

BIOGEOGRAPHY, DIVERSITY, AND EVOLUTION THROUGH VICARIANCE OF THE HYDROTHERMAL VENT APLACOPHORAN GENUS *HELICORADOMENIA* (APLACOPHORA, MOLLUSCA)

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ABSTRACT Species of the neomenioid aplacophoran genus *Helicoradomenia* Scheltema & Kuzirian are found only in areas of hydrothermal vents, oceanic ridges, and back-arc basins and have been collected widely in the East Pacific, Southwest Pacific, and the Triple Junction in the Indian Ocean, but not in the Atlantic. As with other vent taxa, species diversity of *Helicoradomenia* in the East Pacific is greatest south of the subduction zone of the Pacific Plate under the North American Plate, which divided the ridge system into two sectors during the Eocene: the northern Juan de Fuca system and southern East Pacific Rise. Diversity of *Helicoradomenia* species reflects, in smaller numbers, the diversity of the vent limpets in the two sectors. Two *Helicoradomenia* sister species are illustrated with the characters that separate them, *H. juani* Scheltema and Kuzirian (1991) from the northern sector and *H. acredema* Scheltema (2000) from the southern. They apparently speciated when the vicariant event of subduction of a once continuous ridge occurred.

KEY WORDS: *Helicoradomenia juani*, *Helicoradomenia acredema*, taxonomy, symbionts, dispersal, Juan de Fuca ridge, East Pacific Rise

INTRODUCTION

Aplacophoran molluscs are a small taxon with fewer than 400 described species including both neomenioids (Neomeniomorpha or Solenogastres) and the chaetoderms (Chaetodermomorpha or Caudofoveata). They are found throughout the world's oceans in an amazing assortment of habitats: level-bottom muds subtidally on the continental shelf to hadal depths >7,000 m in deep-sea trenches, interstitially in sands, upon isolated seamounts rising from the seafloor at 4,000-m depths, upon octocorals, and from the tropics to polar regions. Included among the habitats where aplacophorans occur are the chemosynthetic, sulfur-based communities of the hydrothermal vents in oceanic spreading ridges and back-arc basins. Species of the genus *Helicoradomenia* have been collected, sometimes in surprisingly large numbers, in the East Pacific, Southwest Pacific back-arc basins, and Indian Ocean (Tables 1, 2), but not in the Atlantic. They live upon hard substrates (e.g., rocks, pebbles, worm tubes, clam beds) away from the hot venting fluids.

EAST PACIFIC RIDGE SYSTEM

Since the first discovery in 1977 of a remarkable community living chemosynthetically in regions of hydrothermal vents (Lonsdale 1977, Woods Hole Oceanographic Inst. 2007), the most studied ridge system over the longest period of time is the north-south oceanic ridge in the East Pacific. The ridge is divided into two sectors where the Pacific-Farallon Plate was subducted under the North American Plate in the Eocene, a zone marked beneath continental California by the San Andreas Fault (Tunnicliffe et al. 1996). The ridge sector north of 35°N is the Juan de Fuca Ridge (itself made up of a subset of segments) and the segment from 21°N and southward, the East Pacific Rise (EPR). At 0° latitude, the Galapagos Rift runs eastward perpendicular to the East Pacific Rise.

Species of *Helicoradomenia*, the genus to which most aplacophoran vent species belong, occur on northern and southern segments and at the Galapagos Rift. They apparently

are endemic to the sulfide-based, chemosynthetic fauna of the hydrothermal vents. Two genera, one perhaps being *Helicoradomenia*, are also found on whalefalls (unpublished). However, *Helicoradomenia* has not been found with the other important sulfide-based fauna in seeps. The *Helicoradomenia* species awaiting description are tallied here unnamed.

THE NEOMENIOID GENUS *HELICORADOMENIA*

Helicoradomenia belongs to the neomenioid aplacophorans, which are narrow or wide cylinder-shaped molluscs ("worm-shaped" in the literature) covered by aragonite sclerites held by body mantle cuticle—the scleritome. There is a narrow ventral groove within which is a ciliated foot-fold that glides upon a mucous track. *Helicoradomenia* is defined by its radula, type of ventrolateral salivary glands, body shape, types of sclerites, and presence of paired copulatory spicules.

Description

Helicoradomenia species are usually 5 mm or less in length when contracted. The *radula* (Fig. 1B, 1C; 2C, 2D) has two mirror-image teeth per row (=distichous). It is carried on a radula membrane in a long radular sac before emerging into the pharynx, where the two sides of the radula separate and spiral into paired anteroventral pockets that usually unite distally. These radula-filled, anteroventral pockets seem to serve as struts to hold open and expand the proboscis (personal observation), which is usually withdrawn. Each tooth has a number of denticles, added during growth, affixed to a bar, with the longest denticle lateral. The denticles overlap indentations on the next adjacent tooth (Fig. 1B, 2C).

The paired *ventrolateral glands*, presumably salivary, are a type particular to *Helicoradomenia* (Handl & Todt 2005, Todt & Salvini-Plawen 2005). Each of the pair is a group of extraepithelial glandular cells bundled together by a thin muscle sheath and emptying individually through long necks into the junction of the pharynx and anteroventral pocket (Fig. 1A). The *body* is short to somewhat elongate and broad, widest

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TABLE 1.

Distribution of *Helicoradomenia* species in the East Pacific based on author's examinations and unnamed, figured species in Desbruyères et al. (2006). Specimens provided by Woods Hole Oceanographic Institution, IFREMER, and Field Museum (Chicago).

Species	Juan de Fuca				East Pacific Rise				Gal.
	Latitude								
	49°N	48°N	41°N	21°N	13°N	9°N	17°S	21°S	0°
<i>H. juani</i>	+	+	+						
<i>H. acredema</i>				+		+	?	?	+
<i>H. bisquama</i>				+					
<i>Helico. sp. 1</i>				+					
<i>Helico. sp. 2</i>					+	+	+		
<i>Helico. sp. 3</i>						?			
<i>Helico. sp. 4</i>					+				

Gal. = Galapagos Rift.

posteriorly (Fig. 1D, 1E, 2A, 2B). The *sclerites* are solid and upright (i.e., not hollow or adpressed against the body), and are short to elongate; there can be few types or many (Fig. 1F, 2H). The appearance of the scleritome ranges from slightly fuzzy to somewhat to very spiny (Fig. 1D, 1E). For individual sclerites, they are best viewed under cross-polarized light, as different thicknesses produce bands of color, or isochromes (e.g., Fig. 1F, 2H sclerites 4a). For line drawings, the bands are indicated by dotted lines (cf. Fig. 1F, 2H). The *copulatory spicules* are species specific, although sister species may be morphologically similar (Fig. 2E to 2G), and are sometimes elaborate and numerous; they grow in length with the growth of an individual.

Because the body shape, appearance of the scleritome, and hard parts together are so characteristic, species are relatively easy to differentiate without recourse to histological sectioning. *Helicoradomenia* species tend to be similar both at the level of cellular studies and in general internal anatomy (*H. acredema* and *Helicoradomenia* sp., Todt & Salvini-Plawen 2005; *H. juani*, Scheltema & Kuzirian 1991). Such studies may give other diagnostic characters in addition to the hard parts. Genetic studies would also be useful, particularly in cases of sister species or for a species from many vent populations along a ridge, such as *H. acredema* from 21°N to 17°S.

Differentiating Morphologies in *H. juani* and *H. acredema*, Sister Species

Hard parts and body shape distinguish these very similar species as follows, *H. juani* listed first (*j*), *H. acredema* second

TABLE 2.

Helicoradomia species examined from the southwest Pacific back-arc basins and Indian Ocean Triple Junction. Specimens provided by Robert Hessler, Cindy Van Dover, and IFREMER.

Southwest Pacific		
No. Fiji Back-Arc Basin	16°–18°S, 173°–179°W	2–3 species, 8 specimens
Lau Back-Arc Basin	22°S, 176°W	1 species, 3 specimens
Mariana Back-Arc Basin	18°S, 144°E	1 species, 3 specimens
Indian Ocean Triple Junction		
Kairei mussel field	25°S, 70°E	1 species, 3 specimens

(*a*). The differences are based on adults of large populations of both species (Scheltema & Kuzirian 1991, Scheltema 2000).

Body: length >5 mm (*j*), <5 mm (*a*); *appearance of scleritome*: fuzzy (*j*), spiny (*a*) (Fig. 1D, 1E; 2A, 2B).

Radula: length of denticle number: 2 < 1/2 length of denticle number 1 (*j*), >1/2 length of denticle no.1 (*a*); *number of denticles*: usually 5, sometimes 6 (*j*); usually 6, sometimes 7 (*a*) (Fig. 2C, 2D).

Copulatory spicules: 2 in each of paired sacs, morphologically very similar but up to 1 mm (*j*), up to 0.7 mm (*a*) (Fig. 2E, 2F); *accessory copulatory spicules*: curve relatively shallow (*j*), relatively deep (*a*), “bumps” 3–4 in both (Fig. 2G).

Sclerites: indicated by numbers 1–4, species by “j” or “a” in Figure 2H. Differences in sclerite size between the two species within a particular type as illustrated here are not significant, e.g., type 4 from the posterior end of the body can be up to ~130 µm in both species. The differentiating sclerites are *type 1 from beside the pedal groove*: convex on one side, straight on the other (*j*), curved on both sides (*a*); and *type 4 over entire body*: tips without swelling (*j*), tips often swollen, as seen under cross-polarized light (*a*) (Fig. 1F). (The species name *acredema* refers to this distinguishing character.)

Feeding

Most aplacophorans are carnivorous, but a few feed on detritus. Most neomenioids are predators on octocorals or hydroids, whose nematocysts are seen in their midguts. *Helicoradomenia* species, however, do not feed on cnidarians, as telltale nematocysts are lacking in their guts. The remains of food in two species, *H. acredema* and *Helicoradomenia* sp., were examined by transmission electron microscopy and found to be of a triploblastic metazoan, most probably a polychaete (Todt & Salvini-Plawen 2005).

Presence of Symbiotic Bacteria

Four types of epibiotic and endocuticular bacteria on sclerites and in body mantle cuticle have been demonstrated as symbionts in *H. cf. acredema* and *Helicoradomenia* sp. (Katz et al. 2006). Unlike the nutritional necessity of symbiotic bacteria for many vent invertebrates, in *Helicoradomenia* the bacteria appear to have all the benefits of the association. Individual

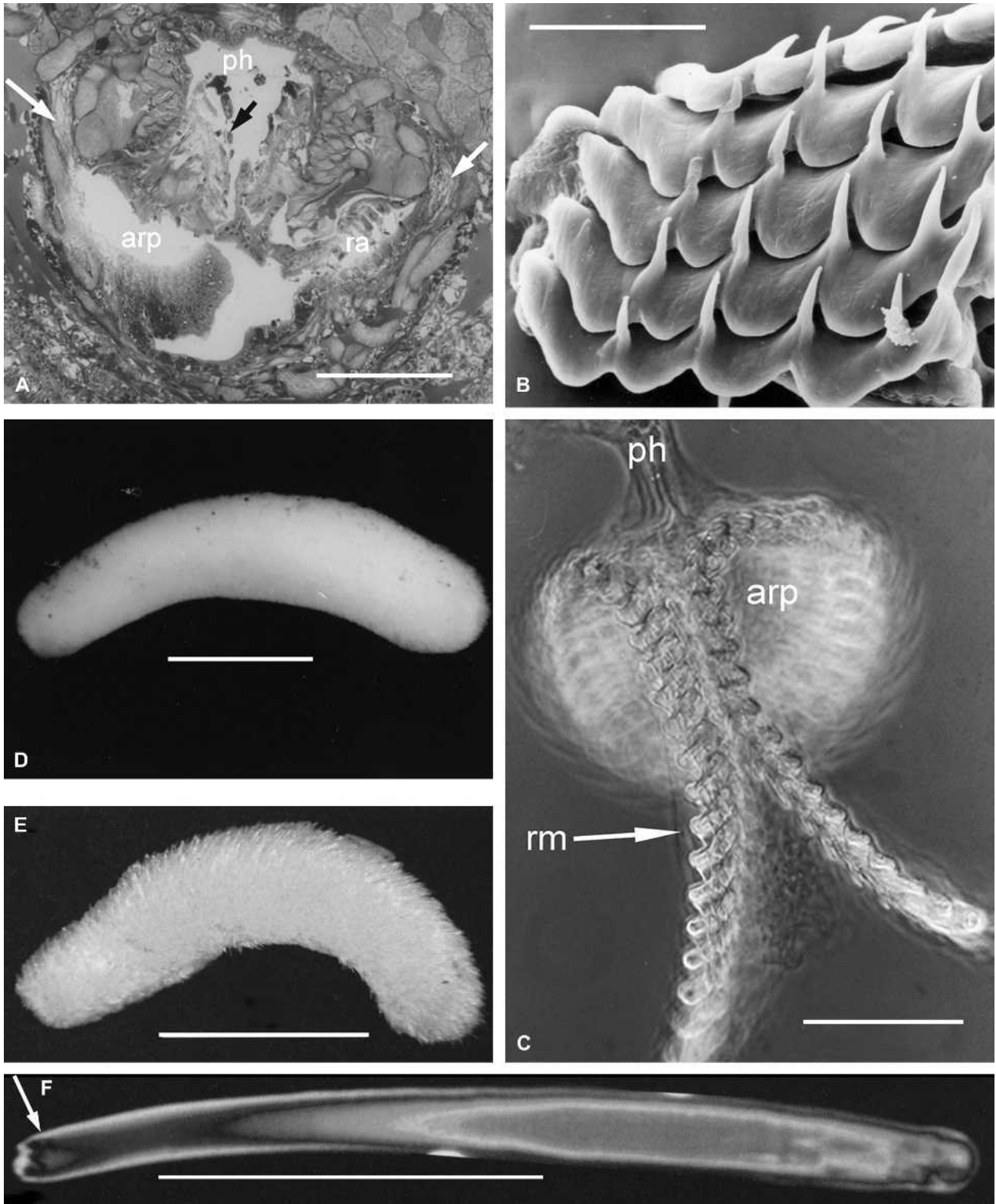


Figure 1. A. Histological cross-section of *Helicoradomenia juani* where pharynx (ph) opens into anteroventral radula pockets (arp); paired ventrolateral glands (white arrows), left arrow, long necks of gland cells, right arrow, gland cells; and radula (black arrow in pharynx, ra in anteroventral radula pocket) (from Scheltema & Kuzirian 1991). Scale 0.1 mm. B. *Helicoradomenia juani* radula, left side of 5 rows (from Scheltema & Kuzirian 1991) (cf. Fig. 2C). Scale 0.05 mm. C. *Helicoradomenia acredema*, entire radula; proximally, medial split between two sides is an artifact of dissection, as teeth are held together by the radula membrane (rm) until radula reaches the pharynx. arp anteroventral radula pocket, ph pharynx (from Scheltema 2000). Scale 0.1 mm. D. *Helicoradomenia juani* holotype (from Scheltema & Kuzirian 1991). Scale 1.0 mm. E. *Helicoradomenia acredema* (specimen from Akademik Keldysh station 4668, 9°N East Pacific Rise; kindly provided to author by Dmitry Ivanov). Scale 1.0 mm. F. *Helicoradomenia acredema* sclerite from E, gray-scale rendition of color image showing isochromes (Scheltema & Ivanov 2004); arrow, swollen tip (cf. Fig. 2H). Scale 0.5 mm.

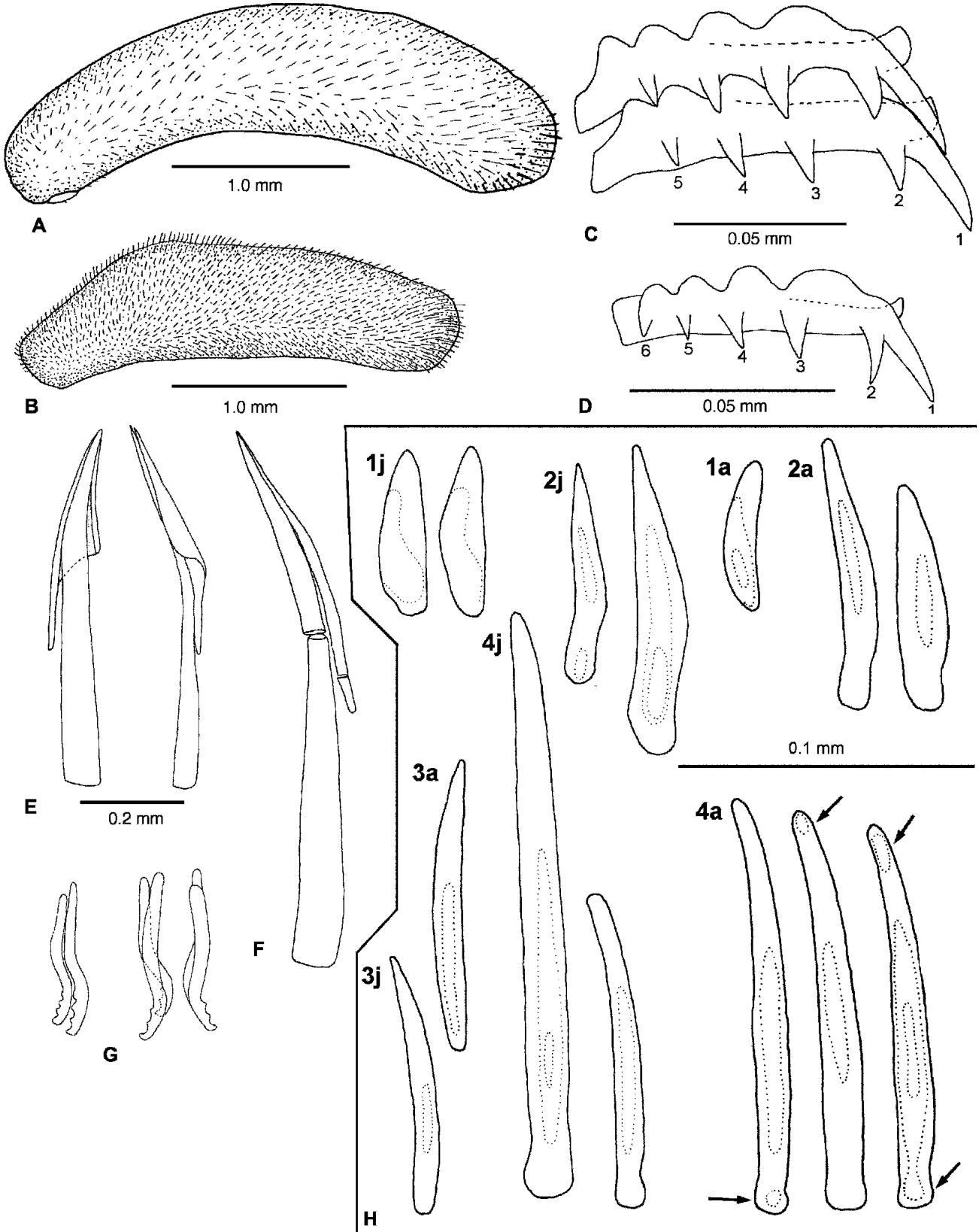


Figure 2. Comparisons between *Helicoradomenia juani* and *H. acredema*. A. (*juani*), B. (*acredema*), at same scale (cf. Fig 1D, E). C. (*juani*), D. (*acredema*), radula teeth from one side of tooth row, not to same scale; denticles numbered from long, lateral denticle. E. (*acredema*), F. (*juani*), copulatory spicules at same scale, both pairs shown in E. G. Accessory copulatory spicules: left, *acredema* with both pairs, right, *juani*. H. Sclerite types 1-4, "j" (*juani*) and "a." (*acredema*), isochromes indicated by dotted lines (cf. Fig. 1F). 1 from beside pedal groove, 2 scimitar-shaped, 3 simple curved, 4 most common; arrows, thickened end in *acredema* (cf. Fig. 1F). (Illustrations of *H. juani* from Scheltema & Kuzirian 1991, of *H. acredema* from Scheltema 2000; some reprinted in Desbruyères et al. 2006).

aplacophoran sclerites are covered by a cuticle as they are extruded from the forming epidermal cell (Haas 1981), a cuticle not related to the formation of the cuticular body mantle. The presence of two different cuticles might afford an explanation for why the symbionts are unusually both epibiotic and endocuticular in these species of *Helicoradomenia*.

Reproduction

All aplacophorans, except for some brooders, seem to have planktonic lecithotrophic larvae (some perhaps demersal), determined from (1) egg size in the gonads (e.g., Scheltema 1987; and personal observations); (2) the occurrence of swimming larvae (Pruvot 1890, Baba 1938, Okusu 2002, Nielsen et al. 2007); or (3) settlement of larvae into experimental, *in situ* settlement boxes (Scheltema 1987) or onto panels (L. Mullineaux, pers. comm.). Active vent sites are ephemeral in that they die and new ones form with noticeable regularity. Recruitment into new areas is thus necessary if the associated fauna is to survive. Ongoing recruitment experiments at vent sites using substrates placed *in situ* demonstrate the ability of *Helicoradomenia* species to disperse.

DIVERSITY AND AGE OF HELICORADOMENIA SPECIES IN THE EAST PACIFIC

Diversity

The diversity of organisms in the East Pacific Rise, in genera and species, is many times greater than that in the Juan de Fuca system (Tunnicliffe 1988). The abundant limpet gastropods afford a good example of a mollusc fauna for comparing the two sectors; their diversity is tabulated from Desbruyères et al. (2006) in Table 3.

Helicoradomenia species have the same dispersal capabilities as the limpets, with lecithotrophic planktonic larvae (for limpets, Desbruyères et al. 2006; for Aplacophora, see earlier). Thus a direct comparison may be made between the limpets and *Helicoradomenia* (Table 3). *Helicoradomenia* has 6-fold greater number of species in the southern *versus* the

northern sector (one species, Juan de Fuca; 6 species, East Pacific Rise). Similarly, limpets have five times more species in the southern sector (8 species, Juan de Fuca; 39 species, East Pacific Rise).

Vicariant Evolution in Helicoradomenia

Helicoradomenia juani and *H. acredema* are so similar morphologically to each other (Figs. 1, 2) and different from other species (examined but not yet described) that they presumably arose from a single species that inhabited hydrothermal vents when the East Pacific ridge was continuous before the Eocene subduction event. The two sectors, Juan de Fuca and East Pacific Rise, separated about 35 million years ago. *Helicoradomenia juani* is common and abundant in the San Juan sector, where there are no *H. acredema*. *H. acredema* is likewise common and abundant in the East Pacific Rise, where there are no *H. juani*. A single mitochondrial gene, CO1 has been sequenced only for *H. juani* (C. Schander, pers. comm.), and differentiation of the two species relies on their morphology (see earlier).

CONCLUSION

- (1) The single most important genus of hydrothermal aplacophorans in number of species is the endemic neomenioid *Helicoradomenia*. It is known to occur in the East Pacific, Southwest Pacific, and Indian Ocean.
- (2) The difference in diversity of *Helicoradomenia* species between the northern and southern sectors of the East Pacific is similar to that of limpets, both dispersing by lecithotrophic, planktonic larvae.
- (3) Subduction of the Pacific plate under the North American plate caused a vicariant evolutionary event resulting in two very similar sister species, *H. juani* and *H. acredema*, that can, nevertheless, be identified from external and hard-part morphology.
- (4) Symbiotic bacteria on sclerites and within the mantle cuticle of two *Helicoradomenia* species seem not to benefit the aplacophorans. Nutritionally, *H. acredema* and another *Helicoradomenia* species probably feed on polychaetes.
- (5) Sectioned *Helicoradomenia* species indicate great similarity among them in internal anatomy and substantiate the adequacy of external and hard-part morphology including body shape and size, appearance of scleritome, sclerites, radula, and copulatory spicules for distinguishing species.

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TABLE 3.

Diversity of genera and species of limpets on the northern and southern sectors of the East Pacific vent and ridge systems, enumerated as occurring in both sectors or as restricted to only one sector or the other. Comparison is made to the aplacophoran genus *Helicoradomenia*, with the same diversity but with fewer species. Limpet data compiled from Desbruyères et al. (2006).

Taxon	North & South		North Only		South Only	
	No. genera	No. species	No. genera	No. species	No. genera	No. species
Lepetosoidea	1	1	—	—	1	5
Lepetodriloidae	3	—	1	5	2	13
Neomphalina						
Neomphalidae	1	—	1	2	5	8
Peltospiridae	—	—	1	1	7	13
Totals	5	1	3	8	15	39
<i>Helicoradomenia</i>	1	—	—	1	—	6

Scheltema was a graduate student there. The author's friendship continued in Woods Hole when Mel directed the Systematics and Ecology program at the MBL. The author remembers the great excitement when Mel's wonderful SEM of a gastropod radula was published, when the blessing of that marvelous

microscope first became available. Surely Mel revolutionized how the gastropod radula was seen and how it functioned. The author thanks Rich Lutz for inviting her to participate in this issue of the *Journal of Shellfish Research* as a memorial to Mel Carriker.

LITERATURE CITED

- Baba, K. 1938. The later development of a solenogastre, *Epimenia verrucosa* (Nierstrasz). *J. Dept. Agric. Kyusu Imperial Univ.* 6:21–40.
- Desbruyères, D., M. Segonzac & M. Bright. 2006. Handbook of Deep-Sea Hydrothermal Vent Fauna. 2nd ed. Denisia 18. Linz, Austria. 544 pp.
- Haas, W. 1981. Evolution of calcareous hardparts in primitive molluscs. *Malacologia* 21:403–418.
- Handl, C. H. & C. Todt. 2005. Foregut glands of Solenogastres (Mollusca): anatomy and revised terminology. *J. Morphol.* 265:28–42.
- Katz, S., C. M. Cavanaugh & M. Bright. 2006. Symbiosis of epi- and endocuticular bacteria with *Helicoradomenia* spp. (Mollusca, Aplacophora, Solenogastres) from deep-sea hydrothermal vents. *Mar. Ecol. Prog. Ser.* 320:89–99.
- Lonsdale, P. 1977. Clustering of suspension-feeding macrobenthos near abyssal hydrothermal vents at oceanic spreading centers. *Deep-sea Res.* 24:857–863.
- Nielsen, C., G. Haszprunar, B. Ruthensteiner & A. Wanninger. 2007. Early development of the aplacophoran mollusca *Chaetoderma*. *Acta Zool.* 88:231–247.
- Okusu, A. 2002. Embryogenesis and development of *Epimenia babai* (Mollusca Neomeniomorpha). *Biol. Bull.* 203:87–103.
- Pruvot, G. 1890. Sur le développement d'un Solenogastre. C. R. hébd. *Séances l'Acad. Sci. Paris.* 111:689–692.
- Scheltema, A. H. 1987. Reproduction and rapid growth in a deep-sea aplacophoran mollusc, *Prochaetoderma yonsei*. *Mar. Ecol. Prog. Ser.* 37:171–180.
- Scheltema, A. H. 2000. Two new hydrothermal vent species, *Helicoradomenia bisquama* and *Helicoradomenia acredema* from the eastern Pacific Ocean (Mollusca, Aplacophora). *Argonauta* 14:15–25.
- Scheltema, A. H. & D. L. Ivanov. 2004. Use of birefringence to characterize Aplacophora sclerites. *Veliger* 47:153–160.
- Scheltema, A. H. & A. M. Kuzirian. 1991. *Helicoradomenia juani* gen. et sp. nov., a Pacific hydrothermal vent Aplacophora (Mollusca: Neomeniomorpha). *Veliger* 34:195–203.
- Todt, C. & L. V. Salvini-Plawen. 2005. The digestive tract of *Helicoradomenia* (Solenogastres, Mollusca), aplacophoran molluscs from the hydrothermal vents of the East Pacific Rise. *Invert. Biol.* 124:230–253.
- Tunnicliffe, V. M. 1988. Biogeography and evolution of hydrothermal vent fauna in the eastern Pacific Ocean. *Proc. R. Soc. Lond. B. Biol. Sci.* 233:347–366.
- Tunnicliffe, V. M., M. R. Fowler & A. G. McArthur. 1996. Plate tectonic history and hot vent biogeography. In: C. J. McLeod, P. A. Tyler & C. L. Walker, editors. Tectonic, magmatic, hydrothermal, and biological segmentation of Mid-Ocean Ridges. Spec. Publ. (Geol. Soc.). pp. 225–238.
- Woods Hole Oceanographic Inst. 2007. The Discovery of hydrothermal vents www.divediscover.whoi.edu/vented/index.html