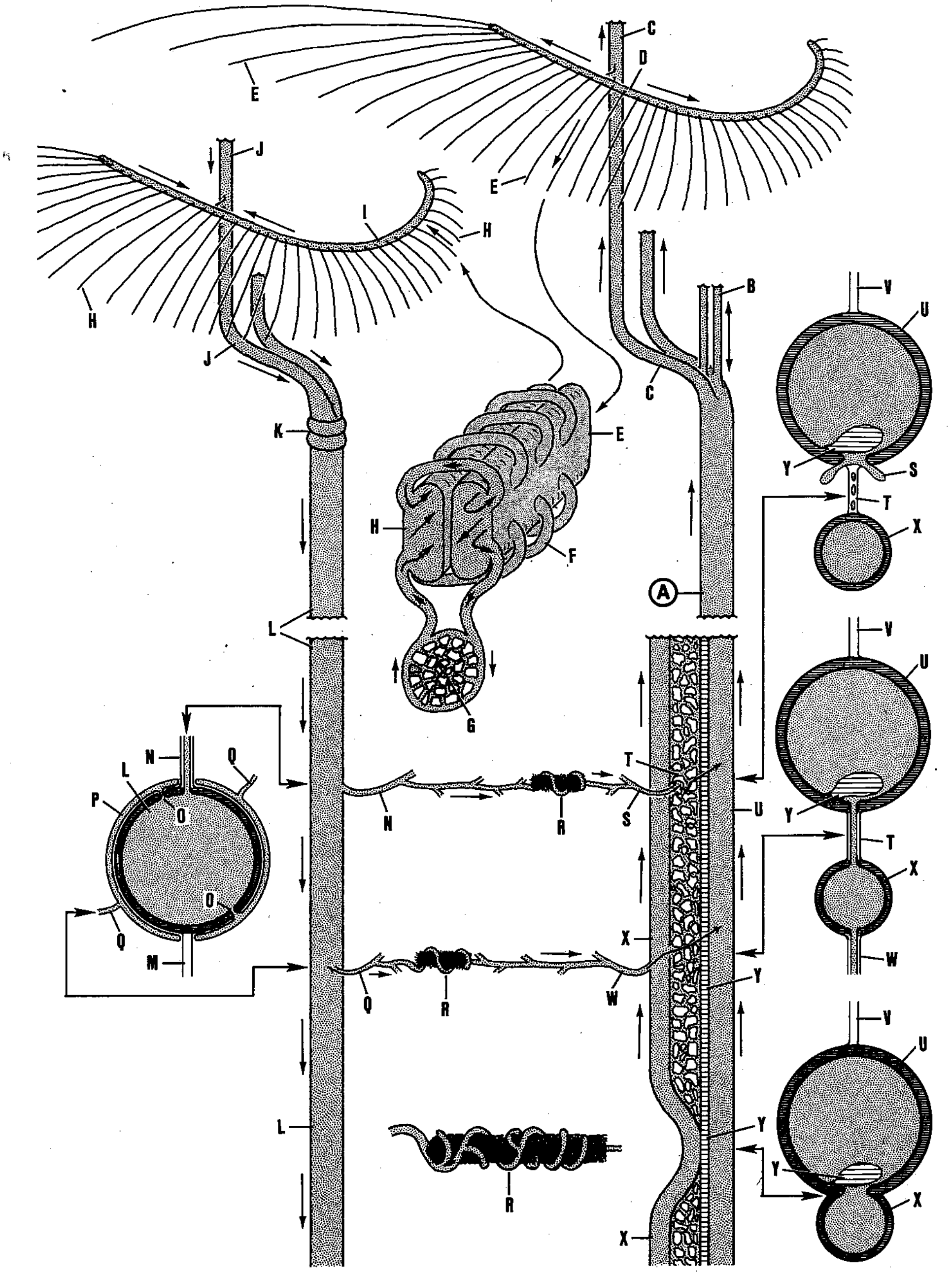


Figure 3
Summary of certain elements of the circulatory system of Riftia pachyptila*; dorsal to right, ventral to left, anterior at top, posterior at bottom; branchial vessels of only one branchial lamella shown; stippled areas blood : blood in dorsal vessel (circled A) propelled anteriorly by muscles in wall of vessel; dorsal vessel branches giving rise to obturacular vessels (B) and afferent plume vessels (C); blood carried anteriorly in plume vessels to afferent lamellar vessels (D) at base of each branchial lamella, then to afferent branchial vessels (E); along length of branchial filament blood may enter intraepithelial capillary loop (F) or pinnular plexus (G), passing then to efferent branchial vessels (H); blood returned via efferent lamellar vessels (I), then to efferent plume vessels (J), which unite at the sinus valvatus (K); blood carried posteriorly in ventral vessel (L), which is supported by ventral mesentery (M); blood may depart ventral vessel directly via dorsal afferent trophosomal vessels (N) or may exit ventral vessel through apertures (O) in wall, to vascular envelope (P) surrounding ventral vessel and extending along its length; blood from envelope carried in lateral afferent trophosomal vessels (Q); dorsal afferent trophosomal vessels service dorsal trophosomal lobules lateral afferent trophosomal vessels service ventral trophosomal lobules; capillary complex (R) formed as afferent trophosomal vessels branch over surface of trophosomal lobules and blood carried centripetally in capillaries among trophosomal bacteria to end-branch of efferent trophosomal vessel; efferent trophosomal vessels from dorsal lobules (S) carry blood to mesenterial blood plexus (T); blood then passes to dorsal vessel (U), which is supported by dorsal mesentery (V); efferent trophosomal vessels from ventral lobules (W) carry blood directly to mesenterial vessel (X) whence it passes to dorsal vessel via mesenterial blood plexus; blood may pass directly from mesenterial vessel to dorsal vessel; back-flow of blood from dorsal vessel into mesenterial vessel and mesenterial blood plexus prevented by flapper-valve action of linearly oriented intravasal body (Y).*

The two species of *Ridgeia* are known only from the northeast Pacific and are associated with hydrothermal vents. *Ridgeia piscesae* (Fig. 1 *h, i*) has a rather flexible transparent to translucent-white tube, up to about 0.9 m in length, with irregularly distributed, moderately developed collars ; it may be provided with one or two white, saucer-like structures on the obturacular face (Fig. 1 *i* : SL) ; at present it is known only from Axial Seamount on the Juan de Fuca Ridge. The smaller *Ridgeia phaeophiale* (Fig. 1 *j, k*) has a somewhat brittle, transparent, brown tube, up to 151 mm in length, with well-developed collars ; on the medial obturacular face there may be as many as 11 brown or golden saucer-like structures, supported by a central rod (Fig. 1 *j, k* : SL); it is known from the Endeavour, middle and southern segments of the Juan de Fuca Ridge at depths of 1599-2380 m.

Additional species of vestimentiferans, as yet undescribed, are known from off the coast of Uruguay (Montero, pers. comm.), from the Explorer and Juan de Fuca Ridge, from a locality south of Louisiana in the Gulf of Mexico, and from the East Pacific Rise at 12°-13° N, 10° N, and 18° S.

GENERAL ASPECTS OF THE CIRCULATORY SYSTEM

Descriptions or pertinent comments concerning vascular patterns have been published (Webb, 1969, 1977; van der Land, Nørrevang, 1975; 1977 ; Jones, 1981 *a; b*; 1985 *a; b* ; Arp *et al.*, 1985; Wittenberg, 1985).

The circulatory system of *Riftia pachyptila* is closed and the primary parts, comprised of the dorsal and ventral vessels and their branches, are connected by capillaries or by intraepithelial capillary loops. Primary blood movement is derived from contractions of the relatively thick layer of circular muscles investing the dorsal vessel in the vestimental and trunk region (Fig. 2 *a, h* : DV, 3 : A, U). There are no obvious branches to or from the dorsal vessel during its transit of the vestimental region and a "heart" region can be recognized here. Near the anterior end of the vestimentum, the dorsal vessel branches to form paired afferent plume vessels [Fig. 3 : C = tentacular blood vessels (Webb, 1975) ; = afferent tentacular vessels (van der Land, Nørrevang, 1977); = anterior branch of dorsal vessel (Jones, 1981 *a ;* 1985 *a*)] and obturacular vessels Fig. 3 : B = cerebral blood vessel (Webb, 1969); = artery of the lophophoral organ (Webb, 1975)]. The obturacular vessels are blind-ending near the anterior face of the obturaculum, are looped throughout their course through the obturaculum, are suspended by mesentery-like structures in coelomic cavities along their entire length and are invested by a layer of circular muscles throughout. They are assumed to function in relieving muscular distortions of the obturaculum (Jones, 1985 *b*).

The paired afferent plume vessels carry blood anteriorly along the ventrolateral length of the obturaculum of *Riftia* and communicate, consecutively, with afferent lamellar vessels (Fig. 3 : D), which are found at the base of each branchial lamella. Along the length of these, arise afferent branchial vessels (Fig. 3 : E), each of which runs the length of a branchial filament. As noted previously (Jones, 1981 *a*, fig. 3 *g*), branchial vessels, both afferent and efferent, are provided with a series of ring muscles at 75-100 µm intervals ; the cumulative function of these linearly arranged sphincters is considered to be that of an auxilliary heart, serving to propel blood the length of the branchial filaments, both distally and proximally. Intraepithelial capillary loops (Fig. 3 : F, Jones, 1981 *a*, Fig. 3 *e*) connect the afferent and efferent branchial vessels on the anterior and posterior faces of the branchial filaments comprising the lamellae, occurring at intervals of about 5 µm; this arrangement affords a capillary interchange with the external milieu via the epithelial cells and their microvilli. At intervals, on the posterior surface of branchial filaments, there occur two rows of pinnules (Jones, 1981 *a*, Fig. 3 c), each of which contains a capillary plexus (Fig. 3 : G) formed as an elaboration of a ventral intraepithelial capillary loop. The branchial filaments of vestimentiferans represent an efficient exchange surface.

Blood returns from the branchial filaments via efferent branchial vessels (Fig. 3 : H), movement being facilitated by action of the ring-muscle sphincters along their length. Blood then enters the efferent lamellar vessels (Fig. 3 : I), thence to the efferent plume vessel (Fig. 3 : J), which carries the blood to the base of the obturacular region ; the pair of efferent plume vessels join at the so-called sinus valvatus (Fig. 3 : K ; van der Land, Nørrevang, 1975; 1977); which would appear to prevent backflow from the ventral vessel to the branchial region (van der Land, Nørrevang, 1977). Blood flows posteriorly in the ventral vessel (Fig. 2 *a, f* : VV, 3 : L), presumably due to hydraulic pressure generated by the auxilliary hearts of the branchial vessels, as well as the contraction of a thin layer of circular muscles investing the ventral vessel. At intervals in the trunk region stout vascular branches depart from the ventral vessel and penetrate deeply to the dorsal portion of the trophosome (Fig. 3 : N), giving off branches as they proceed. Alternatively, blood may leave the ventral vessel via occasional apertures (Fig. 3 : O) in the wall ; these lead immediately into what might be called a vascular envelope (Fig. 3 : P), *i.e.*, a narrow, thin-walled vascular space, closely applied to the ventral vessel over its outer surface and extending along its length. From the lateral surface of this envelope extend thin-walled blood vessels (Fig. 3 : Q) that appear to be restricted to the ventral portion of the trophosome. Both types of branches from the ventral vessel, the afferent trophosomal vessels, ramify over the outer surface of individual trophosomal lobules (Fig. 2 *g-l* : BVV); van der Land and Nørrevang (1977) have noted that efferent trophosomal vessels are to be found on the surface of lobules of *Lamellibrachia luymesi.* From these superficial vessels numerous smaller blood vessels (= capillaries, Fig. 2 *j-l* : CA) carry blood centripetally to the center of the trophosomal lobule, passing close by the contained endosymbiotic bacteria. In transmission electron micrographs (Gardiner, pers. comm.) it has been noted that blood vessels 2-3 µm in diameter are present among trophosomal endosymbionts ; in one particular micrograph no more than three bacteria separate a given bacterium from the closest capillary. Thus, blood is carried through the trophosomal lobule with its endosymbionts and passes into the single efferent trophosomal vessel (Fig. 2 *j, k* : BVD) (= vaisseau axial, Bosch, Grassé, 1984) that runs the length of the trophosomal lobule and joins other such efferent vessels (Fig. 2 *l* : BVD). Those serving the dorsal portion of the trophosome (Fig. 3 : S) pass dorsally to a blood plexus in the mesentery connecting the mesenterial and dorsal vessels (Fig. 2 *h* : MPL, 3 : T) ; efferent trophosomal vessels serving the ventral portion of the trophosome (Fig. 3 : W) pass dorsally and connect directly with the mesenterial vessel (Fig. 2 *g, h* : MV, 3 : X) whence blood passes to the mesenterial blood plexus. Blood from both types of efferent trophosomal vessels passes from the mesenterial blood plexus to the dorsal vessel ; occasionally the mesenterial vessel connects directly to the dorsal vessel. Blood in the dorsal vessel is propelled forward by means of contractions of the thick layer of circular muscles ; back flow from the dorsal vessel into the mesenterial blood plexus and the mesenterial vessel is prevented by the flapper-valve action of the intravasal body (Fig. 3 : Y), which is attached to the inner ventrolateral wall of the dorsal vessel, along its length.

Collateral trophosomal vessels, reported in *Lamellibrachia luymesi* (van der Land, Nørrevang, 1975; 1977), have not been observed in *Riftia* nor vascular connections between the trophosome and the longitudinal "feather" muscles of the body wall, as were reported by these authors for *Lamellibrachia luymesi.*

Whereas the afferent and efferent plume vessels of *Riftia* are axially oriented along the length of the obturaculum, afferent and efferent plume vessels of all other vestimentiferans lie in a transverse plane at the base of the obturacular region (Jones, 1985 *b*, Fig. 1, 2) ; this difference has morphological and taxonomic implications that will be discussed below.

THE TROPHOSOME AND ITS ORIGIN

In their paper describing *Lamellibrachia luymesi*, van der Land and Nørrevang (1975) noted and named the trophosome of this vestimentiferan : later (van der Land, Nørrevang, 1977) they presented a more detailed account of the morphology and vascularization of this structure ; their assumption was that the trophosome plays a role in the sustenance of sperm and, possibly, serves as a storage site for waste products. In describing the reproductive systems of *Lamellibrachia barhami*, Webb (1977, 474) observed the trophosome as "... spongy tissue (of unknown function) which fills most of the trunk coeloms."

The first report that the trophosome of *Riftia pachyptila* might be comprised mainly of chemoautotrophic bacteria was made by Cavanaugh (1980) ; this was followed by a study of the trophosomal endosymbionts of this species (Cavanaugh *et al.*, 1981). A number of observations, pertinent to the following discussion, have been made :

— the presence of free-living bacteria at and near hydrothermal vents has been documented (*inter al.*, Jannasch, Wirsen, 1979; 1985; Karl, 1985 ; Tuttle, 1985 ; Baross, Deming, 1985) ;

— trophosomal bacteria have been observed to be intracellular symbionts in *Riftia pachyptila* (Cavanaugh, 1983 ; Bosch, Grassé, 1984), *Ridgeia piscesae* (Tunnicliffe *et al.*, 1985), and *Escarpia spicata* (Cavanaugh, 1985);

— a number of researchers have suggested that trophosomal bacteria represent a mixture of several kinds (Fisher, Childress, 1984 ; Jannasch, Nelson, 1984 ; Jannasch, Mottl, 1985 ; Jannasch, Wirsen, 1985), while others (Lane *et al.*, 1985 ; Nelson *et al.*, 1984) consider that trophosomal bacteria are of a single type ;

— Nelson *et al.* (1984, 271) note that "... the genome size of the prokaryotic symbiont of *Riftia pachyptila* trophosome (based on DNA base composition) is ... typical for that of free-living bacteria...";

— examination of unfertilized eggs from the oviduct of *Riftia pachyptila*, by transmission electron microsopy, has not revealed the presence of bacteria (Cavanaugh, 1985 ; Cavanaugh *et al.*, 1981 ; Gardiner, pers. comm.).

In their monographic account of *Lamellibrachia luymesi* van der Land and Nørrevang (1977) noted the presence of a "...strong muscle, which runs through the central hole in the brain...". They suggest that this so-called obturacular muscle moves the paired obturacula.

In the course of early histological observations of adult and young adult specimens of *Riftia pachyptila*, I was able to confirm the presence of such a structure, but its appearance was that of a central strand of basophilic cells accompanied by a few muscle fibers, rather than a muscle, *per se*. I was able to trace it from a ventral extension of the internal cuticular boundary between the developing branchial lamellae of the obturacular region and the brain (= thick cuticular plate, van der Land, Nørrevang, 1977, 47, 64), into the brain, where it became associated with an anterior extension of the ciliated-tubule portion of the excretory organ, but lost track of it in the complexities of the main portion of the excretory organ ; van der Land and Nørrevang (1977) do not comment on the origin of their obturacular muscle, but do suggest, in their Figure 18, that it originates in the musculature of the vestimentum.

It was felt that more of the details of the nature and course of this structure might be revealed in a histological examination of juvenile specimens. Such studies showed that in earlier stages it was actually a ciliated duct that culminated anteriorly in an external medial process, open to the exterior. Internally, the ciliated duct could be traced posteriorly to the vicinity of the trophosome, in the anterior extensions of the trunk coelom that overlie the posterior portion of the vestimentum.

Externally the medial process is seen to arise at the base of the obturacular region (Fig. 4 *c, d* : MP) in the mid-line, just posterior to the most basal series of developing branchial filaments (Fig. 4 *d*: BF). There is an external opening of the duct and an overhanging upper lip (Fig. 4 *d* : MP) ; SEM micrographs at higher magnifications show that cilia extend from the opening of the duct to the outer surface of the sides and the upper and lower lips of the aperture.

Internally, the aperture of the medial process (Fig. 5 *k, l* : MP) leads to a medial duct that passes through the brain (Fig. 5 *b, c, k, l* : MD, BR) in a dorsoposterior direction and emerges in a cleft on the posterior surface of the brain, invested by an anterior extension of the excretory organ (Fig. 5 *l* : EXO). Passing through the excretory organ, the medial duct continues posteriorly between the joining efferent plume vessels, above the sinus valvatus, and through the muscle and connective tissue of the vestimentum, between the dorsal and ventral vessels (Fig. 5 *b, d, k, l* : EPV, SV, VS, DV, VV, respectively). In earlier observations of the morphology of *Riftia pachyptila* it was evident that the trunk and its paired coelomic cavities extended anteriorly and dorsally over the posterior portion of the vestimentum (Fig. 1 *b, c* ; Jones, 1985 *a*). Histological sections of juveniles reveal the presence of paired cavities, separate from and ventral to these trunk coelom extensions (Fig. 5 *e - l* : TRC, ATC). Careful examination of the posterior medial duct shows that it opens into these paired cavities, *i.e.*, paired trophosomal chambers (Fig. 5 *f, h - j* : MD, X, TRC). Further examination shows that there is communication between the trophosomal chambers and what appears to be a sac-like structure investing the presumptive trophosome (Fig. 5 *g - j* : TRC, large arrow, TR).

On the basis of the relationship of the medial process, the ciliated medial duct and its connection to the trophosome, I suggest that bacteria, which come to comprise the trophosomal symbionts of *Riftia*, are obtained from the immediate microenvironment of developing juvenile/larval individuals. I suggest that such bacteria are picked up by the ventral medial process, somewhat in the manner of a vacuum cleaner, and are carried posteriorly within the medial duct to the trophosome. I suggest that any and all types of free-living bacteria are taken in and that those capable of surviving in the internal milieu of the young *Riftia* do so; those which can not, do not.

Although the probability of finding even a few bacteria in an unfertilized egg is small, the presence of such a neat collecting and delivering mechanism, and the isolation of the trophosome from the vestimentiferan reproductive system, would strongly suggest that young vestimentiferans obtain their endosymbionts by active collection, not by maternal gift. It is pertinent to mention that in extensive examinations of developing spermatozoa, by transmission electron microscopy (Gardiner, Jones, 1985), nothing resembling bacteria was seen.

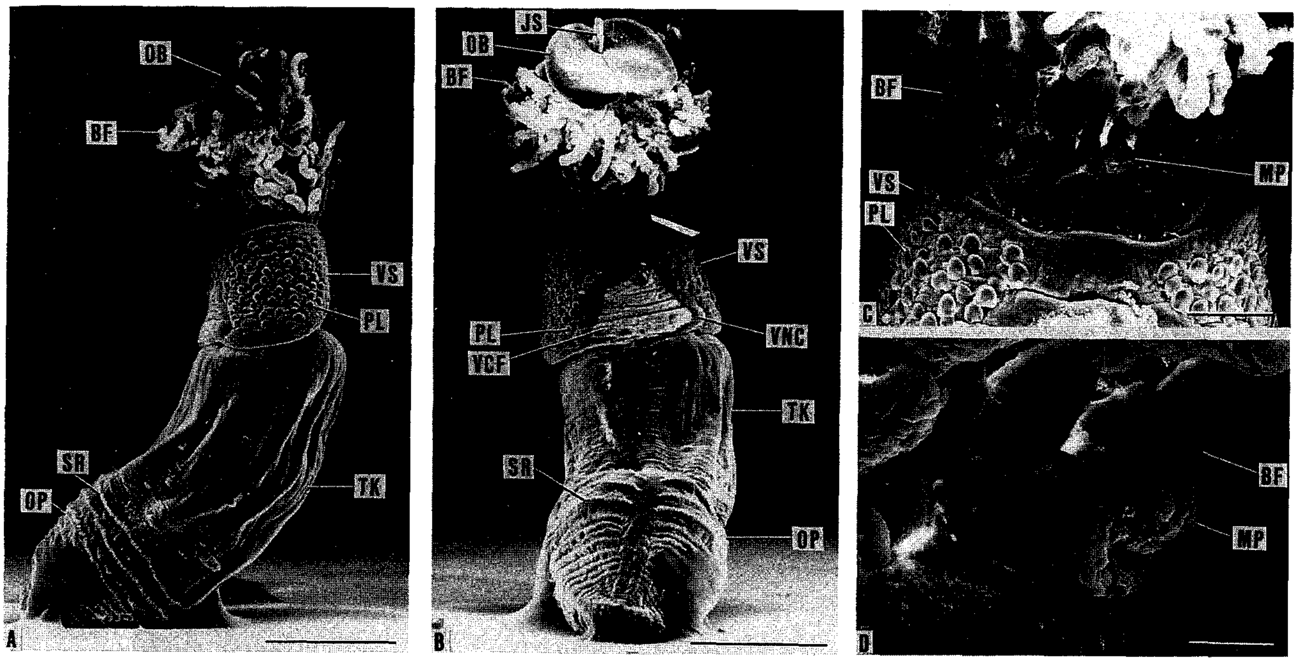


Figure 4
SEM micrographs of juvenile specimen of Riftia pachyptila *(from Rose Garden, Galapagos Rift, USNM 99038), length : 2.1 mm : A) Left lateral view ; scale bar: 400 µm. B) Ventral view; obturacular region bent posteriorly, obscuring ventral medial process; scale bar: 400 µm. C) Ventral view of base of obturacular region and anterior portion of vestimentum; scale bar : 100 µm. D) Ventrolateral view of ventral medial process; scale bar : 20 µm. BF : branchial filaments; JS : juvenile obturacular spine; MP : ventral medial process; OB : obturaculum; OP : opisthosome; PL : plaque; SR : setal row; TK: trunk; VCF : ventral ciliated field; VNC : ventral nerve cord; VS : vestimentum.*

The conflicting results as to whether there is a mixture of several kinds of bacteria in the trophosome or but a single type might be explained by the random nature of the suggested mode of obtaining bacteria ; so long as the crucial bacteria survive, *i.e.*, those which allow the mouthless and gutless adult worms to obtain indirect nutrition, all other bacteria may or may not survive ; if they do not, then there is left a trophosomal bacterial complement of but a single kind ; if they do, then there is left a complement of mixed bacteria. Fisher and Childress (1984) have noted differences in color and the activity of ATP sulfurylase along the length of the trophosome of *Riftia* ; an alternative explanation of finding a single type of bacterium or a mixed lot is that this is a reflection of linear heterogeneity along the length of the trophosome, a possibility that will require careful examination by transmission electron microscopy.

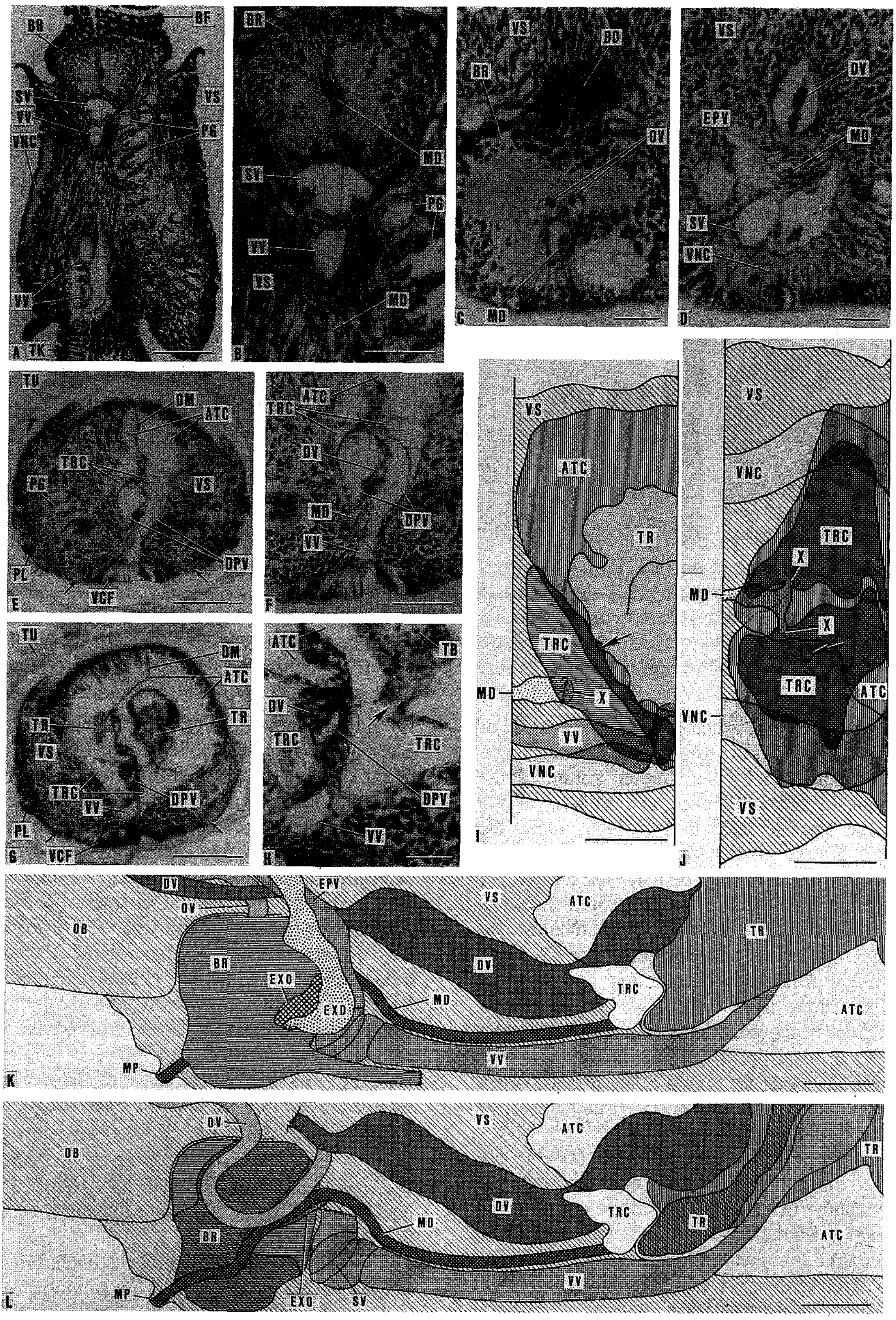
Cavanaugh (1983), Bosch and Grassé (1984) and Tunnicliffe *et al.* (1985) have demonstrated the intracellular nature of the symbiotic relationship of vestimentiferans and their trophosomal bacteria, in that the bacteria are found in bacteriocytes, within membrane-bound peribacterial spaces. We also have found such to be the case in *Riftia pachyptila* (pers. observ. ; Gardiner, pers. comm.). In view of the proposed mechanism for the acquisition of bacteria by juvenile vestimentiferans, it must be assumed that, after bacteria have passed through the trophosomal chambers into the sac-like structures leading from the latter, the prospective bacteriocytes acquire the bacteria, perhaps by phagocytosis. The elaborate, short-lived procedure for obtaining the bacteria, the necessity of bacterial intercession for the survival of a vestimentiferan worm and the vascular adaptations of the worms, all point to a close relationship between host and symbiont, probably of long standing.

We do not know how early in development the process takes place. In young juveniles of 0.8 mm total length, living in their own tubes, with all four regions formed and with trophosomes visible through the body wall, a ventral medial process is present. It is still present in specimens of up to 15.5 mm total length. It may well be that in older juveniles the internal mechanism malfunctions even though the external medial process still exists. Further development results in the loss of the external ventral medial process, the appearance of the medial duct transiting the brain as an "obturacular muscle" or as a "strand of basophilic cells accompanied by a few muscle fibers" and the isolation of the trophosome in the trunk coelom.

Nine juveniles from among tubes of *Ridgeia piscesae* from Axial Seamount on the Juan de Fuca Ridge, examined by SEM, ranging from 170 µm to 5.18 mm total length, have a ventral medial process. I think that all vestimentiferans possess such an external structure and internal duct system for the acquisition of trophosomal bacteria.

The success of a hydrothermal vestimentiferan juvenile in finding proper prospective endosymbiotic bacteria in its immediate environment would seem most likely. It must be assumed that prospective endosymbiotic bacteria do occur, as well, at non-hydrothermal sites.

A similar internal distribution of endosymbiotic bacteria occurs in species of the phylum Pogonophora. Southward *et al.* (1981), Southward (1982) and Flügel and Langhof (1983) have documented the presence of bacteria in bacteriocytes, which form a trophosome, in eight species of four genera of pogonophorans. The details of the architecture of the trophosome of the pogonophores differs from that of the vestimentiferans, as well as the morphological types of bacteria found there. Southward



(1982) has noted that if bacteriocytes are shown to be mesodermal in origin, then the central cavity found in some pogonophorans is a coelom ; if bacteriocytes are endodermal, then the cavity is the lumen of a vestigial gut. Flügel and Langhof (1983) have suggested that trophosomal bacteria of pogonophores are derived from free-living forms in muds from the sea bottom. It is tempting to suggest that in this phylum, one would find an analogue/homologue of the ventral medial process at some point in pogonophore development. Such would not seem to be the case, for in the reports by Ivanov (1963), Webb (1964), Nørrevang (1970), and Bakke (1977), illustrations of juveniles, of greater than about 0.4 mm total length, of six species of pogonophoran genera, show no structure that might be construed as anything similar to a ventral medial process. Perhaps the mechanism for acquiring bacteria is different in the Pogonophora and the Vestimentifera.

There are similar chemoautotrophic symbiotic relationships among certain of the bivalved molluscs and the oligochaetous annelids (Cavanaugh, 1985). It would be of interest to examine the early stages of these taxa, *i.e.*, *Calyptogena, Bathymodiolus, Solemya*, and several of the Lucinidae, among the bivalves, and certain species of the oligochaete genus *Phallodrilus*, in search of a ventral medial process or some other means of bacterial acquisition.

THE HIGHER CLASSIFICATION OF THE VESTIMENTIFERA

In the course of earlier studies, a number of morphological features of the vestimentiferans were recognized as bearing on their higher classification (Jones, 1985 *b*). Two of these have been mentioned above, in passing.

The first of these is the disposition of the ring muscles of the obturacular matrix. In certain genera these muscles may be parasagittal in orientation (Jones, 1985 *b*, fig. 7), in others, frontal (Jones, 1985 *b*, fig. 10) ; in one genus the frontally oriented muscles are augmented by a second complex of muscles, generally longitudinal (Jones, 1985 *b*, fig. 12).

The second morphological feature is the disposition of the afferent and efferent plume vessels (Fig. 3 : C, J). On the one hand they may proceed along the length of the obturaculum, with successive connections to and from lamellar vessels (Fig. 3 : D, I); the result is axially arranged branchial lamellae, distributed along the length of the obturaculum (Fig. 1 *b, c* ; Jones, 1985 *b*, fig. 1). On the other hand the plume vessels may remain in a transverse plane at the base of the obturacular region, with successive connections to and from lamellar vessels restricted to this plane (Jones, 1985 *b*, fig. 2); the result is basally arranged branchial lamellae, distributed concentrically around the obturaculum (Fig. 1 *a, d - k*).

Only two of the six vestimentiferan genera have an unpaired, medial excretory pore formed by the union of internally paired excretory ducts ; the pore opens at the base of the dorsal side of the obturacular region. In the remaining four genera there are paired excretory pores.

Opisthosomal setae are comprised of a posterior and an anterior group of denticles separated by a central boss (Jones, 1985 *b*, fig. 15 *c*). For five of six genera the denticles of the posterior group are arranged mainly in three vertical rows ; in the remaining genus the denticles are in two rows (Jones, 1985 *b*, fig. 44).

Riftia is the only genus with axially arranged plume vessels and branchial lamellae ; I have assigned it to the class Axonobranchia (Fig. 6). All other vestimentiferans, with their basally situated branchial vessels and branchial lamellae, are members of the class Basibranchia, this includes the genus *Ridgeia* (Fig. 1 *h - k*) which, although exhibiting a *Riftia*-like branchial complex, has basal plume vessels and lamellae.

At the ordinal level *Riftia* is the sole member of the Riftiida (Fig. 6). On the basis of the nature of the excretory pore(s) the orders Lamellibrachiida (with *Lamellibrachia* and *Escarpia*) and Tevniida (with *Tevnia, Oasisia* and *Ridgeia*) are separated, the former with an unpaired excretory pore and the latter with paired pores. This character serves to separate hydrothermal from cold-water vestimentiferans. It may be noted that *Riftia*, a hydrothermal genus, has paired excretory pores.

Riftia is the only member of the family Riftiidae (Fig. 6). In the order Tevniida, *Tevnia* and *Oasisia*, with parasagittally oriented obturacular ring muscles, comprise the family Tevniidae ; *Ridgeia* is the only member of the family Ridgeidae and has its obturacular ring muscles oriented in frontal planes. Both *Lamellibrachia* and *Escarpia* have frontally oriented obturacular ring muscles; however, *Escarpia* has an additional set of longitudinal muscles anterior and peripheral to the frontal ring muscles (Jones, 1985 *b*, fig. 12) ; this is the basis of differentiation between the families Escarpiidae and Lamellibrachiidae. *Riftia* has parasagittally oriented ring muscles.

Thus, all families are monogeneric at this time, except for the Tevniidae (Fig. 6). In this instance *Tevnia* has opisthosomal setae with denticles of the posterior group, for the most part, in three vertical rows (Jones, 1985 *b*) and *Oasisia*, in two rows (Jones, 1985 *b*). The disposition of these denticles in *Riftia* and *Ridgeia* is similar to that of *Tevnia* (Jones, 1985 *b*) ; opisthosomes and their setae are not known, as yet, for *Lamellibrachia* and *Escarpia.*

THE PHYLUM VESTIMENTIFERA

It has been noted above that the original placement of *Lamellibrachia*, the first vestimentiferan described, was in a new class in the phylum Pogonophora (Webb, 1969) ; subsequently van der Land and Nørrevang (1975; 1977) considered the Vestimentifera and Pogonophera to be separate classes in the phylum Annelida ; later (Jones, 1981 *a*) I retained the vestimentiferans in the phylum Pogonophora in the subphylum Obturata, the remaining

Figure 5

Medial duct of Riftia pachyptila (A, B : USNM 81950; C-H : USNM 99037); Masson's trichrome : A) Frontal section of juvenile, from base of obturacular region to trunk, left side more ventral than right; scale bar : 200 mm. B) Same section, higher magnification; scale bar : 100 mm. C) Transverse section, at level of brain and bases of obturacula; scale bar : 25 mm. D) Same, 40 mm posterior to Fig. 5c at level of sinus valvatus; scale bar : 25 mm. E) Overview, transverse section, 95 mm posterior to Fig. 5d, at level of beginning of trophosomal chambers; four series of dots, right of mid-line, connect points torn during sectioning; scale bar : 100 mm. F) Same section, higher magnification; scale bar: 50 mm; G) Overview, transverse section, 35 mm posterior to Fig. 5e, at level of connection of trophosomal chamber and trophosome; scale bar: 100 mm. H) Same section, higher maginfication; scale bar: 50 mm. I) Reconstruction, lateral view, based on sections of specimen of Fig. 5 c, h; dorsal vessel omitted; scale bar : 50 mm. J) Same, dorsal view; trophosome, dorsal and ventral vessels omitted; scale bar : 50 mm. K) Reconstruction, lateral view, based on sections of specimen of Fig. 5a,b; scale bar : 100 mm. L) Same, with certain obscuring structures removed; scale bar : 100 mm. Diagonal lines, Fig. 5I -L : cut surfaces; ATC : anterior extensions of trunk coelom; BF : branchial filaments; BO : bases of obturacula; BR : brain; DM : dorsal mesentery; DPV : perivascular cavity of dorsal vessel; DV: dorsal vessel; EPV: efferent plume vessel; EXD : excretory duct; EXO : excretory organ; MD : medial duct; MP : medial process; OB : obturaculum; OV : obturacular vessel; PG : pyriform gland; PL : plaque papilla; SV : sinus valvatus; TB : trophosomal bacteria; TK : trunk; TR : trophosome; TRC : trophosomal chamber; TU : tube; VCF : ventral ciliated field; VNC : ventral nerve cord; VS : vestimentum; VV : ventral vessel; X : passage from medial duct to trophosomal chamber; small arrows (Fig. 5 e, g) : ventral nerve cords; large arrows (Fig. 5 i, j) : passage from trophosomal chamber to trophosome.

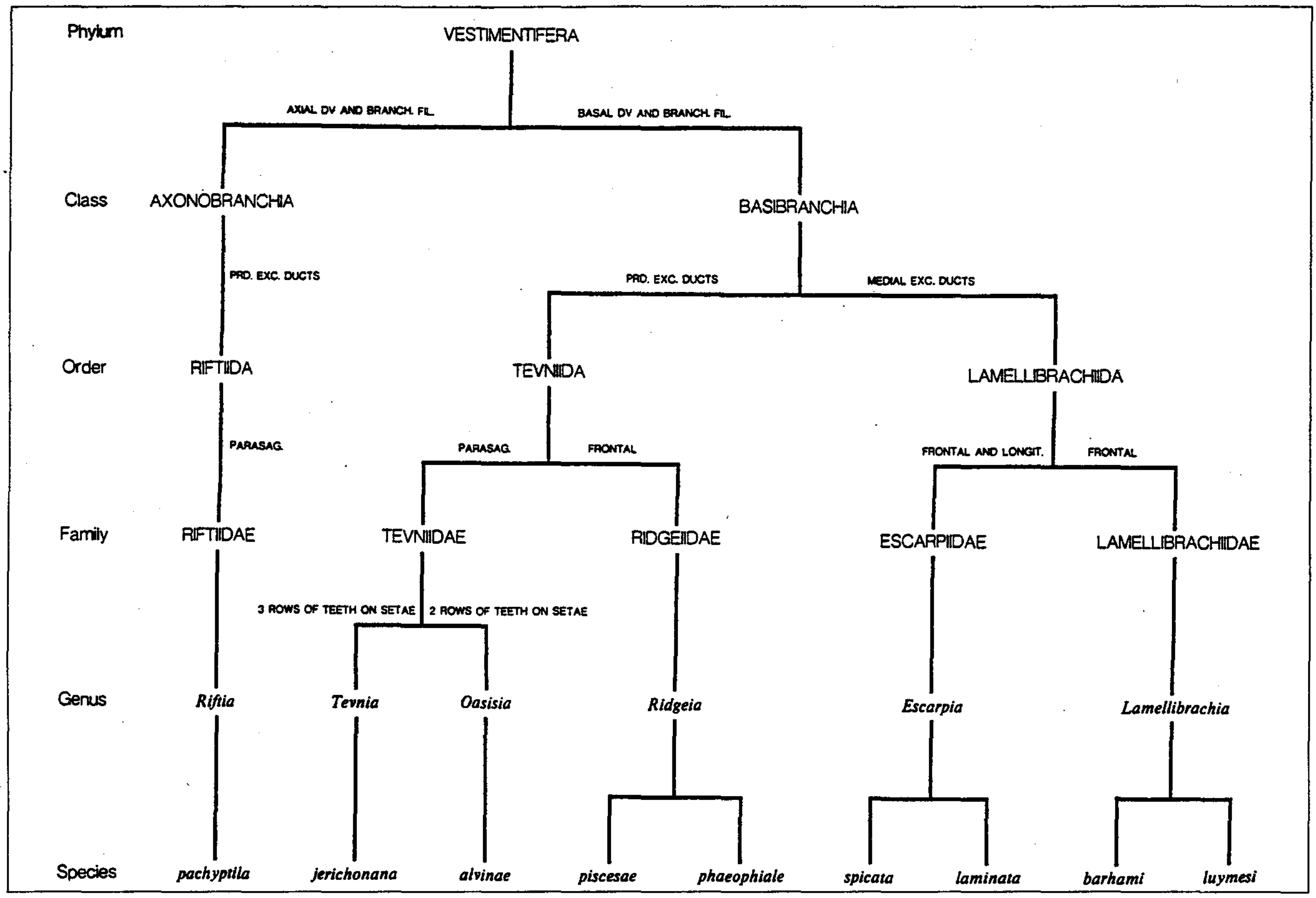


Figure 6
Classification of the Vestimentifera with discriminating characters noted.

pogonophores being placed in the subphylum Perviata ; finally (Jones, 1985 *b*), I have recently felt that a latter day consideration of the morphology and anatomy of the vestimentiferans necessitated their being separated in their own phylum, Vestimentifera, and the former perviate pogonophorans being restored to their own phylum Pogonophora.

Throughout this paper I have referred to *regions* of the vestimentiferan body. Earlier (Jones, 1981 *a*) I considered that the similar body plan of the pogonophorans and the vestimentiferans overrode other morphological differences between the two groups, and, thus, I considered it necessary to keep them in the same phylum. Anatomical differences observed subsequently (Jones, 1985 *a*) weakened the argument for the close affinity of the two groups based on superficial similarity of body regions.

The conclusions reached in a study of the various cavities of *Riftia* and *Tevnia* (Jones, 1985 *a*) were that:

- the perivascular cavities of the obturacular vessels were the remnants of the coeloms of a first segment ;
- the perivascular cavities of the anterior dorsal vessel, the afferent and efferent plume vessels, the afferent and efferent lamellar vessels and the afferent and efferent branchial vessels were the remnants of the coeloms of a second segment ;
- the perivascular cavities of a posterior, vestimental portion of the dorsal vessel were the remnants of the coeloms of a third segment (comparable perivascular cavities of the ventral vessel have not yet been recognized) ;
- the paired trunk cavities are the coeloms of a fourth segment ;
- the segmented cavities of the opisthosome represent an accrual of coeloms of posterior segments, from the fifth onward (Jones, 1985 *a*).

If Southward's (1980) interpretation of pogonophoran segmentation is accepted, then :

- the branchial complex, its coelomic cavity and the pericardium, if the presence of the latter is confirmed throughout the phylum, comprise the first segment of the Pogonophora ;
- the paired trunk coeloms, together with the paired cavities set apart secondarily by the diaphragm, anterior to the trunk coeloms, represent the second segment ;
- the segmented cavities of the opisthosome represent an accrual of coeloms of posterior segments, from the third onward (Southward, 1980; Jones, 1985 *a*).

It is difficult to reconcile the disparity in number of segments in the two groups of worms, *i.e.*, four segments anterior to the opisthosome among the vestimentiferans and two such segments in the case of the pogonophores, assuming the opisthosomes are homologous.

There are a number of, perhaps, less substantial differences between the two groups, *i.e.*, the vestimentiferans are provided with multicellular pinnules on the branchial filaments, they lack setae on the trunk of the adult, have setae with *vis-à-vis* denticles on opisthosomal segments, have basally closed tubes and lack spermatophores ; the pogonophorans, on the other hand, have unicellular pinnules, have setae with *vis-à-vis* denticles in the mid-trunk region (the girdle) and peg-like setae on opisthosomal segments, have a tube open at both ends and, with one exception (Flügel, Langhof, 1983), have spermatophores.

There is yet another, and to my mind, more important, series of differences between the two groups. The opisthosome of *Siboglinum fiordicum* Webb has been described in detail by Southward (1975 *a; b*; 1980). She found that:

- there are three ventral nerve trunks in the opisthosome ;
- these nerve cords appear to be ganglionated ;
- muscles associated with opisthosomal septa are on the posterior septal face, only ;
- the coeloms of opisthosomal segments are unpaired, *i.e.*, there is no medial mesentery separating right and left halves.

In the case of the opisthosome of *Riftia pachyptila* :

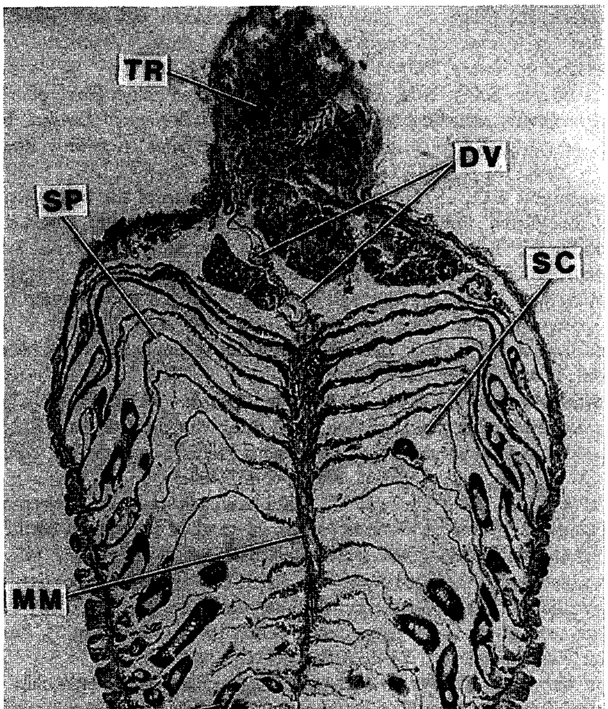


Figure 7
Frontal section, opisthosome of juvenile Riftia pachyptila *(USNM 81950, Rose Garden, Galapagos Rift); Masson's trichrome; scale bar : 200 µm.*
DV : dorsal vessel in trunk; MM : medial mesentery of opisthosome; SC : segmental coelom; SG : segmental gland; SP : septum; TR : trophosome.

- there is a single ventral nerve cord (Jones, 1985 *b*);
- the nerve cord is without apparent ganglia ;
- there are septal muscles on both anterior and posterior septal faces ;
- coeloms of opisthosomal segments are paired, owing to the presence of a medial mesentery that runs the length of the opisthosome, separating right and left halves (Fig. 7).

I attach special importance to the opisthosomal contrasts because they occur in the nervous system, considered to be evolutionarily conservative, and in the end product (segmented coeloms) of a conservative process (coelom formation).

The differences in disposition of septal musculature, on the posterior septal face as opposed to both anterior *and* posterior faces, would suggest that different methods of segment formation are at work here. The presence or absence of a medial mesentery suggests that in the vestimentiferans, coelom formation is a classical schizocoely and that in the pogonophorans, coelom formation is some kind of total, transverse splitting of the mesoderm to form coelomic cavities, segments and septa ; in effect, segmentation by septation.

Together, the differences in number of coelomic segments, particularly in the anterior regions, the considerable differences in the nervous system of the opisthosome and the basic formational differences implicit in the structure of the opisthosomal segments convince me that the phylum Vestimentifera stands apart from the phylum Pogonophora.

In consideration of the affinities of the Vestimentifera, I must say that they are most closely related to the Pogonophora and that these two phyla are most closely allied to the Annelida, primarily on the basis of their segmentation, most readily seen in the architecture of their opisthosomes. It would seem most reasonable that the phyla Pogonophora and Vestimentifera arose from the stock that gave rise to the Annelida ; however, whether a common ancestor between the pogonophorans and the vestimentiferans was their link, whether these phyla arose independently, or whether all three phyla, Annelida, Pogonophora and Vestimentifera, diverged at a much earlier point in time, remains to be elucidated.

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