THE VELIGER

The Veliger 42(2):117–123 (April 1, 1999)

Calyptogena diagonalis, a New Vesicomyid Bivalve from Subduction Zone Cold Seeps in the Eastern North Pacific

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Abstract. A new vesicomyid bivalve species, *Calyptogena* ***diagonalis,*** is described from cold seep communities in the Cascadia subduction zone off the Oregon coast and accretionary wedge sediments along the Pacific coast of Costa Rica. Live bivalves and shells were collected at sulfide seeps near 2021 m depth in Oregon and from 2900 to 3800 m depth in Costa Rica. Shell morphology of *C.* ***diagonalis*** differs considerably from sympatric congeneric and confamilial species of the northeastern Pacific. Shells are large (to 24.0 cm) and elongate (H/L = 0.42), with one or more ridges on the external shell surface extending diagonally from the umbo to near the posteroventral margin. Enlarged, sulfur-colored ctenidia and micrographs of endosymbiotic bacteria held in ctenidia suggest that this species, like other vesicomyids, is a sulfur-based chemolithoautotroph.

INTRODUCTION

The bivalve family Vesicomyidae, first established by Dall & Simpson (1901) includes more than 50 species found nearly exclusively in sulfide-rich habitats such as cold seeps, hydrothermal vents, and accumulations of organic debris (e.g., whale carcasses) from 450 to greater than 3000 m depth. All species investigated have been shown to rely nutritionally on sulfide-oxidizing endosymbiotic chemoautotrophic bacteria held in ctenidia (Fiala-Médioni et al., 1994).

Fossil representatives of the Vesicomyidae are known from as early as the Eocene from the Pacific Northwest, and span the Paleogene and Neogene from collections at several locations (Boss & Turner, 1980; Kanno et al., 1989; Niitsuma et al., 1989; Goedert & Squires, 1993). Although several genera have been erected, most extant species fall under two genera (*Vesicomya* and *Calyptogena*). *Vesicomya* was established in 1886 within the Veneridae (Dall, 1886), and the genus *Calyptogena,* originally placed in the Carditidae, was described in 1891 (Dall, 1891). Assignment of species among genera has resulted in considerable taxonomic confusion within the family, particularly at the generic level (Kojima et al., 1995; Vrijenhoek et al., 1995; Peek & Vrijenhoek, in press). Molecular studies concerning taxonomic affinities within the Vesicomyidae may soon resolve the alignment of species among genera (R. Vrijenhoek, personal communication).

Increased exploration and sampling of vent and seep habitats (and other sulfidic environments) since their discovery in the late 1970s have greatly expanded our understanding of the natural history and biology of vesicomyids, including description of many new species. Early trawl and dredge samplers were deployed most commonly over soft sediments, thereby undersampling geologically rugged terrain where seep and vent habitats often occur. In addition, these habitats are highly localized, further reducing the likelihood of collections using surface-deployed devices. Recent increases in access to these sites by manned submersibles and remotely operated vehicles have allowed focused investigations of environments typically inhabited by vesicomyids, as well as detailed studies of their natural history. In this paper we describe a new species of vesicomyid bivalve collected from cold seeps associated with accretionary sediments along subduction zones off Oregon and Costa Rica.

COLLECTION INFORMATION

Specimens analyzed for the erection of *Calyptogena* ***diagonalis*** sp. nov. were obtained from newly discovered cold seeps in the Cascadia Trough along the Oregon subduction zone (D. Orange, unpublished data), and along the Costa Rica accretionary wedge. A total of 15 live clams or articulated shells were collected at the Oregon site (44°40.56″N, 125°7.08″W) during *ALVIN* dives (# 2644, 2659, and 2663) at a depth of 2021 m. The Cascadia fauna was dominated by several species of vesicomyid clams (mainly *C.* ***diagonalis***) and bacterial mats, as well as columbellid snails typical of sulfide-rich habitats (e.g., *Mitrella permodesta*). Vestimentiferan worms (*Lamellibrachia* sp.) were also common, but less abun-

Table 1

Paratypes of *Calyptogena diagonalis*

Length (mm)	Height	Width	Site	Valves	Dive #	USNM #
74.2	35.0	30.4	Oregon	Left, Right	2644	(880308)
210.0	86.6	55.1	Oregon	Right	2644	(880309)
226.0	91.0	63.0	Oregon	Right	2644	(880310)
231.0	93.0	58.0	Oregon	Left	2663	(880311)
201.0	77.9	52.1	Coasta Rica	Left, Right	2719	(880312)

dant than vesicomyids. Seepage of fluids presumed to be rich in sulfide, methane, or both, appears to be related to dewatering of accretionary sediments during tectonic compression along the Cascadia subduction zone (D. Orange, unpublished).

Twenty-six individuals of *Calyptogena* ***diagonalis*** were obtained from seep locations from 2900 to 3800 m depth off Costa Rica, during *ALVIN* dives # 2715, 2719, and 2728. The Costa Rican site (9°42.28″N, 86°4.38″W) is geographically distant but geologically similar to the Oregon locale, as both are positioned in accretionary complexes undergoing sediment compression owing to tectonic subduction, leading to dewatering of sediments and fluid expulsion at the sea floor (Kahn et al., 1996). The chemosynthetic communities in Costa Rican waters include several species of vesicomyid clams, as well as dense aggregations of serpulid polychaete worms and lamellibrachid vestimentiferans.

Specimens from both sites were compared to vesicomyids housed at the U.S. National Museum of Natural History, the Museum of Comparative Zoology at Harvard University, Los Angeles County Museum of Natural History, and the Santa Barbara Museum of Natural History, and all available published descriptions of vesicomyids. Specimens of *Calyptogena* ***diagonalis*** were also sent to other vesicomyid taxonomists for inspection. Owing to the dissimilarity of these specimens from any described extant or fossil vesicomyid species, we concluded that the erection of a new species within the genus *Calyptogena* is justified. Assignment of the new species to the genus *Calyptogena* was based both on its morphological similarity to congenerics as well as recent unpublished data from molecular studies confirming the close relationship of *C.* ***diagonalis*** to several congeneric species inhabiting the north Pacific (Vrijenhoek, personal communication).

SPECIES DESCRIPTION

Calyptogena ***diagonalis*** Barry & Kochevar, sp. nov.

(Figures 1, 2)

Holotype: Length—215.0 mm, height—78.0 mm, width—53.1 mm, sex unknown, collected from Costa Rican cold seep, *ALVIN* Dive # 2719, 14 February 1994; USNM # 880307, Smithsonian Institution U.S. National Museum of Natural History, Division of Mollusks.

Paratypes: See Table 1.

Type locality: Cold seeps along the Costa Rica subduction zone (9°42.28″N, 86°4.38″W) from 2980 to 3800 m depth. *C.* ***diagonalis*** occurs in clusters of 10 to hundreds of individuals partially buried in sediment, in association) with other vesicomyid clams and bacterial mats.

Description: Shell whitish, chalky, and covered by dehiscent yellowish brown periostracum. Shell large (to 240 mm long, 95 mm high, and 63 mm wide), elongate, inequilateral, heavy, solid (Figure 1). Valves strongly inequilateral, with slightly inflated, incurved umbo positioned far anterior (18–20% of length). Anterior margin short, rounded, slightly gaping due mainly to outward flexure of left valve. Anterodorsal margin short, slightly convex. Umbonal cavity moderate; beaks mildly inflated. Posterior margin subangular, pointed near ventral end, especially in Costa Rican specimens. Lunule short, sublanceolate, poorly defined anteriorly. Posterodorsal margin elongate, convex, angular near distal end. Escutcheon incised steeply immediately posterior to umbo in some specimens. Margin of incision near umbo forming posteriorly directed ridge extending toward postero ventral margin. Ligament deeply embedded, highly inflated, dark brown, lanceolate, calcified along hinge plate in large individuals, encompassing ~16–25% (calcified portion) or ~38–41% (calcified and uncalcified portion) of posterodorsal margin. Ventral shell margin nearly straight along midpoint in small individuals, mildly concave in large specimens. Sculpture consisting of strong radial ridge from umbo to posteroventral tip, with similar adjacent ribs on some specimens, poorly defined commarginal lirations on shell and periostracum, most crowded near anterior end. Commarginal ridging suggestive of growth rings weakly evident on some specimens. Viewed ventrally, slight flexure evident along ventral margin, most notably near posterior end. Large individuals with flaky, mostly dehiscent periostracum, except along shell margin, where periostracum overlaps shell margin to provide

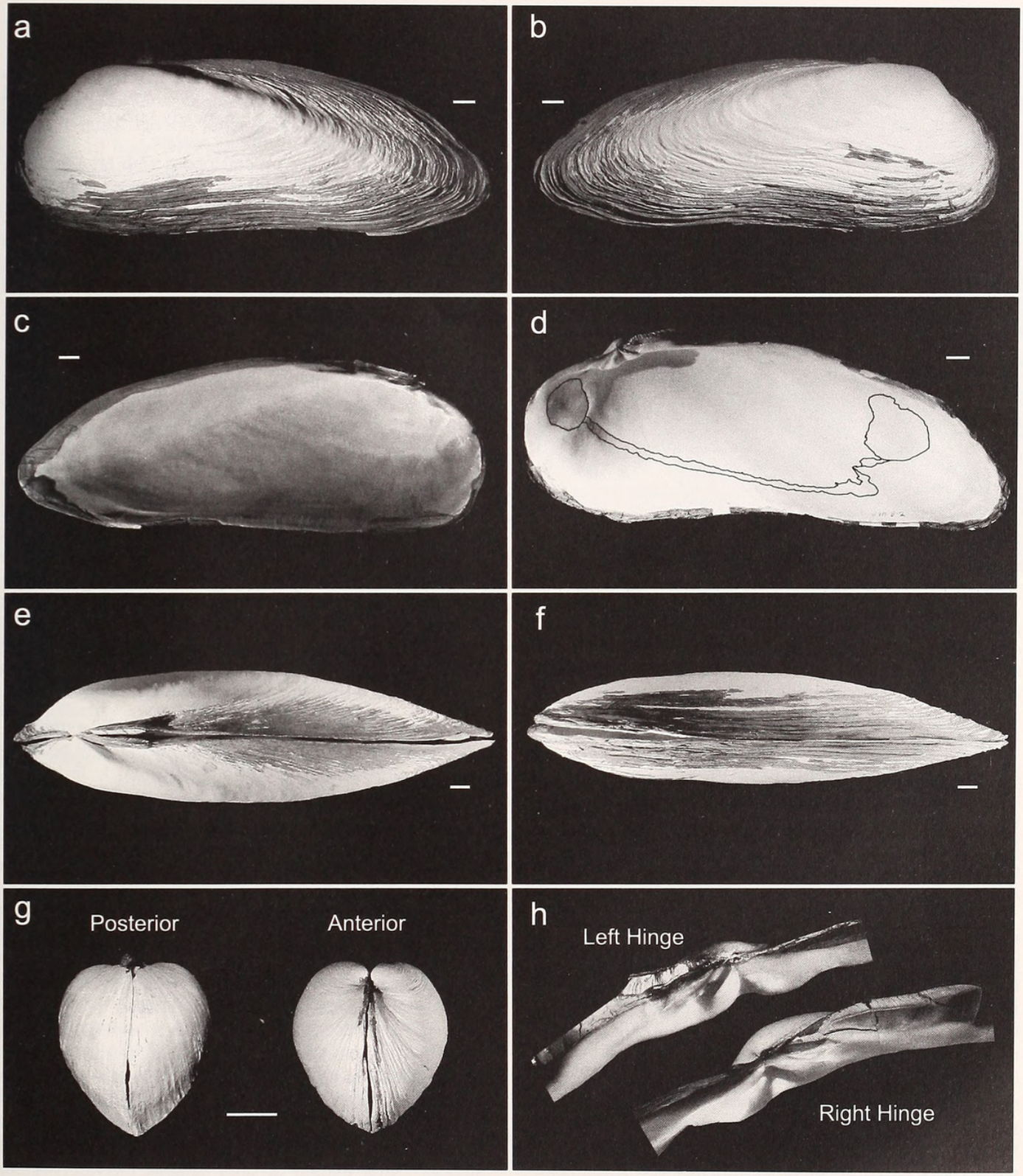

Figure 1

Diagnostic shell characteristics of *Calyptogena* ***diagonalis*** Barry & Kochevar, sp. nov. Scale bars = 1 cm. a. External view of left shell valve of holotype (USNM# 880307) from Costa Rican collection. b. External view of right shell valve of holotype. c. Internal view of left shell valve of holotype. d. Internal shell valve of paratype (USNM# 880312) from Costa Rican site, with pallial line and adductor muscle scars highlighted in black. e. Dorsal view of holotype. f. Ventral view of holotype. g. Anterior and posterior views of juvenile specimen (paratype; USNM# 880308) from Oregon seeps. h. Hinge structure of left (paratype; USNM# 880311) and right (holotype) valves.

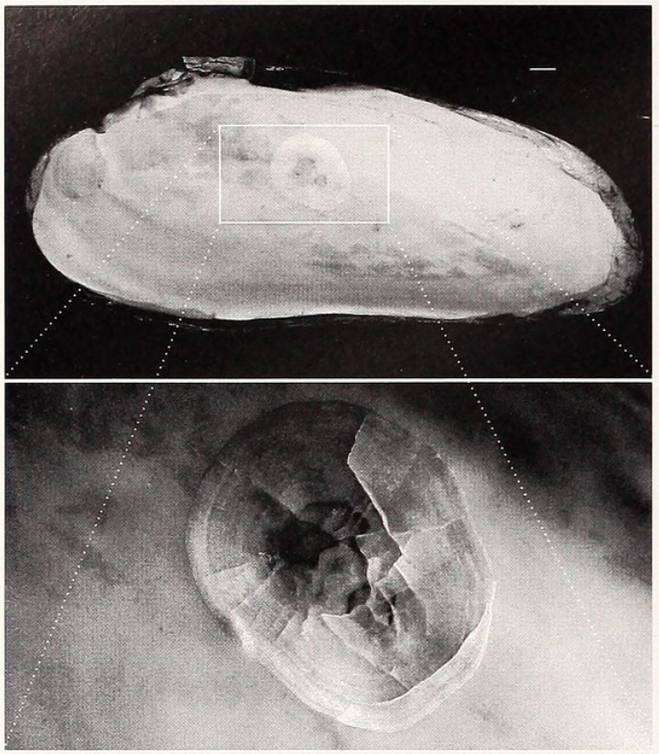

Figure 2

Repaired internal surface of shell valve from Oregon specimen (paratype; USNM# 880310). Scale bar = 1 cm. a. Overall view of internal valve, with repaired shell area highlighted. b. Magnified view of shell repair.

complete seal when shell valves closed. Periostracum inflated, ruffled along anterior to anteroventral margin. Dissolution of external shell moderate to extreme in some specimens, principally ventral and posterior to umbones. Fenestrations resulting from dissolution occasionally repaired by localized calcification of inner shell (Figure 2) in some specimens.

Right valve with two cardinal teeth beneath umbo (Figure 1d, h). Anterior cardinal tooth strongly protuberant, with parallel to subtrigonal borders, pointing ventrally from umbo, and convex to slightly concave medial surface. Posterior tooth dorsal to anterior cardinal, protuberant, narrow, and slightly bifid in some. Anterior and posterior cardinals joined under beak. Three sockets formed by cardinal teeth and umbonal shell margin to accept cardinal teeth from left valve, central socket deepest, triangular. Posterior hinge plate massive, forming nymph subtending and partially enveloping ligament; longest relative to shell length in small specimens.

Left valve with three cardinal teeth and two sockets to accept central and dorsal cardinal teeth of right valve (Figure 1c, h). Anterior cardinal strongly protuberant, narrow to massive, rounded medially; convex anterior margin merges ventrally with hinge plate, flat posterior face contacts anterior cardinal of right valve. Central cardinal tooth massive, strongly protuberant, trigonal, pointed to nearly blunt; anterior surface convex, posterior contact surface flat. Posterior cardinal positioned dorsally, small compared to other teeth, long, narrow, produced only slightly above hinge plate, nearly horizontal; medial surface nearly smooth to mildly serrate.

Internal shell surface porcellaneous with faintly developed radial internal riblets and minor commarginal undulations. Anterior adductor muscle scar recessed dorsally and posteriorly, ovately conic to subelliptical, with minor concentric lirations, extending to anterior shell margin in small individuals (Figure 1d). Posterior adductor muscle scar larger, irregularly ovate, teardrop-shaped, or pear-shaped, pointed dorsally, lacking supportive shell sculpture found in anterior scar. Pallial line weakly evident, broad, with sinuous and irregular margins, mildly convex anteriorly and ventrally, and angular posteriorly, forming small pallial sinus (Figure 1d).

Soft anatomy: Our general description of the soft anatomy of *Calyptogena* ***diagonalis*** is based on dissections of two adult-sized individuals. Soft anatomy is generally similar to that reported for *C. pacifica* Dall, 1891; *C. kilmeri* Bernard, 1974; *C. magnifica* Boss & Turner, 1980; *Ectenagena extenta* Krylova & Moskalev, 1996; and *C. packardana* Barry et al., 1997. The most conspicuous features of all six species are the greatly enlarged and often sulfur-colored ctenidia, large and heavily vascularized foot, reduced digestive system, and red, hemoglobin-rich blood, which all relate to their chemosynthetic life style.

Mantle and siphons. Mantle lobes bilaterally symmetrical, thickened around shell margin, particularly near anteroventral margin, attached to shell by thick, broad pallial muscles. Mantle cavity opens to create pedal gape from ventral margin of anterior adductor muscle to ventral anterior margin of incurrent siphon. Thick folds of inner mantle fused posteriorly to form separate incurrent and excurrent siphons; fusion extends dorsally between adductor muscles. Mantle margin thickened and inflated along anterior margin. Band of sensory papillae along thickened anterior mantle margin, similar to that described for *C. magnifica* (Boss & Turner 1980).

Incurrent and excurrent siphons formed by fusion of the mantle, conical to cylindrical in side view, ovate in cross section, positioned in pallial sinus formed by folds of thickened mantle musculature. Highly developed pallial musculature near posteroventral shell margin in siphonal region, as in *C. magnifica* (Boss & Turner, 1980). Incurrent siphon larger and more ovate than excurrent siphon. Distal margin of both siphons uneven, slightly serrate, lacking papillae found in *Calyptogena packardana* (Barry et al., 1997). Densely branched structure near base of incurrent siphon functions as filter to reject large particles. Excurrent siphon smaller in cross section than incurrent siphon, with mildly serrate distal margin, thin collar of tissue lining internal siphonal walls to form

one-way valve similar to other vesicomyids (Bernard, 1974; Barry et al., 1997).

Ctenidia: Greatly enlarged ctenidia enveloping body along length, from umbonal cavity ventrally through much of shell cavity. Inner and outer demibranchs on each side of body with ascending and descending lamellae. Inner demibranchs fused along distal margins to middle of visceral mass and joined posteriorly, isolating incurrent and excurrent pallial chambers. Ctenidia variously colored among specimens, from bright sulfur yellow to purplish red, presumably depending upon content of elemental sulfur in endosymbiont bacteriocytes (Kochevar & Barry, 1994). We have observed ctenidia of *C. packardana, C. pacifica,* and *C. kilmeri* to change gradually from sulfur-colored to deep red in laboratory aquaria, apparently due to endobacterial oxidation of elemental sulfur deposits. Micrographs of ctenidial tissues show endosymbiotic bacteria similar to those in related chemosynthetic vesicomyids (R. Kochever, unpublished data).

Foot and visceral mass: Foot large, generally conical, highly muscular and distensible, particularly in its ventral half; highly vascularized, deep red owing to hemoglobin content. Dorsally, foot grading into visceral mass, housing large gonad surrounded laterally and ventrally by foot musculature, and dorsally by stomach, digestive gland, intestinal tract, and heart. Labial palps, stomach, and intestine greatly reduced, similar to other vesicomyids (Bernard, 1974; Boss & Turner, 1980; Barry et al., 1997).

Reproductive system: Microscopic inspection of gonad samples from several specimens indicates that *Calyptogena* ***diagonalis*** is gonochoristic. Ovary or testis found directly dorsal to foot and surrounded by foot musculature. No evidence of sexual dimorphism in shells or soft anatomy other than the gonad was observed.

REMARKS

Calyptogena ***diagonalis*** inhabits seep communities associated with accretionary complex sediments near 2021 m depth off Oregon and from 2900 to 3800 m off Costa Rica. Owing to its broad latitudinal range, we suspect that this species inhabits other sulfide-rich seeps along continental borderlands of the northeastern Pacific. Observations during *ALVIN* dives found *C.* ***diagonalis*** in clusters including ~10 to 100 individuals, buried partially in sediments presumed to be the locus of seeping sulfide-rich pore fluids. *Calyptogena pacifica* and other vesicomyid clams cohabit seeps with *C.* ***diagonalis.***

The principal diagnostic shell characters of *Calyptogena* ***diagonalis*** are its large size, elongate shape, diagonal ridge along the posterior apex of each valve to near the posteroventral shell margin, and somewhat angular posterodorsal margin.

Allometric changes in shell morphology, determined from comparisons of three juvenile shells with five to 10 adult-sized shells, is evident in several shell characteristics of *C.* ***diagonalis.*** Juveniles are considerably less elongate (H/L ~0.55 [juveniles] versus ~0.39 [adults]), more inflated (W/L ~0.41 [juveniles] versus ~0.25 [adults]), and less inequilateral (umbo ~24% along length [juveniles] versus ~19% [adults]).

While direct measures of chemosynthetic physiology in *C.* ***diagonalis*** are lacking, all available evidence indicates that this species relies on sulfur-oxidizing endosymbiotic bacteria for most or all of its nutrition. All species of vesicomyid bivalves investigated have been shown to derive their nutrition from thiotrophic endosymbionts (Fiala-Médioni et al., 1994). *C.* ***diagonalis*** inhabits seep environments and has morphological (size, soft anatomy, endosymbiotic bacteria, elemental sulfur in ctenidial tissues, hemoglobin) and behavioral (inhabits seeps, aggregates at sites presumed to have sulfide-rich pore fluids) characteristics very similar to known chemosynthetic vesicomyids. Analysis of stable carbon isotopic ratios of foot tissues for *C.* ***diagonalis*** also suggest chemosynthesis as the primary nutritional pathway, with values near 36‰, similar to confamilial species known to rely on chemosynthetic production.

Geographic Variation in the Morphology of *Calyptogena* ***diagonalis***

Calyptogena ***diagonalis*** from sites off Oregon and Costa Rica differs slightly in shell morphology and may warrant the specification of distinct subspecies for the two groups, though additional collections are required to resolve consistent differences among these geographical groups. Shells of Oregon specimens are slightly deeper-bodied than their Costa Rican counterparts, with height/length ratios averaging 0.41 (s.d. = 0.02) and 0.38 (s.d. = 0.03), respectively (shells > 150 mm length; t-test = ns). Southern material also has a less inflated ligament, and more prominent secondary diagonal ridge dorsal to the primary ridge, leading from near the umbo to the angle in the posterodorsal margin. Dentition is very similar, with minor variation in shape and orientation of cardinal teeth. The anterior cardinal of southern specimens is more protuberant and directed more anteriorly, compared to the nearly vertical orientation of northern specimens.

Comparison with Other Vesicomyids

Calyptogena ***diagonalis*** is similar to few extant described vesicomyids, owing principally to its large size. *Ectenagena extenta* inhabits seep communities with *C.* ***diagonalis,*** but is considerably more elongate (H/L ~ 0.22), and lacks the characteristic diagonal ridge of *C.* ***diagonalis*** (Table 2). Similarly, *Calyptogena phaseoliformis* Métivier et al., 1986, at present known only from the western Pacific, may be confused with *C.* ***diagonalis,*** but is also highly elongate (H/L ~ 0.24). Morphometric ratios of *C.* ***diagonalis*** are more similar to *Calyptogena mag-*

Table 2

Comparison of morphometric ratios among described extant vesicomyid species similar in morphology to *Calyptogena* ***diagonalis***

Species	Height/Length (H/L)			Width/Length (W/L)			Width/Height (W/H)		
	Mean	S.D.	N	Mean	S.D.	N	Mean	S.D.	N
Calyptogena ***diagonalis,*** sp. nov.	0.42	0.07	38	0.29	0.07	36	0.69	0.07	35
Calyptogena elongata	0.45	0.02	12	0.26	0.08	12	0.58	0.19	12
Calyptogena kilmeri	0.51	0.03	1805	0.33	0.03	1826	0.65	0.06	1825
Calyptogena magnifica	0.44	0.02	14	0.27	0.02	5	0.61	0.05	5
Calyptogena packardana	0.53	0.03	210	0.31	0.03	210	0.58	0.04	210
Calyptogena phaseoliformis	0.24	0.01	6	0.16	0.01	4	0.65	0.04	4
Ectenagena extenta	0.22	0.01	4	0.17	0.01	4	0.78	0.05	4

nifica than any materials examined, but these species differ greatly in shell outline and sculpture, ligament size and shape, and periostracum morphology. Valves of *C. magnifica* are subelliptical with similarly rounded anterior and posterior margins, and lack either the pointed posterior margin or diagonal ridge sculpture characteristic of *C.* ***diagonalis.*** The ligament of *C. magnifica* is massive and much more extensive than *C.* ***diagonalis,*** extending from the umbo to the posterior pedal retractor muscles (~ 48–50% of posterodorsal margin versus 38–41% in *C.* ***diagonalis***). The periostracum of both species develops complex and inflated folds along the anterior margin, but these appear to be more extensive in *C. magnifica* as reported by Boss & Turner (1980). In addition, *C.* ***diagonalis*** and *C. magnifica* inhabit different environments and appear to be endemic to cold seeps and hydrothermal vent sites, respectively. *Calyptogena elongata* Dall, 1916, is similar in shape, but does not reach the large size of *C.* ***diagonalis,*** is thinner, and lacks a diagonal ridge. *Calyptogena packardana* is generally similar to small specimens of *C.* ***diagonalis,*** but is easily distinguished by its very narrow width to length ratio (0.31) and deeply incised escutcheon. Finally, two morphologically similar species, *Calyptogena kilmeri* and *Calyptogena soyoae* Okutani, 1957, from the northeastern and northwestern Pacific, respectively, could be confused with small *C.* ***diagonalis.*** However, like *C. packardana,* both species lack a diagonal ridge, and have very different hinge dentition than *C.* ***diagonalis.*** The posterior (dorsal) cardinal tooth of the right valve in these smaller species is directed at nearly 45° toward the posteroventral margin. In *C.* ***diagonalis,*** this tooth inclined only about 20 to 30 degrees from parallel with the dorsal shell margin.

ACKNOWLEDGMENTS

We are grateful to Dr. K. J. Boss, E. V. Coan, and P. H. Scott for providing access to specimens and literature important to this project and for their advice concerning the assignment of a new species. Two referees provided valuable comments concerning the content and organization of the manuscript. Funding for the project was provided by grants from the National Science Foundation, and the Monterey Bay Aquarium Research Institute.

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