

Calyptogena packardana, A New Species of Vesicomimid Bivalve from Cold Seeps in Monterey Bay, California

by

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Abstract. *Calyptogena packardana*, a new bivalve species of the family Vesicomimidae, is described from specimens collected from sulfide seeps near 600 m depth in the Monterey Submarine Canyon, Monterey Bay, California. Shell characteristics of *C. packardana* differ considerably from those of sympatric confamilial species (*Calyptogena pacifica*, *C. kilmeri*, *C. gigas*, and *Vesicomima stearnsii*) found at cold seeps in Monterey Bay and elsewhere in the northeastern Pacific. They are most similar to those of two fossil species (*C. gibbera*, *C. lasia*), from Pleistocene and Pliocene deposits in southern California. The soft anatomy, including mantle and siphons, ctenidia, and foot, are discussed. Ratios of stable carbon isotopes near-36‰ PDB units and presence of endosymbiotic bacteria in ctenidial tissues indicate that chemosynthesis, via thiotrophic chemoautotrophic endosymbiotic bacteria, is the primary nutritional source for *C. packardana*, as reported for other vesicomimids.

INTRODUCTION

The family Vesicomimidae was erected by Dall & Simpson (1901) to include a number of large, thick-shelled species with heterodont dentition and dehiscent periostraca. Fossil representatives of the Vesicomimidae are known from as early as the Eocene from the Pacific Northwest (Goedert & Squires, 1990, 1993), and span the Paleogene and Neogene from collections at several locations (Kanno et al., 1989; Niitsuma et al., 1989; Goedert & Squires, 1993). While the taxonomic relationships among species within the family are not completely understood (Kojima et al., 1995; Vrijenhoek et al., 1995), extant species are presently assigned to five genera (Krylova & Moskalev, 1996; Goto & Poppe, 1996). Most species belong to the genera *Vesicomima* Smith, 1885 and *Calyptogena* Dall, 1891. Vesicomimid bivalves have been collected principally or perhaps exclusively (exact location of dredge samples are not known) in sulfide-rich habitats (e.g., hydrothermal vents, cold seeps, whale falls) from 400 m to greater than 3000 m depth.

Prior to the discovery of hydrothermal vent and cold seep communities, vesicomimids were regarded as noteworthy for their large size and robust shells, collected from deep sea habitats where the bivalve fauna typically included small, thin-shelled species (Boss, 1970). Recent

studies have shown that all living species examined contain sulfur-oxidizing endosymbiotic bacteria from which much of their nutrition derives (Fiala-Médioni et al., 1994). Knowledge that vesicomimid nutrition is based largely or entirely on thioautotrophic production by endosymbiotic bacteria, thereby potentially increasing the energy available to sustain high rates of metabolism and growth compared to non-chemosynthetic deep sea species, resolves the paradox of differences between vesicomimids and other deep sea bivalves.

Discoveries of new vesicomimid species have been frequent in the past 20 years, owing to investigations of seep and vent communities using submersibles and ROVs. The relatively recent discovery of many sulfide-rich environments inhabited by vesicomimids partially explains the rarity of their collection and poor representation in museum collections. Historically, most collections were from bottom trawls, which are not deployed in areas of rough terrain where vesicomimids often occur. Much new information concerning the diversity, biology, and ecology of vesicomimids is arising from studies of seep and vent sites.

Several cold seep sites have been discovered recently in the Monterey Bay region from 600 m to 1000 m depth, in which the fauna is dominated by up to five species of vesicomimid clams (Barry et al., 1996). In this paper we

describe a new species of vesicomyid bivalve which inhabits two of these cold seep sites.

COLLECTION INFORMATION

Observations and collections were made at the "Mt. Crushmore" cold seep site (36°46.9'N, 122°2.6'W) in Monterey Canyon, Monterey Bay, California (Barry et al., 1996), during dives of the remotely operated vehicle (ROV) *Ventana*, operated by Monterey Bay Aquarium Research Institute. This site includes numerous small seeps distributed near 600 m depth along exposures of the Purisima Formation sandstones in Monterey Canyon. Clusters of vesicomyids are common at these seeps. Following close examination of 210 living and dead unidentified specimens of vesicomyids collected from 1992 to 1994, coupled with review of the taxonomic literature concerning vesicomyids, comparisons with specimens housed at the United States National Museum of Natural History (USNM), the Museum of Comparative Zoology at Harvard University (MCZ), Los Angeles County Museum of Natural History (LACM), and the Santa Barbara Museum of Natural History (SBMNH), and consultations with experts on vesicomyid taxonomy, we concluded that these specimens differed significantly from any described vesicomyid species. Although the taxonomic affinities within the family Vesicomyidae remain unresolved, the unidentified specimens were most similar morphologically (i.e., periostracum, dentition, and other characters) to other species assigned to the genus *Calyptogena*. In addition, unpublished genetic analyses also indicate high relatedness of the new species to other *Calyptogena* sp. (G. Matsumoto, personal communication). We therefore propose the following new species of *Calyptogena*.

SPECIES DESCRIPTION

Calyptogena packardana, Barry, Kochevar, Baxter & Harrold, sp. nov.

(Figure 1)

Holotype: Length—77.8 mm, height—42.1 mm, width—27.8 mm, sex unknown (Figure 1), USNM, Department of Invertebrates, Mollusks, no. 880188.

Paratypes: Length—46.4 mm, height—22.7 mm, width—12.4 mm, sex, unknown, USNM, no. 880189; Length—52.7 mm, height—28.4 mm, width—15.4 mm,

sex, female, USNM, no. 880190; Length—72.1 mm, height—37.9 mm, width—23.3 mm, sex, male, USNM, no. 880191; Length—79.2 mm, height—40.5 mm, width—25.7 mm, sex, unknown, USNM, no. 880192; Length—69.3 mm, height—35.4 mm, width—19.9 mm, sex, female, USNM, no. 880193; Length—78.9 mm, height—43.5 mm, width—29.2 mm, sex, unknown, USNM, no. 887520.

Paratypes are accessioned at the LACM, SBMNH, and the MCZ at Harvard University.

Type-locality: "Mt. Crushmore" cold seep, (36°47.1'N, 122°2.6'W), Monterey Bay, California, in 635 m depth.

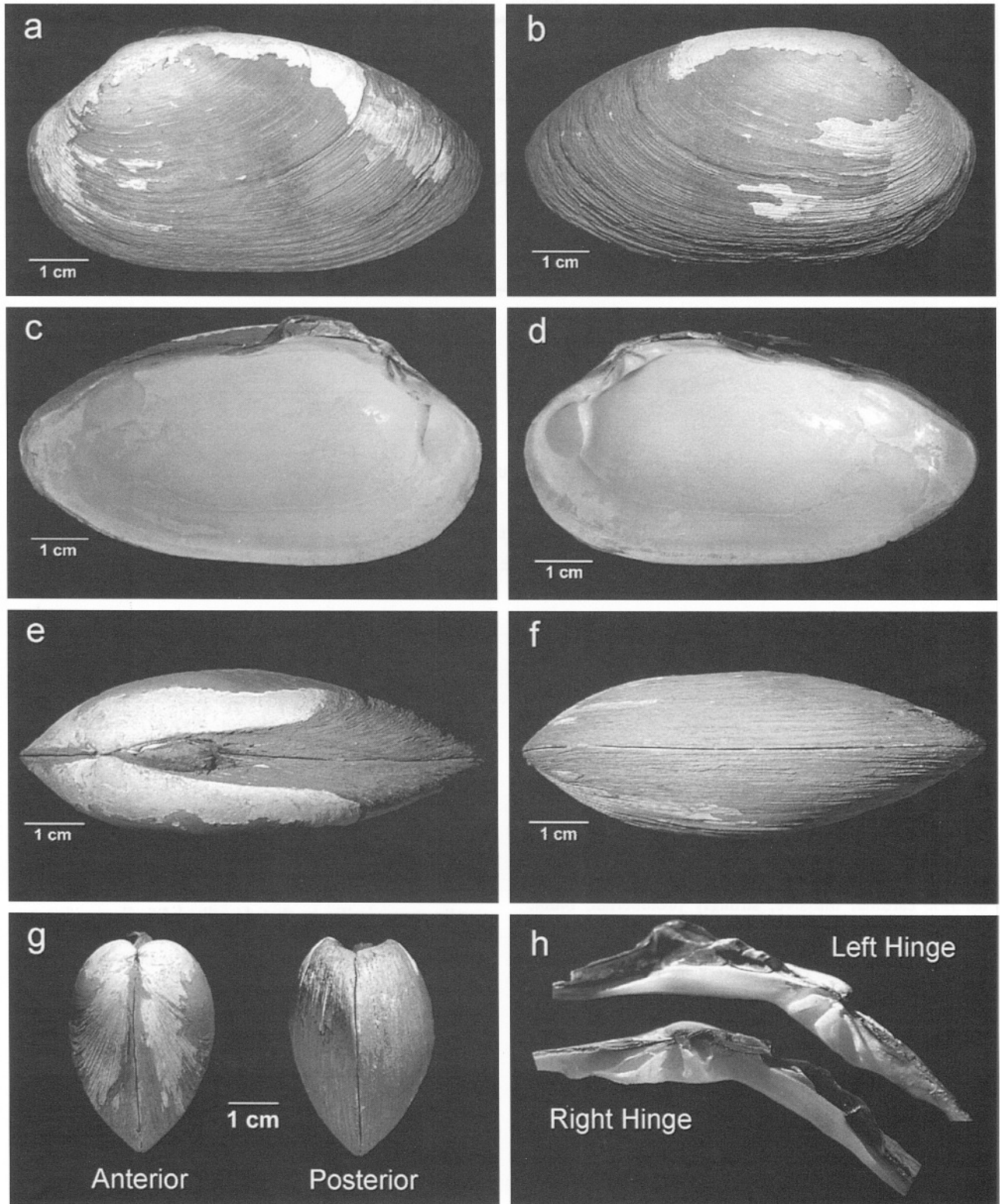
Description: Shell whitish, chalky, covered by yellowish brown periostracum. Juvenile color light brown, with intact, smooth periostracum. Large individuals with flaky dehiscent periostracum. Periostracum overlapping shell margin slightly to provide complete seal when shell valves close. Shell (Figure 1) to 87.2 mm long, 46.8 mm high, and 31.0 mm wide, subtrigonal, elongate, inequilateral, heavy and solid, slightly compressed. Small individuals have a more transparent and indehiscent periostracum, and a lower W/L ratio. Large individuals are more inflated and have a slightly greater height/length ratios than shorter, presumably younger individuals.

Valves strongly inequilateral, with slightly inflated and introrse umbo positioned far anterior (20–25% of total shell length [TL]) along shell length. Umbonal cavity moderately deep; beaks mildly inflated. Anterior margin short, rounded, with very slight or no gape; posterior margin pointed in largest specimens. Ventral margin generally convex, nearly flat medially. Anterodorsal margin short, slightly convex in small individuals, flat to slightly concave in large individuals. Lunule short, sublanceolate, deeply incised in large individuals. Posterodorsal margin elongate, convex. Escutcheon little developed in small specimens, becoming deeply incised, steeply walled in larger, presumably older specimens, extending from umbo to posterior end of shell (Figures 1, 2). Ligament opisthodontic, dark brown, lanceolate, inflated, deeply embedded, extending 38 to 45% of posterodorsal margin. Sculpture consisting of weak commarginal lirations, most crowded and conspicuous near anterior end and within escutcheon. Growth rings weakly evident; no obvious radial sculpture. Viewed ventrally, slight flexure evident along ventral margin, most notably near posterior end. From dorsal perspective, mild flexure along posterodorsal

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Figure 1

Shell characteristics of the holotype of *Calyptogena packardana* Barry, Kochevar, Baxter & Harrold, sp. nov. (USNM, no. 880188) a. Left valve, external view; b. Right valve, external view; c. Left valve, internal view; d. Right valve, internal view; e. Dorsal view of shell; f. Ventral view of shell; g. Anterior and posterior view of shell; h. View of hinge structure for left and right valves.



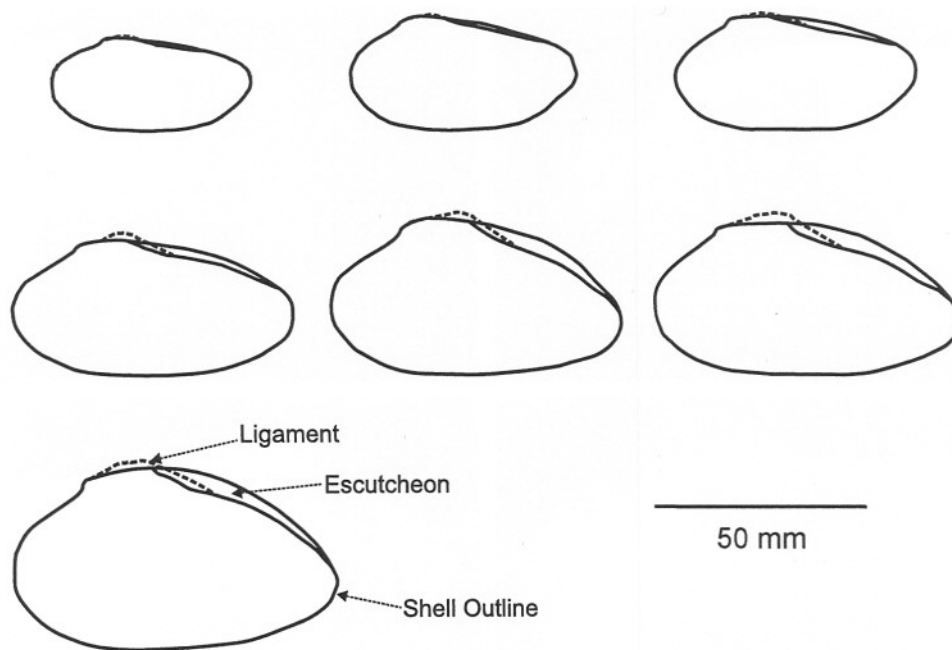


Figure 2

Size series of *Calyptogena packardana* Barry, Kochevar, Baxter & Harrold, sp. nov. showing allometric changes in the depth of the escutcheon.

shell margin apparent, as is slight overlap (~1-1.5 mm in 75 mm long specimen) of right valve over left valve near posterior third of escutcheon, particularly in larger specimens.

Right valve with three cardinal teeth radiating from the umbo (Figure 1). Anterior cardinal tooth thin, only mildly protuberant, with nearly parallel dorsal and ventral margins, pointed ventrally and merging with hinge plate. Medial tooth nearly parallel to and positioned ventrally to anterior tooth; strongly protuberant, blunt on medial face, but narrow and massive compared to anterior cardinal. Posterior cardinal massive, strongly protuberant, blunt, bifid, subtrigonal, subconvex along dorsal margin, mildly concave along anterior face. Anterior and posterior cardinals joined at beak. Three sockets are formed amongst the right cardinal teeth and posterior-dorsal margin, to accept cardinal teeth from the left valve. The central socket is deepest and pyramidal. Right posterior hinge plate massive, forming wide solid nymph subtending the ligament. Left valve (Figure 1) with three cardinal teeth forming two sockets to accept central and posterior cardinal teeth of the right valve. Anterior cardinal thin, pointed, ventral to and merging with hinge plate. Central tooth protuberant, massive, slightly bifid in most specimens, trigonal. Posterior cardinal protuberant, subconvex along dorsal margin, roughly parallel to dorsal shell margin. Anterior and posterior cardinal teeth joined at or slightly anterior to beak.

Internal surface of shell porcelaneous, white, without internal ribs. Anterior adductor muscle scar incised dorsally and posteriorly, subovate, slightly pointed dorsally (Figure 1). Posterior adductor muscle scar irregularly ovate. Pallial line weakly to moderately impressed, subarcuate anteriorly; sinuous and angular posteriorly, forming small pallial sinus. Anterior pedal retractor muscle scar deeply recessed, subtending anterior margin of hinge plate immediately posterior to dorsal end of adductor scar.

Soft anatomy: The anatomy of *C. packardana* is generally very similar to that described for *C. pacifica* and *C. kilmeri* by Bernard (1974), and *C. magnifica* by Boss & Turner (1980). The most conspicuous features of *C. packardana* are the greatly enlarged ctenidia, often yellow in color owing to their content of elemental sulfur; large and heavily vascularized foot; reduced digestive system; and presence of red, hemoglobin-rich blood, all of which relate to the life style of this group, which harbor chemoautotrophic bacteria.

Mantle and siphons: The mantle lobes are bilaterally symmetrical, and slightly thickened anteriorly. The mantle is attached to the shell ventrally by broad pallial muscles, and dorsally by smaller pallial muscles, except near the hinge plate, where pallial musculature is enlarged. The mantle cavity opens ventrally, leaving a pedal gape which extends from the ventral margin of the anterior

adductor muscle to the ventral anterior margin of the incurrent siphon. The inner mantle folds are fused posteriorly to form inhalant and exhalant siphons and continue fused dorsally between the adductor muscles. The mantle lobes of *C. packardana*, as in *C. kilmeri* and *C. pacifica*, are thickened along their ventral margin and hypertrophied along the posteroventral margin, but do not exhibit the greatly thickened anterior and posterior margins observed in *C. magnifica* (Boss & Turner, 1980).

The siphons are conical to cylindrical in shape and elliptical in cross section. The inhalant siphon is larger and more elliptical in cross section than the exhalant siphon, with two to three rows of papillae on its distal margin. The inner row includes approximately 35 short papillae. An outer row has about 35 long, similar sized, club-shaped papillae along its inner edge, and about 85 variably sized, club-shaped papillae along its outer edge. The base of the inhalant siphon includes internally a branched flaplike structure apparently acting as a filter for rejecting large particles. The exhalant siphon is smaller and more ovate in cross section than the inhalant siphon, and has a single row of approximately 60 papillae of variable size on its distal margin. Like *C. kilmeri* and *C. pacifica*, the base of the exhalant siphon of *C. packardana* also bears an inner collar of thin translucent epithelium, which acts as a one-way valve.

Ctenidia: The ctenidia are greatly enlarged, enveloping the body and extending dorsally into the umbonal cavity and ventrally greater than half the distance to the ventral shell margin. Ctenidia lie on either side of the body and have nearly equally sized inner and outer demibranchs, both with ascending and descending lamellae. The inner demibranchs are fused along their distal margins to the midline of the visceral mass and joined together posteriorly, thereby isolating the inhalant and exhalant pallial chambers. Ctenidia are sulfur-laden, varying in color among specimens from bright sulfur-colored to purplish red.

Foot and visceral mass: The foot is large, conical, pointed distally, highly muscular, and distensible, particularly in its ventral half. It is also highly vascularized, and in live specimens is a deep red color, owing to its hemoglobin content. Live animals have been observed to extend the foot through the pedal gape greater than 1 body length. Dorsally, the foot grades into the visceral mass, which includes a large gonad surrounded laterally and ventrally by the foot musculature, and dorsally by the stomach, digestive glands, intestinal tract, and heart. The stomach and intestine are greatly reduced, as are the labial palps, similar to that described for other vesicomysids by Bernard (1974) and Boss & Turner (1980).

Reproductive system: A fairly large gonad is embedded in the dorsal portion of the visceral mass, adjacent to and partially merging with the digestive glands. The species

is dioecious, with little difference in size among sexes (Figure 3) and no apparent sexual dimorphism of the shells.

Etymology: *Calyptogena packardana* is named in honor of David and Lucille Packard, the founders of the Monterey Bay Aquarium Research Institute.

DISCUSSION

Calyptogena packardana inhabits cold seeps in Monterey Bay, California, near 600 m depth. The clams house endosymbiotic thioautotrophic bacteria in their ctenidia (Kochevar & Barry, 1994). Sulfide levels at the center of these cold seeps are near 200 μM (Barry et al., 1997). Shell length reaches 87.2 mm in Monterey Bay, but the average size of 210 specimens examined was 63.5 mm (Figure 3). Shells of *C. packardana* have also been collected by dredge from 800 m in southern California (C. Fisher, personal communication). Inspection of approximately 35 shell valves collected by dredge near Point Conception, California (housed in the MCZ at Harvard University) showed their maximum length near 70 mm.

The most diagnostic shell characters of *Calyptogena packardana* are its moderate to large size and stout shell thickness, narrow width, long, deep escutcheon, and pointed posterior margin. The depth of the escutcheon and sharply pointed posterior are most evident in the largest specimens, while small individuals are characterized by a remarkably narrow width, and a smooth and almost pearly periostracum.

Comparison with Other Vesicomysids

Few extant sympatric species can be confused with *Calyptogena packardana*. *Calyptogena pacifica* Dall, 1891, inhabits the same cold seeps as *C. packardana*, but is considerably smaller in size (maximum length near 62.1 mm; Table 1), and has a more ovate outline. Recent data concerning *C. pacifica* indicate that shell morphology differs between the sexes (Barry, unpublished data); males of *C. pacifica*, have a slightly pointed posterior shell margin, and may therefore be confused with *C. packardana*, especially among smaller individuals. These species are easily differentiated, however, by the smoother periostracum and very narrow width/length ratio of *C. packardana* (~ 0.31) compared to *C. pacifica* (W/L ~ 0.38), and the greatly pronounced escutcheon, especially in large specimens, unlike that of *C. pacifica*. *Calyptogena pacifica* can also be distinguished by the presence of a long narrow posterior cardinal tooth on the hinge plate of the right valve subtending the length of the ligament, which is absent in *C. packardana*.

Calyptogena kilmeri Bernard, 1974, is also found amongst *C. packardana* (Barry et al., 1996). *Calyptogena kilmeri* has a generally smoother and transparent periostracum, a rounded shell margin both anteriorly and pos-

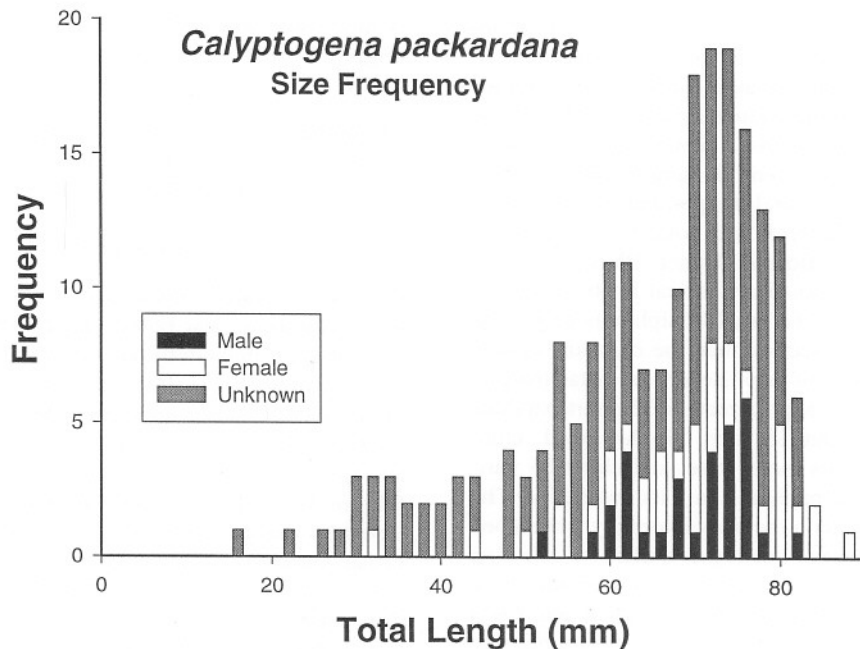


Figure 3

Size frequency of *Calyptogena packardana* Barry, Kochevar, Baxter & Harrold, sp. nov. (total length), collected from cold seeps in Monterey Bay, California.

teriorly, lacks a posterior cardinal tooth in the right valve, and is considerably greater in width/length ratio (Table 2); *C. kilmeri* also attains a much greater size (Table 1).

Calyptogena gigas Dall, 1896, is sympatric with and co-occurs at seeps with *C. packardana*, and attains a similar length in Monterey Bay (Barry unpublished data). *C. gigas* is considerably more similar to *C. kilmeri* than to *C. packardana*, however, and is easily distinguished by its greatly inflated shell compared to both *C. kilmeri* and *C. packardana* (Table 2).

Vesicomya stearnsii Dall, 1895, is a small vesicomyid found rarely at cold seeps in Monterey Bay (Barry et al., 1996), though it may be common elsewhere. Its shell morphology is quite dissimilar to *C. packardana*. *Vesi-*

comya stearnsii attains a total length of only ~33 mm, has a nearly transparent periostracum, and a much greater width/length ratio (0.52).

Ectenagena extenta Krylova & Moskalev, 1996, was described from Monterey Canyon and is found elsewhere in the North Pacific, but is difficult to confuse with *C. packardana*, owing to its great length (to 174 mm) and low width/length ratio (0.18). *Ectenagena extenta* also appears to inhabit deeper depths (> 3000 m) than *C. packardana*.

Shells of *C. packardana* have also been collected from dredge collections off southern California, where *Calyptogena elongata* Dall, 1916, has also been found. *Calyptogena elongata* is similar in height/length ratio (0.58) to *C. packardana* (0.53), but has a much thinner shell and lacks an escutcheon.

Two fossil species, *Calyptogena lasia* Woodring, 1938, from the Pliocene Towsley formation of Ventura County, California, and *Calyptogena gibbera* Crickmay, 1929, from the Timms Point Silt Pleistocene deposits of Los Angeles County, California (Squires, 1991), have shell morphologies similar to *C. packardana*. Although *C. lasia* and *C. gibbera* were recently synonymized (Squires, 1991), we treat them separately here, owing to the greater morphological variation between the three fossil specimens inspected for each of the former species, compared to intraspecific variation within *C. packardana*.

Calyptogena lasia is easily distinguished from *C. pack-*

Table 1

Maximum dimensions (total length, height, and width) for vesicomyid bivalves from collections at cold seeps in Monterey Bay, California. Dimensions in millimeters.

Species	Length	Height	Width
<i>Calyptogena gigas</i>	100.3	49.0	46.2
<i>Calyptogena kilmeri</i>	129.4	60.6	46.9
<i>Calyptogena pacifica</i>	62.1	36.6	26.6
<i>Calyptogena packardana</i> , sp. nov.	87.2	46.8	31.0
<i>Ectenagena extenta</i>	174.0	44.2	30.6
<i>Vesicomya stearnsii</i>	33.0	22.8	17.5

Table 2

Morphometric comparisons among vesicomymid species inhabiting the eastern Pacific, including species from Monterey Bay cold seeps, seep communities in Costa Rica (*C. angulata* Dall 1896), dredged *C. elongata* from near Pt. Conception, California, and fossil species (*C. gibbera*, *C. lasia*) deposits.

Species	Height/length (H/L)			Width/length (W/L)			Width/height (W/H)		
	Mean	SD	N	Mean	SD	N	Mean	SD	N
<i>Calyptogena angulata</i>	0.61	0.02	2	0.38	0	2	0.62	0.02	2
<i>Calyptogena elongata</i>	0.45	0.02	12	0.26	0.08	12	0.58	0.19	12
<i>Calyptogena gibbera</i>	0.53	0.03	3	0.31	0.04	3	0.58	0.03	4
<i>Calyptogena gigas</i>	0.56	0.05	14	0.46	0.04	14	0.84	0.11	14
<i>Calyptogena kilmeri</i>	0.51	0.03	1805	0.33	0.03	1826	0.65	0.06	1825
<i>Calyptogena lasia</i>	0.54	0.05	3	0.37	0.05	3	0.67	0.08	4
<i>Calyptogena pacifica</i>	0.58	0.03	1275	0.38	0.02	1272	0.66	0.05	1272
<i>Calyptogena packardana</i> , sp. nov.	0.53	0.03	210	0.31	0.03	210	0.58	0.04	210
<i>Ectenagena extenta</i>	0.25	—	1	0.18	—	1	0.69	—	1
<i>Vesicomya stearnsii</i>	0.70	0.04	69	0.52	0.05	68	0.74	0.07	68

ardana by its greater W/L ratio (0.37 vs. 0.31) and greater W/H ratio (0.67 vs. 0.58). Furthermore, *C. lasia* lacks a deep escutcheon and sharply pointed posterior outline, which are distinguishing characters of *C. packardana*.

Inspection of three specimens of *C. gibbera* show that this species is similar in general outline to *C. packardana*, with a pointed posterior margin and deep escutcheon, but these features are less pronounced than in *C. packardana*. The W/L, W/H, and H/L ratios for both species are very similar (Table 2); however, these measures do not reflect shell differences in margin shape, escutcheon, etc. The cardinal teeth of *C. packardana* differ greatly from *C. gibbera*. On the left valve, the anterior cardinal of *C. packardana* is not as heavy, being narrower and longer. The middle cardinal of *C. packardana* is triangular, with the anterior vertex displaced steeply anteriorly, such that the anterior margin of the tooth is nearly parallel to the anterior cardinal, forming a steep lanceolate recess between them. In contrast, the middle cardinal of the left valve of *C. gibbera* is strongly bifid, with a strong, posteriorly directed posterior ridge, which is entirely lacking in the modern species. Furthermore, the anterior ridge of the middle cardinal in *C. gibbera* is set at a much greater angle from the anterior cardinal, pointing almost directly away from the beak, thus forming a nearly ovate recess to accept the middle cardinal of the right valve. The posterior cardinal in the left valve of *C. packardana* is considerably shorter than in *C. gibbera*, and is set at 20 to 30 degrees to the dorsal margin, compared to nearly parallel in *C. gibbera*. In the right valve of *C. packardana*, the anterior cardinal is slender and set nearly parallel to the anterodorsal margin. This feature is not easily distinguished on *C. gibbera* fossils, due to poor preservation. Nevertheless, the recess formed by the anterior and middle cardinal teeth of the right valve is narrowly and sharply lanceolate in *C. packardana*, and wide and triangular in *C. gibbera*. The middle cardinal of *C. packardana* is

longer and less massive or bifid, than in *C. gibbera*. The posterior cardinal of the right valve in *C. packardana* is massive, slightly bifid, broadly trigonal, and set at nearly 45 degrees from the dorsal margin. In *C. gibbera*, this tooth is slightly bifid, but is set at an angle near 10 degrees from the dorsal surface (nearly parallel). No details of the pallial line or other interior shell characteristics are available from specimens of *C. gibbera*.

Natural History of the Vesicomymidae

Although numerous species of vesicomymids were described prior to the discovery of chemosynthetic communities at hydrothermal vents and cold seeps, little was known of the life style of most species of this group. Because most specimens have been collected from dredge samples, little information was available regarding characteristics of the environments inhabited by vesicomymids. Recent observations and collections using manned and unmanned submersibles have shown that nearly all species are associated with sulfide-rich environments at hydrothermal vents (e.g., *Calyptogena magnifica* Boss & Turner 1980), cold seeps (various species; Paull et al., 1984; Kennicutt et al., 1985; Laubier et al., 1986; Hashimoto et al., 1987; Embley et al., 1990; Barry et al., 1996), and whale carcasses on the sea floor (Bennett et al., 1994). Moreover, all living species of vesicomymids investigated to date have been shown to rely on endosymbiotic thioautotrophic bacteria harbored in gill tissues as their principal source of nutrition (Fiala-Médioni et al., 1994). Observations by Vetter (1985) and Kochevar & Barry (1994) suggest that variation in the color of gill tissues is due to their content of elemental sulfur, apparently related to the physiology of endobacterial symbionts. The frequency of yellowish gill coloration among specimens held in laboratory aquaria for weeks decreased, apparently related to utilization by endosym-

biotic bacteria of sulfur stored in the ctenidia. Bacteria in gill tissues of *C. packardana* have features characteristic of other thiotrophic bacteria studied by Kochevar & Barry (1994). Their sulfur-laden ctenidia and stable carbon isotopic ratios ($\delta^{13}\text{C}$) near -36‰ PDB units (expressed here as per mil [‰] values relative to Peedee belemnite) further suggest bacterial thioautotrophic production.

Evidence for the uniformity of thioautotrophic-based nutrition for vesicomids largely explains the paradox of large size and robust shell morphology for a deep sea bivalve species. While much of the deep sea may be food limited, thus favoring reduced metabolism, small body size, and perhaps reduced shell calcification, chemosynthetic systems in the deep sea are comparatively food-rich, thus enabling the existence of large species with high metabolic needs. Although little information is available concerning rates of metabolism and growth for *C. packardana*, rapid growth and high nutritional requirements identified for chemosynthetic fauna (i.e., the vestimentiferan worm, *Riftia pachyptila*, 85 cm/y; Lutz et al., 1994) from hydrothermal vents at 2500 m along the East Pacific Rise, and for vesicomids from Monterey Bay (*Calyptogena kilmeri*, 2 cm/y; Barry unpublished data), supports the notion that these sulfide-rich sites are truly deep sea oases. Similarly, vesicomids appear to have been released from food limitation characteristic of much of the deep sea, owing to their chemosynthetic nutritional mode.

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