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# COCCULINIFORM LIMPETS (COCCULINIDAE AND PYROPELTIDAE) LIVING ON WHALE BONE IN THE DEEP SEA OFF CALIFORNIA

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## ABSTRACT

Cocculiniform limpets of the families Cocculinidae and Pyropeltidae are here reported for the first time on whale bone in the deep sea. The new species and records of previously described species are from four whale-falls at bathyal depths on the continental margin off California, from Monterey Bay to the Catalina Basin. The family Cocculinidae is represented by the new species *Cocculina craigsmithi*. With few exceptions, the previously known species of Cocculinidae are known from wood substrates. The family Pyropeltidae is represented by three species: *Pyropelta musaica* McLean & Haszprunar, 1987, originally described from the Juan de Fuca hydrothermal vents, *Pyropelta corymba* McLean & Haszprunar, 1987, originally described from the hydrothermal vent habitat at the Guaymas Basin, and one new species, *P. wakefieldi*. The two previously known species of *Pyropelta* have heretofore been regarded as obligate members of the sulfide habitat of hydrothermal vents. *Pyropelta* species are the first gastropods known from both habitats. Like the hydrothermal-vent habitat, the newly reported habitat on whale bone is also a sulfide-rich, reducing environment.

## INTRODUCTION

During the course of exploration of the seafloor at a depth of 1,240 m in the Santa Catalina Basin, observers aboard the deep-submersible *Alvin* located an intact, 20 m long skeleton of a blue or fin whale in November 1987 (identification by Dale Rice, National Marine Fisheries Service, Seattle). A unique biological community associated with the whale skeleton (termed the whale-fall habitat) was reported by Smith *et al.* (1989) and further described by Allison *et al.* (1991). Samples of bone were recovered and limpets collected on the bone were forwarded to me by Craig R. Smith. These specimens were determined as a new species of *Cocculina* Dall, 1882. In November, 1988, the site was revisited. Two dives were made and additional specimens of the same species were collected along with two species of yet another limpet genus, *Pyropelta* McLean & Haszprunar, 1987. Two further dives were made on a third visit to the site in February, 1991.

Early in 1989, Waldo Wakefield forwarded limpet specimens that he had found on two skulls of gray whales that had been left to dry on the grounds of Scripps Institution of Oceanography. The skulls had been trawled two years earlier off central California by the National Marine Fisheries Service vessel R/V *David Starr Jordan*, one from Monterey Bay off Santa Cruz and another to the south of Monterey Bay off Point Sur. Bodies of the limpet specimens had dried in place, but I was able to rehydrate the specimens and prepare radulae for SEM, which established that the same new species of *Cocculina* and three species of *Pyropelta* were represented. Wakefield also brought to my attention an additional record for *Pyropelta* that came from a third whale skull, which was trawled off Point Lobos (between Monterey Bay and Point Sur) in 1985. Two preserved limpet specimens from that find had been deposited at the California Academy of Sciences and were subsequently borrowed for study. These records form the basis for this paper and are listed below for each whale-fall.

The *Cocculina* species described here is the first member of its genus and family to be reported from whale bone. The records of *Pyropelta* are even more unexpected, as the family Pyropeltidae had previously been known only from two species, which were thought to be restricted to the hydrothermal-vent habitat. Similarities between the hydrothermal-vent and the whale-fall habitats are treated further in the discussion section.

## MATERIALS AND METHODS

Locality information for each of the four whale-falls is given here and not repeated further in the text except for citation of type localities of new species:

Catalina Basin, California (33°12.0'N, 118°30.0'W), 1,240 m. *Alvin* dives: 1949, 10 November 1987; 2138, 11 November 1988; 2333, 21 February 1991; 2334, 22 February 1991. Species: *Cocculina craigsmithi, Pyropelta corymba, P. musaica.*

Off Point Sur, California (36°17.6'N, 122°12.2'W), 940 m. R/V *David Starr Jordan*, trawl 48, January-February 1987. Species: *Cocculina craigsmithi, Pyropelta musaica, P. corymba, P. wakefieldi.*

Off Point Lobos, California (36°26.2'N, 122°15.8'N), 1,400 m. R/V *Cayuse*, sta. 6, May 1985. Species: *Pyropelta musaica.*

Monterey Bay, California (36°56.4'N, 122°37.9'W), 1,100 m. R/V *David Starr Jordan*, trawl 21, January-February 1987. Species: *Cocculina craigsmithi, Pyropelta musaica.*

Radulae were extracted from dried specimens after rehydration in detergent, followed by dissolution of tissues in 10% NaOH at room temperature for 48 hours. Radulae from preserved specimens were extracted after direct treatment in 10% NaOH. Radular ribbons were washed in distilled water, air dried and coated with gold or gold/palladium for examination with SEM.

Abbreviations of institutions mentioned in the text: CAS, California Academy of Sciences, San Francisco; LACM, Los Angeles County Museum of Natural History; USNM, National Museum of Natural History, Washington, D.C.

## SYSTEMATICS

### Superfamily Cocculinoidea
### Family Cocculinidae Dall, 1882
### Genus *Cocculina* Dall, 1882

*Type species* (subsequent designation of Dall, 1908): *C. rathbuni* Dall, 1882. Western Atlantic. Generic definitions of cocculinids were provided by Marshall (1986) based on radular characters and external anatomy, and by Haszprunar (1987) based on internal anatomy. *Cocculina rathbuni*, the type species of *Cocculina*, was treated by McLean (1987). Until now the genus has been represented in the northeastern Pacific by two species living on submerged logs described by McLean (1987): *C. cowani* and *C. baxteri*. A third species that is probably restricted to the whale-fall habitat is here added to the northeastern Pacific fauna.

### ***Cocculina craigsmithi*** new species
(Figs 1–8)

*Description:* Shell (Figs 1–3) relatively large for family (maximum length 10.7 mm), white with moderately thick, pale brown periostracum. Height low, that of holotype 0.30 times that of length. Anterior slope slightly convex; lateral slopes nearly straight, posterior slope slightly concave. Outline in dorsal view elongate-oval, anterior end slightly broader than posterior, margin of shell nearly in one plane. Apex slightly posterior to center, at highest point of shell. Protoconch unknown; apical area eroded in all specimens. Teleoconch sculpture of fine radial striae, slightly curved and faintly beaded on crossing concentric growth lines. Shell margin sharp, easily shipped. Interior white, muscle scar faintly indicated even in largest specimens, scar broken into bundles; anterior tips of scar continuous with pallial attachment scar; apical area thickened within to compensate for erosion of outer surface.

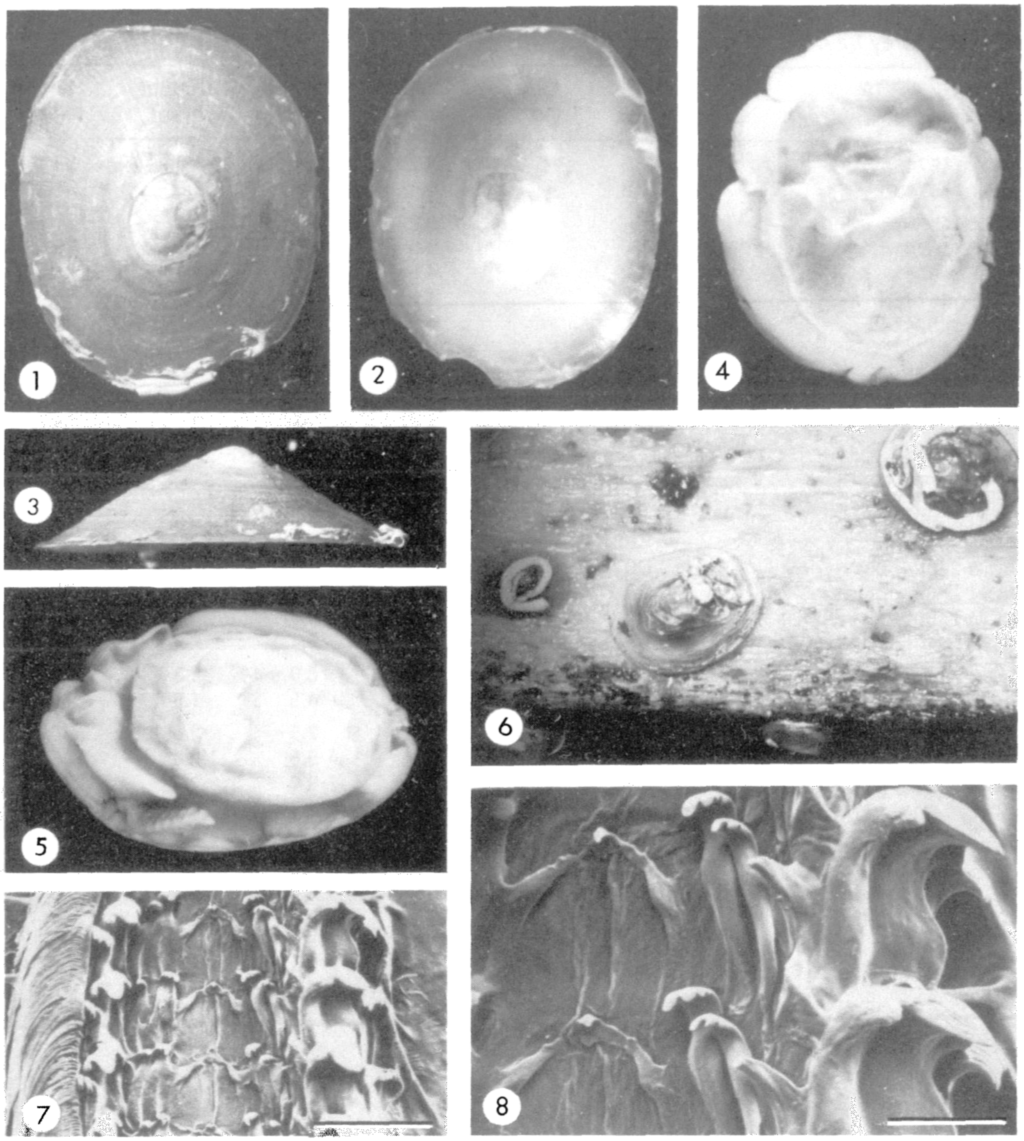
Dimensions: Length 8.6, width 6.9, height 2.6 mm (holotype); length 10.7, width 9.6, height 2.9 mm (largest paratype, LACM). See Table 1 for measurements of paratypes and other specimens.

External anatomy (Figs 4, 5): Hypobranchial gland lacking; pair of posterior epipodial tentacles present; oral lappets broad and projecting posteriorly, penis represented by posterior extension of right lappet; gill attached to neck above right oral lappet. The cephalic tentacles are relatively short in preserved material and do not show in the illustrations.

Radula (Figs 7, 8): Rachidian tooth poorly developed, represented by cusp outline that terminates in a small beaklike overhanging tip; tip subtended by two wrinkled ridges. First lateral tooth with curved shafts and up to five cusps on overhanging tip. Second lateral tooth shorter and straighter, with three cusps, innermost the largest. Third lateral tooth narrow, lacking cusp. Outer lateral tooth robust, with large primary cusp and smaller secondary cusps on inner and outer sides.

*Type locality*: On whale bone from 1,240 m in Santa Catalina Basin between Santa Catalina Island and San Clemente Island, California (33°12.0'N, 118°30.0'W).

*Type material* (Table 1): 23 specimens from the type locality, collected with deep-submersible *Alvin* on four dives, received from Craig Randall Smith. Holotype, LACM 2459 and 7 paratypes, dive 1949, 10 November 1987; 2 paratypes LACM 2461, dive 2138, 11 November 1988; 5 paratypes LACM 2391, dive 2333; 21 February 1991; 8 paratypes LACM 2392, dive 2334, 22 February 1991.



**Figures 1–8.** *Cocculina craigsmithi* new species. All from type locality, the Catalina Basin whale-fall. Anterior at top in vertical views. **1–3.** Holotype, LACM 2459, exterior, interior, and left lateral views. Length 8.6 mm. **4.** Dorsal view of holotype body, showing transparent mantle skirt over head, lacking hypobranchial gland. Length 6.2 mm. **5.** Right-ventral view of holotype body showing elongation of right oral lappet to serve as copulatory organ, pinnate gill exposed in mantle groove, and posterior pair of epipodial tentacles. **6.** In-situ photograph of limpets on whale bone, showing eroded surfaces of shell and attached serpulid worm tubes (C.R. Smith photo). Horizontal length of field ca. 50 mm. **7.** LACM 2460b, paratype, full width of radula ribbon, marginal teeth stripped away on right side. Scale bar = 100 μm. **8.** Same specimen, half-row of radular ribbon, rachidian at left, outer lateral tooth at right. Scale bar = 40 μm.

The holotype was selected as the specimen that best preserves the original exterior sculpture, although other specimens in the type lot are larger than the holotype. Many of the specimens are deeply eroded; in some specimens the shell erosion extends under the periostracum. Shells of most specimens also serve as an attachment substrate for an unidentified serpulid

**Table 1.** Localities (north to south) and measurements for *Cocculina craigsmithi.* CB = Catalina Basin; MB = Monterey Bay; PS = Point Sur.

| Museum catalog no. | Site | Dive no. | Length (mm) | Width (mm) | Height (mm) | Height/ length |
|---|---|---|---|---|---|---|
| LACM 145743a | MB | – | 9.2 | 7.1 | 3.0 | .33 |
| LACM 145743b | MB | – | 8.4 | 6.8 | 2.6 | .31 |
| LACM 145741a | PS | – | 9.2 | 6.4 | 2.8 | .30 |
| LACM 145741b | PS | – | 9.0 | 6.6 | 2.6 | .29 |
| LACM 145741c | PS | – | 4.6 | 3.5 | 1.1 | .24 |
| LACM 145741d | PS | – | 4.6 | 3.2 | 1.2 | .26 |
| LACM 145741e | PS | – | 4.2 | 3.5 | 1.1 | .26 |
| LACM 145741f | PS | – | 3.8 | 2.9 | 1.0 | .26 |
| LACM 145741g | PS | – | 3.6 | 2.9 | 1.0 | .28 |
| LACM 145741h | PS | – | 3.0 | 2.3 | 0.9 | .30 |
| LACM 145741i | PS | – | 2.1 | 1.5 | 0.7 | .33 |
| LACM 2459, holotype | CB | 1949 | 8.6 | 6.9 | 2.6 | .30 |
| LACM 2460a, paratype | CB | 1949 | 10.7 | 9.6 | 2.9 | .27 |
| LACM 2460b, paratype (radula) | CB | 1949 | 9.5* | 7.9 | 3.0 | .32 |
| LACM 2460c, paratype | CB | 1949 | 10.1 | 8.1 | 3.3 | .33 |
| LACM 2460d, paratype | CB | 1949 | 8.9 | 6.8 | 2.6 | .29 |
| LACM 2460e, paratype | CB | 1949 | 8.1 | 6.2 | 2.3 | .28 |
| LACM 2460f, paratype | CB | 1949 | 8.0 | 6.5* | 2.3 | .29 |
| LACM 2460g, paratype | CB | 1949 | 7.7 | 6.4 | 2.2 | .29 |
| LACM 2461a, paratype | CB | 2138 | 7.8 | 6.0 | 2.3 | .29 |
| LACM 2461b, paratype | CB | 2138 | 6.0 | 4.6 | 1.8 | .30 |
| LACM 2391a, paratype | CB | 2333 | 9.5 | 7.5 | 2.8 | .29 |
| LACM 2391b, paratype | CB | 2333 | 7.2 | 5.5 | 2.0 | .27 |
| LACM 2391c, paratype | CB | 2333 | 5.1 | 3.0 | 2.2 | .43 |
| LACM 2391d, paratype | CB | 2333 | 4.1 | 3.2 | 1.0 | .24 |
| LACM 2391e, paratype | CB | 2333 | 3.6 | 2.2 | 1.6 | .44 |
| LACM 2392a, paratype | CB | 2334 | 9.7 | 7.4 | 3.4 | .35 |
| LACM 2392b, paratype | CB | 2334 | 7.9 | 6.2 | 2.0 | .25 |
| LACM 2392c, paratype | CB | 2334 | 7.2 | 5.8 | 2.1 | .29 |
| LACM 2392d, paratype | CB | 2334 | 7.1 | 5.8 | 2.2 | .31 |
| LACM 2392e, paratype | CB | 2334 | 6.4 | 5.1 | 1.8 | .28 |
| LACM 2392f, paratype | CB | 2334 | 6.0 | 4.7 | 1.5 | .25 |
| LACM 2392a, paratype | CB | 2334 | 4.8 | 3.8 | 1.3 | .27 |
| LACM 2392a, paratype | CB | 2334 | 3.1 | 2.3 | 0.8 | .26 |

* Shell edge damaged, measurement estimated.

worm, which seems not to attach directly to the whale bone (Fig. 6).

*Referred material* (Table 1): LACM 145743, 2 specimens on Monterey Bay whale-fall; LACM 145741, 9 specimens on Point Sur whale-fall.

*Remarks: Cocculina craigsmithi* has a combination of shell and radular characters unlike that of other known eastern Pacific species of *Cocculina.* As in *C. cowani* McLean, 1987, and *C. baxteri* McLean, 1987, the rachidian is weakly defined, but unlike those species, the upper edge of the tooth has a distinctly defined cusp. In this respect it is more comparable to the Caribbean type species, *C. rathbuni.* Its profile is lower than that of either *C. cowani* or *C. baxteri.* It has curving radial sculpture similar to that of *C. cowani*, but lacks the prominent hypobranchial gland of that species illustrated by McLean (1987: fig. 13).

The erosional pattern is similar to that typical of other Cocculinidae, Pseudococculinidae and Pyropeltidae. The limpets apparently are mobile on the substrate, as no depressions or home scars made by the limpets are evident in a photograph supplied by C.R. Smith (Fig. 6).

This is the first member of Cocculinidae to be reported to live on whale bone. Except for the cocculinid *Teuthirostra cancellata* Moskalev, 1976, which lives on chitinous beaks of cephalopods, other members of Cocculinidae live on decaying wood.

The fact that the present species is quite typical for the genus *Cocculina* in characters of shell, radula, and external anatomy is unexpected, considering that adaptation to substrates other than wood is so infrequent in the Cocculinidae.

*Etymology*: The name honours Craig R. Smith, the principal investigator of the whale-fall site in the Santa Catalina Basin.

Superfamily Lepetelloidea
Family Pyropeltidae McLean & Haszprunar, 1987

Details about the internal anatomy and the systematic position of the Pyropeltidae were given by McLean & Haszprunar (1987) and Haszprunar (1988b) and are not repeated here.

Genus ***Pyropelta*** McLean & Haszpunar, 1987

*Type species: P. musaica* McLean & Haszprunar, 1987. Hydrothermal vents of Axial Seamount on Juan de Fuca Ridge off Washington, 1,575 m.

*Revised diagnosis*: Shell outline oval to nearly circular, strongly elevated to low in profile. Apex at highest elevation of shell. Protoconch unknown (all specimens eroded). Sculpture of fine concentric ridges where retained, but most specimens partially to completely eroded, showing varying pattern of wavily etched lines. Shell interior thickened on inner side; muscle scar horseshoe-shaped, with inwardly directed hook-shaped processes.

External anatomy: Lappets lacking, cephalic tentacles of similar size, gill tips prominent on right side, visible attached to mantle skirt above head in ventral view. Right cephalic tentacle serving as copulatory organ, seminal groove open.

Radula: Rachidian tooth with broad basal portion of shaft, upper area of shaft lacking or rudimentary. First lateral tooth broad, extending behind rachidian, outer edge with strong elbow, upper portion of shaft tapered, overhanging tip long to short. Second and third lateral teeth similar, each with pronounced elbow on outer side and deeply grooved inner arm of shaft for accommodation of adjacent tooth; cutting area long, usually serrated, tip rounded or acute. Fourth lateral tooth unlike first three, outer edge of shaft curved rather than elbowed, overhanging tip well developed, both edges usually serrate. Fifth lateral similar to fourth. Marginals numerous, not separated at base, gradually decreasing in size toward outer edge of ribbon.

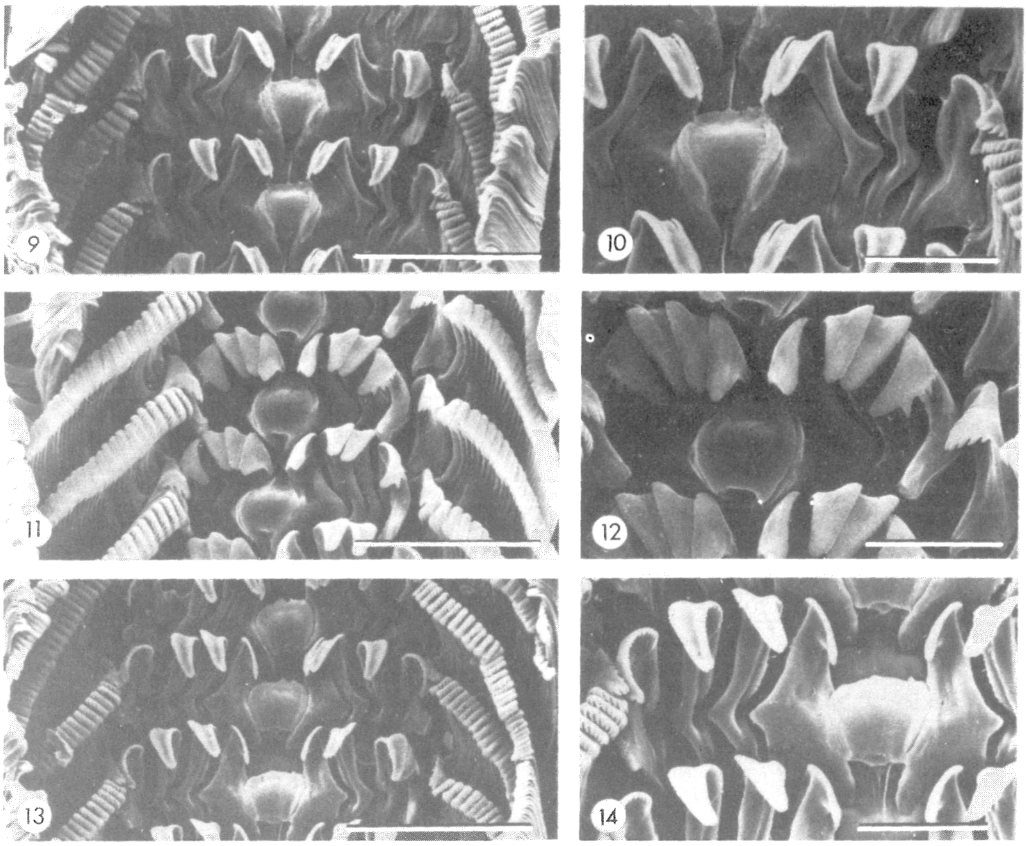
*Remarks: Pyropelta* was based on two species, the type species *P. musaica* from Axial Seamount on the Juan de Fuca Ridge (depth 1,575 m) and *P. corymba* from hydrothermal vents at the Guaymas Basin (depth 2,022 m). Although there were numerous original specimens of the type species, there was only a single specimen of *P. corymba*, the soft parts of which were sectioned, confirming that the anatomy agreed with that of the type species. Consequently, the radula of *P. corymba* was not available for SEM examination and the radular description for the genus was based solely on that of the type species. Fortunately, a second specimen of *P. corymba* from the type locality was recovered on a return expedition to the Guaymas Basin and the radula of this topotypic specimen is figured herein (Figs 23, 24). A third species, *P. wakefieldi*, is described herein.

The original generic description given by McLean & Haszprunar (1987) lacked information about the surface sculpture and the radular description was based solely on that of the type species. The above diagnoses have been modified in order to include new information derived from the three species now known. All specimens reported by Haszprunar & McLean lacked the original surface layer of the shell, but this is now revealed in specimens of the new species *Pyropelta wakefieldi*. The revised radular diagnosis given here is based on the essential characters shared by the three species now known. The protoconch remains unknown.

Radular morphologies of the three species are very different. Radular characters, particularly the morphology of the rachidian tooth, therefore provide the most reliable means for determination of species. Each of the three species may be recognized by its morphologically distinct rachidian tooth.

There are some differences among the species in shell proportions, although surface appearance is similar in its eroded, irregular pattern of concentric lines. Gill differences noted by McLean & Haszprunar (1987) are also important, but the new species described herein can not be compared for lack of preserved material.

Much to my surprise, radular evidence now indicates that both of the two original species,




**Figures 9–14.** *Pyropelta musaica* McLean & Haszprunar, 1987. SEM views of radulae from widely separated whale-fall and hydrothermal sites. **9, 10.** LACM 2276, paratype from type locality, Axial Seamount on Juan de Fuca Ridge. Scale bar for 9 = 50 μm, for 10 = 20 μm. **11, 12.** CAS 066894b, Point Lobos whale-fall. Scale bar for 11 = 50 μm, for 12 = 20 μm. **13, 14.** LACM 146910a, Catalina Basin whale-fall. Scale bar for 13 = 50 μm, for 14 = 20 μm.

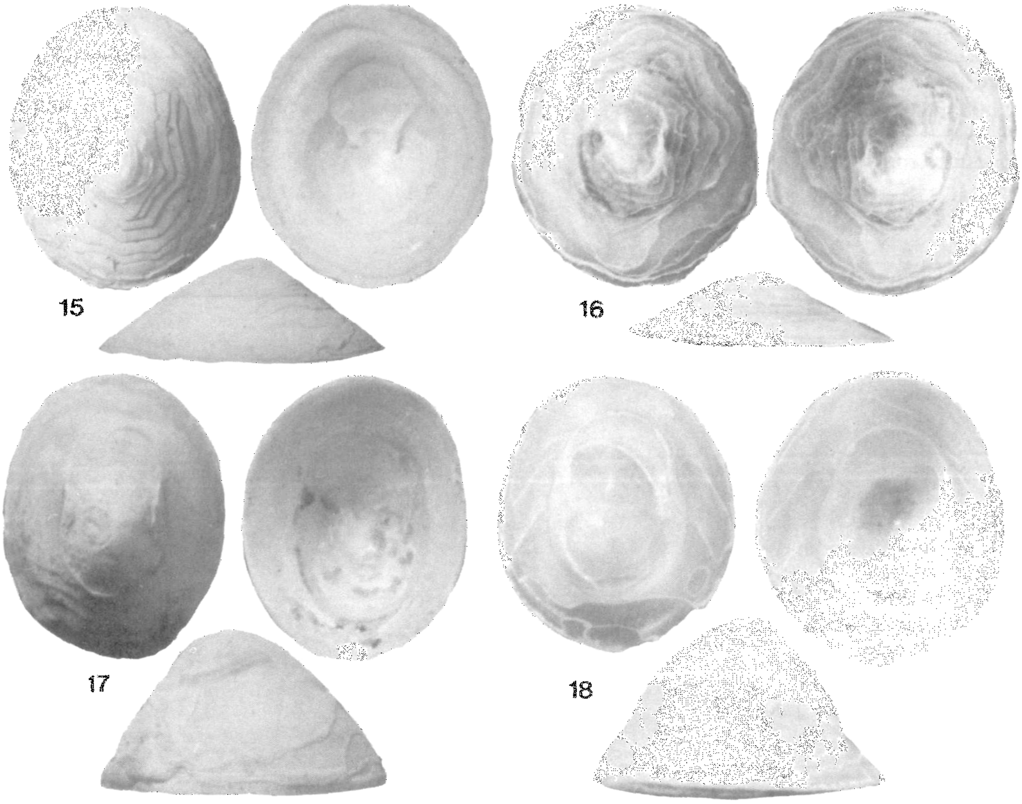
*P. musaica* and *P. corymba*, also occur on whale-falls off the coast of central and southern California. The new species described here is known only from one of the whale-falls off central California.

***Pyropelta musaica*** McLean & Haszprunar, 1987
(Figs 9–16)

*Pyropelta musaica* McLean & Haszprunar, 1987:198, figs 1–8, 9A. Type locality: hydrothermal vents at Axial Seamount, Juan de Fuca Ridge, off Washington (45°59.5′N, 130°03.5′W), 1575 m, *Pisces* IV dive 1733. Holotype: LACM 2275. Numerous additional paratypes were reported from other vents on Axial Seamount by McLean & Haszprunar (1987).

*New records* (Table 2): LACM 145744, 1 specimen on Monterey Bay whale-fall; CAS 066894, 2 specimens on Point Lobos whale-fall (one specimen with shell in fragments used for radular SEM, Figs 11, 12; one preserved specimen remains intact); LACM 146907, 2 specimens on Point Sur whale-fall; LACM 146908, 2 specimens on Catalina Basin whale-fall, *Alvin* dive 2138; LACM 146909, 5 specimens on Catalina Basin whale-fall, *Alvin* dive 2333; LACM 146910, 4 specimens on Catalina Basin whale-fall, *Alvin* dive 2334 (one specimen used for radular SEM, Figs 13, 14).

*Description*: Shell (Figs 15, 16) elongate-oval and moderately elevated. Apex at highest elevation of shell. Protoconch and exterior sculpture eroded, surface showing irregular




**Figures 15–18.** Shells of two previously described species of *Pyropelta*. Exterior, interior and left lateral views, anterior at top in exterior and interior views. **15, 16.** *Pyropelta musaica* McLean & Haszprunar, 1987. **15.** CAS 066894a, Point Lobos whale-fall, length 4.5 mm. **16.** LACM 146910a, Catalina Basin whale-fall, length 3.7 mm. 17, 18. *Pyropelta corymba* McLean & Haszprunar, 1987. **17.** LACM 145742a, Point Sur whale-fall, length 2.6 mm. **18.** LACM 145740a, Catalina Basin whale-fall, length 2.8 mm.

pattern of unevenly etched lines. Shell interior thickened on inner side; muscle scar horseshoe-shaped, with inwardly directed hook-shaped processes.

Dimensions: See Table 2.

External anatomy: Lappets lacking, cephalic tentacles of similar size, gill tips prominent on right side, visible on mantle skirt above head in ventral view.

Radula (Figs 9–14): Rachidian tooth broad, with rounded lateral extremities; base truncate, anchored with lateral prongs; upper portion of shaft of rachidian seeming to emerge behind broad basal plate; overhanging tip rudimentary or lacking. Shaft and base of first lateral tooth broad, extending behind rachidian, inner edge excavated to accommodate base of rachidian, outer edge with strong elbow, overhanging tip relatively long. Second and third lateral teeth similar, each with pronounced elbow on outer side and deeply grooved inner arm of shaft for accommodation of adjacent tooth; cutting area long, serrate, tip rounded. Fourth lateral tooth unlike first three, outer edge of shaft curved, inner edge of overhanging tip finally serrate, outer edge with about five strong, deeply cut serrations, those near tip the largest. Fifth lateral tooth similar to fourth in having broad shaft and undulating cutting edge, its tip with strong serrations. Marginals numerous, not separated at base, gradually decreasing in size.

*Remarks: Pyropelta musaica*, which has heretofore been known only from Axial Seamount on the Juan de Fuca Ridge, is recognized in the California whale-fall habitat on the basis of

**Table 2.** Localities (north to south) and measurements for three species of *Pyropelta*. AS = Axial Seamount; CB = Catalina Basin; GB = Guaymas Basin; MB = Monterey Bay; PL = Point Lobos; PS = Point Sur.

| Museum catalog no. | Site | Dive no. | Length (mm) | Width (mm) | Height (mm) | Height/ length |
|---|---|---|---|---|---|---|
| *Pyropelta musaica* | | | | | | |
| LACM 2275, holotype | AS | 1733 | 3.0 | 2.7 | 1.0 | .33 |
| LACM 2276, paratype (radula) | AS | 1733 | 3.0 | 2.3 | 1.4 | .46 |
| LACM 145744 | MB | – | 3.6 | 3.1 | 1.7 | .47 |
| CAS 066894a | PL | – | 4.5 | 3.7 | 1.6 | .35 |
| CAS 066894b (radula) | PL | – | – | – | – | – |
| LACM 146907a | PS | – | 2.4 | 2.1 | 0.9 | .38 |
| LACM 146907b | PS | – | 2.2 | 1.9 | 0.8 | .36 |
| LACM 146908a | CB | 2138 | 2.8* | 2.5 | 1.0 | .36 |
| LACM 147908b | CB | 2138 | 2.6 | 2.3 | 0.9 | .35 |
| LACM 146909a | CB | 2333 | 3.7 | 3.4 | 1.1 | .30 |
| LACM 146909b | CB | 2333 | 3.6 | 3.2 | 1.1 | .31 |
| LACM 146909c | CB | 2333 | 3.1 | 2.9 | 0.8 | .26 |
| LACM 146909d | CB | 2333 | 2.9 | 2.5 | 0.7 | .24 |
| LACM 146909e | CB | 2333 | 2.7 | 2.5 | 0.9 | .33 |
| LACM 146910a (radula) | CB | 2334 | 3.7 | 3.3 | 1.1 | .30 |
| LACM 146910b | CB | 2334 | 3.5 | 3.1 | 1.0 | .29 |
| LACM 146910c | CB | 2334 | 3.3 | 2.9 | 1.0 | .30 |
| LACM 146910d | CB | 2334 | 2.9 | 2.6 | 0.9 | .31 |
| *Pyropelta corymba* | | | | | | |
| LACM 145742a (radula) | PS | – | 2.6 | 2.1 | 1.6 | .62 |
| LACM 145742b | PS | – | 2.8 | 2.3 | 1.7 | .61 |
| LACM 145742d | PS | – | 2.5 | 2.1 | 1.3 | .52 |
| LACM 145742c | PS | – | 2.3 | 1.8 | 1.4 | .61 |
| LACM 145742e | PS | – | 1.8 | 1.4 | 0.9 | .50 |
| LACM 145740a (radula) | CB | 2138 | 2.8 | 2.0 | 1.6 | .57 |
| LACM 145740b | CB | 2138 | 2.2 | 1.7 | 1.4 | .64 |
| LACM 145740c | CB | 2138 | 2.0 | 1.7 | 1.2 | .60 |
| LACM 145740d | CB | 2138 | 2.0 | 1.7 | 1.1 | .55 |
| LACM 146911a | CB | 2333 | 2.9 | 2.5 | 1.7 | .58 |
| LACM 146911b | CB | 2333 | 2.8 | 2.4 | 1.8 | .64 |
| LACM 146911c | CB | 2333 | 2.8 | 2.4 | 1.8 | .64 |
| LACM 146911d | CB | 2333 | 2.7 | 2.3 | 1.6 | .59 |
| LACM 146911e | CB | 2333 | 2.7 | 2.2 | 1.5 | .55 |
| LACM 146911f | CB | 2333 | 2.5 | 2.1 | 1.5 | .60 |
| LACM 146911g | CB | 2333 | 2.3 | 2.0 | 1.6 | .69 |
| LACM 146911h | CB | 2333 | 2.3 | 2.0 | 1.3 | .56 |
| LACM 2277, holotype | GB | 1176 | 3.0 | 2.5 | 2.5 | .83 |
| LACM 145745 (radula) | GB | 1614 | 2.7 | 2.2 | 1.9 | .70 |
| *Pyropelta wakefieldi* | | | | | | |
| LACM 2462, holotype (radula) | PS | – | 5.1 | 4.8 | 1.6 | .31 |
| LACM 2463a, paratype | PS | – | 6.1 | 5.5 | 1.7 | .28 |
| LACM 2463b, paratype | PS | – | 6.0 | 5.5* | 1.7* | .28 |
| LACM 2463c, paratype | PS | – | 4.7 | 4.2 | 1.7 | .36 |
| LACM 2463d, paratype | PS | – | 4.1 | 3.9 | 1.3 | .32 |
| LACM 2463e, paratype | PS | – | 4.2 | 3.9 | 1.6 | .38 |
| LACM 2463f, paratype | PS | – | 3.5 | 3.1 | 1.0 | .29 |
| LACM 2463f, paratype | PS | – | 2.9 | 2.6 | 1.0 | .34 |

* Shell edge damaged, measurement estimated.

radular characters. The morphology of the broad basal portion of the shaft and the way that it abuts the shafts of the innermost pair of laterals is highly characteristic and unique. These features are remarkably similar in the radula of typical specimens from the Juan de Fuca Ridge (Figs 9, 10) and whale-fall specimens from Point Lobos (Figs 11, 12) and the Catalina Basin (Figs 13, 14). The original description referred to a small overhanging tip on the rachidian (see McLean & Haszprunar, 1987: fig. 3), but I now consider that to be either an artifact or so rudimentary that it is insignificant. The radular description given above is based on a new interpretation of radular morphology and replaces that given in the original description.

Specimens from the Point Lobos whale-fall attain 4.5 mm in length, larger than the 3.0 maximum length of typical specimens from Axial Seamount. The outline of *P. musaica* is more oval than that of the new species *P. wakefieldi*. The specimen from the Monterey Bay whale-fall is identified as this species on the basis of shell proportions; it has the oval outline and it is too large for *P. corymba* and has a higher profile than specimens of *P. wakefieldi*.

Although *Pyropelta musaica* was abundantly represented from Axial Seamount on the Juan de Fuca Ridge, it was not among the limpets recently collected from the Escanaba Trough on the Gorda Ridge, from which limpets of the families Neolepetopsidae and Pseudococculinidae have recently been described (McLean, 1990, 1991).

### ***Pyropelta corymba*** McLean & Haszprunar, 1987 (Figs 17–24)

*Pyropelta corymba* McLean & Haszprunar, 1987:200, figs 9b, 10, 11. Type locality: Hydrothermal vents, Southern Trough, Guaymas Basin, Gulf of California (27°01.0′N, 111°25.0′W), 2,022 m, *Alvin* dive 1176, 19 January 1982. Holotype: LACM 2277.

*New records* (Table 2): LACM 145742, 5 specimens on Point Sur whale-fall (dried body of one specimen rehydrated and used for radular SEM, Figs 19, 20); LACM 145740, 4 specimens on Catalina basin whale-fall, *Alvin* dive 2138 (body of one specimen used for radular SEM, Figs 21, 22); LACM 146911, 8 specimens on Catalina Basin whale-fall, *Alvin* dive 2333; LACM 145745, 1 specimen, Guaymas Basin hydrothermal vents (27°00.7′N, 111°24.4′W), 2,004 m, *Alvin* dive 1614, 6 August 1985 (body used for radular SEM, Figs 23, 24).

*Description*: Shell (Figs 17, 18) moderately elevated, basal outline oval. Apex at highest elevation of shell. Protoconch and exterior sculpture eroded, showing irregular pattern of unevenly etched lines. Shell interior thickened on inner side; muscle scar horseshoe-shaped, with inwardly directed hook-shaped processes.

Dimensions: See Table 2.

External anatomy: Lappets lacking, cephalic tentacles of similar size, gill tips prominent on right side, visible on mantle skirt above head in ventral view.

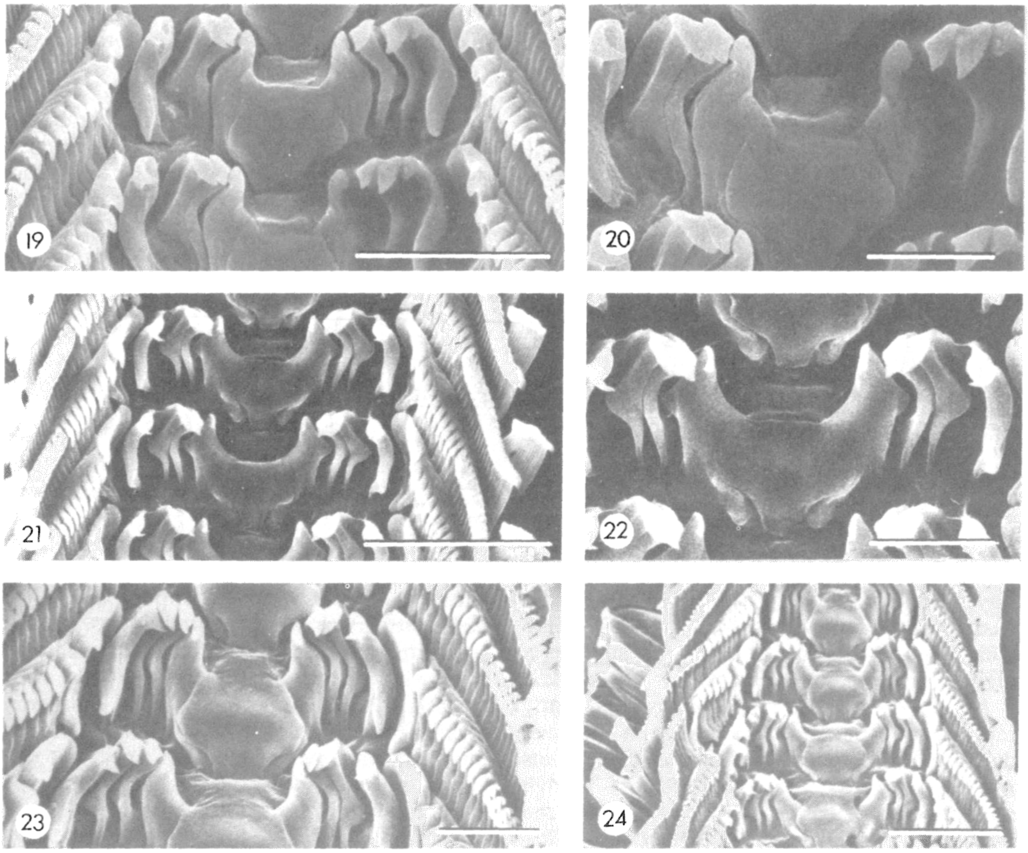
Radula (Figs 19–24): Rachidian tooth broad, with rounded lateral extremities, truncate at upper portion of shaft, basal portion narrowing and seeming to emerge straight across. Shaft of first lateral tooth broad, inner edges extending behind rachidian, concealing most of base, outer edge broadly curved, upper extension of shaft with blunt, weakly hooked tip. Second and third lateral teeth with narrow shaft, outer edge with strong elbow at mid-length, overhanging tips acutely tapered, of moderate length. Fourth lateral tooth standing apart from third and fifth, curved on both sides, not with elbow on outer edge, overhanging tip narrow and curved to point inwardly. Fifth lateral similar to fourth in having broad shaft and undulating cutting edge, its tip acutely pointed. Marginals numerous, not separated at base, gradually decreasing in size toward edge of ribbon.

*Remarks*: The radula of *P. corymba* differs from that of *P. musaica* in major ways: the basal portion of the rachidian tooth is broader and its upper edge is sharply truncate. The overhanging tips of the first three lateral teeth have smooth edges on both sides and the tip is acutely pointed, rather than long with round tips and serrations on both edges.

There are no essential differences among the examined radulae from the three widely separate localities, including the type locality at the Guaymas Basin, and the whale-falls at the Santa Catalina Basin and off Point Sur.

The holotype of *P. corymba* has a relatively high profile (length 3.0 mm, height 2.5 mm), which led to the original assumption that the species may have a higher shell profile than that of *P. musaica*. That assumption is here confirmed. Specimens of *P. corymba* from the whale-falls also are relatively high in profile.

As indicated in Table 2, specimens of high




**Figures 19–24.** *Pyropelta corymba* McLean & Haszprunar, 1987. SEM views of radulae from widely separated whale-fall and hydrothermal sites. **19, 20.** LACM 145742a, Point Sur whale-fall. Scale bar for 19 = 50 μm, for 20 = 20 μm. **21, 22.** LACM 145740a, Catalina Basin whale-fall. Scale bar for 21 = 50 μm, for 22 = 20 μm. **23, 24.** LACM 145745, Guaymas Basin hydrothermal vents. Scale bar for 23 = 20 μm, for 24 = 40 μm.

profile with a height to length ratio of .50 to .83 are identified as *P. corymba*, whereas those with a low profile with a height to length ratio of .47 to .24 are identified as *P. musaica*. There may, in fact, be some overlap in shell height profile between the two species, but the matter is not further explored.

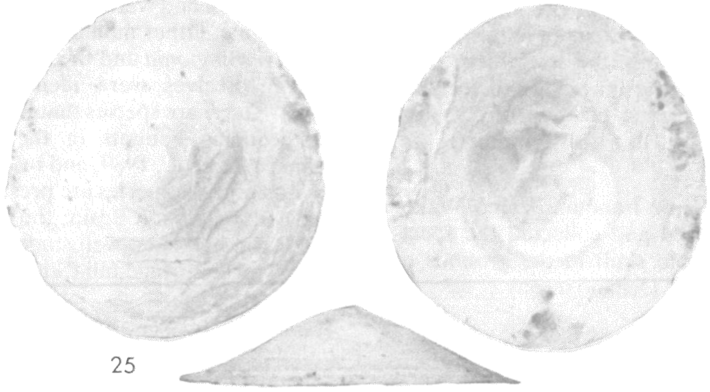
### *Pyropelta wakefieldi* new species
(Figs 25–27)

*Description*: Shell (Figs 25) large for genus (maximum length 6.1 mm), low in profile, nearly circular in outline. Apex at highest elevation of shell. Protoconch unknown. Periostracum thin, light brown where present at margin. Exterior sculpture of closely spaced concentric ridges retained at margin in some specimens; most of shell surface eroded and showing irregular pattern of unevenly etched lines. Shell interior thickened on inner side; muscle scar horseshoe-shaped, with inwardly directed hook-shaped processes.

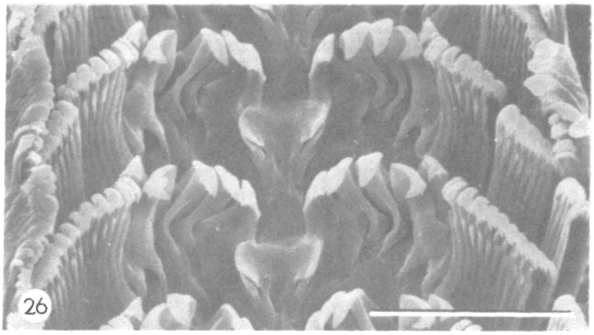
Dimensions: Length 5.1, width 4.8, height 1.6 mm (holotype). For measurements of paratypes see Table 2.

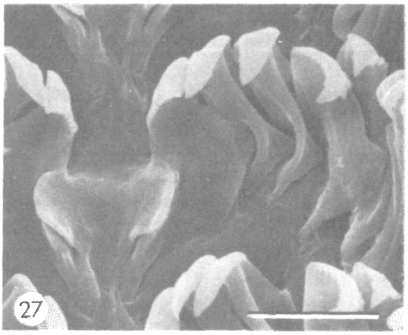
External anatomy unavailable (bodies desiccated).

Radula (Figs 25, 27): Rachidian tooth broad, with rounded lateral extremities, upper portion of shaft merging with ribbon base, lower edge also merging. Shaft of first lateral tooth broad, inner edges extending behind rachidian, except at uppermost junction with rachidian, where it appears to be fused with edge of rachidian; basal area of first lateral broadly exposed, outer



25





**Figures 25–27.** *Pyropelta wakefieldi* new species. Holotype, LACM 2462, from type locality, the Point Sur whale-fall. **25.** Exterior, interior, and left lateral views of shell. Note whale fat residue at margins and traces of original sculpture at 4 o'clock position on exterior view. Length 5.1 mm. **26.** Full width of radular ribbon. Scale bar = 50 μm. **27.** Half-row of radular ribbon, rachidian at left. Scale bar = 20 μm.

edge elbowed, overhanging tip acutely pointed, inner edge of tip strongly serrate. Second and third lateral teeth with narrow shaft, outer edge with strong elbow at mid-length, inner edges deeply excavated to receive elbow of adjacent teeth, overhanging tips of moderate length, acutely pointed, edges not serrate. Overhanging tips and outwardly projecting elbows of first four laterals higher than broadest extremity of rachidian, giving cusp rows a prominent dip toward the rachidian. Fourth lateral tooth standing apart from third and fifth, curved on both sides, with elbow on outer edge, overhanging tip narrow and curved to point inwardly, both edges strongly serrate. Fifth lateral tooth displaced behind fourth, with narrower shaft, overhanging tip acutely pointed, serrate on both edges. Marginals numerous, not separated at base, gradually decreasing in size toward edge of ribbon.

*Type locality*: On whale bone off Point Sur, California (36°17.6′N, 122°12.2′W), 940 m.

*Type material* (Table 2): 8 specimens from whale skull trawled by R/V *David Star Jordan*, trawl 48, January-February, 1987. Received from Waldo Wakefield, who removed specimens from whale skull left to dry on grounds of Scripps Institution of Oceanography early in 1989. Holotype, LACM 24652; 7 paratypes LACM 2463.

*Remarks: Pyropelta wakefieldi* is characterized by its relatively large size, low profile, nearly circular outline and unique radula. The maximum shell length is 6.1 mm, compared to the maximum of 4.5 recorded here for *P. musaica*. This is also the only species for which original exterior sculpture is retained near the margin in some specimens. The rachidian is relatively short in its vertical dimension. This is the only species in which the elbow of the lateral teeth and the cusp tips rise and then fall on successive teeth moving out from the rachidian. The strong serrations on the inner side of the first lateral and the displaced position of the fifth lateral behind the fourth are also unique.

*Etymology*: The name honours Waldo Wakefield, who discovered and collected the specimens from the whale skull in the grounds of Scripps Institution of Oceanography.

## DISCUSSION

Cocculiniform limpets live on a variety of biogenic substrates, including wood, other plant remains, cephalopod beaks, egg cases of sharks and skates, fish bone, and whale bone (Moskalev, 1976; Hickman, 1983; Marshall, 1983, 1986, 1987; McLean, 1985, 1987, 1988; Haszprunar, 1988b). The use of whale bone by cocculiniform limpets was first reported by Marshall (1987), who proposed the family Osteopeltidae for *Osteopelta mirabilis* Marshall, 1987, from 880 m on the Chatham Rise off New Zealand. Warén (1989) described an additional species of *Osteopelta* from southwestern Iceland, depth unknown. The anatomy of *Osteopelta* has been treated by Haszprunar (1988a). Considering the broad distribution of *Osteopelta*, it is noteworthy that no record of that genus is known from the whale-fall habitat in the northeastern Pacific.

The addition of species of *Cocculina* and *Pyropelta* to the whale-bone habitat brings the number of genera making use of this habitat to three, although *Osteopelta* remains the only genus unknown on other biogenic substrates. Each genus has similarly proportioned shells, but radulae and anatomies are sufficiently different to place them in different families.

Following its discovery in November, 1987, the biological community associated with the Santa Catalina Basin whale-fall has been visited in subsequent years and subjected to intensive study (Smith *et al.*, 1989; Allison *et al.*, 1991). As reported by these authors, many of the partially buried bones were covered with microbial mats (*Beggiatoa* sp.). Recovered bones were impregnated with whale oil and smelled of hydrogen sulfide. The bacterial mats were considered to be supported by the chemical reducing power of bone oil seepage.

Vesicomyid clams (*Vesicomya gigas* and *Calyptogena pacifica*) were nestled in crevices on the skeleton and were living in the surrounding sediments. Other mollusks were the mytilid *Idasola washingtonia* and the lucinid *Lucinoma annulata* (bivalves were identified by R.D. Turner). These are species that are known from other reducing habitats in the northeastern Pacific (Smith *et al.*, 1989, and references therein). None of these species are present elsewhere in the Santa Catalina Basin; the benthic fauna of the Basin had been well studied prior to the discovery of the whale fall (Smith & Hamilton, 1983; Smith, 1986).

Smith *et al.* (1989) considered it 'not surprising that a whale carcass on the energy-poor deep-sea floor should produce a community with ecological and taxonomic similarities to other deep-sea reducing habitats. Microbial degradation of organic-rich whale remains appears certain to yield sulphide from sulphate reduction and putrefaction. The consequent occurrence of sulphides with a nearby source of oxygen (in bottom water) should provide a habitat analogous to seeps and vents in its suitability for sulphide-oxidizing bacteria and their metazoan hosts.'

The genus *Pyropelta* joins such genera as *Calyptogena* in being present in reducing habitats other than hydrothermal vents. It has not been found at cold-seep habitats, but its discovery at such sites would not be unexpected. Unlike most of the bivalves of reducing environments, there is no evidence that *Pyropelta* supports chemoautotrophic symbionts. The only vent-associated gastropod known to harbor chemosynthetic symbionts is *Alvinoconcha hessleri* as reported by Stein *et al.* (1988). Vent limpets of various families have been assayed for chemoautotrophic symbionts but none have been detected (J.L. Stein, pers. comm.).

Four cocculiniform families are now known to be represented in strong sulfide-reducing habitats in the deep sea: the family Osteopeltidae, known only from the whale-fall habitat; the family Pyropeltidae, in which the three known species are obligate members of either the whale-fall habitat or the hydrothermal habitat (two of the three species are known from both habitats); the family Pseudococculinidae (usually occurring on decaying wood), represented by *Amphiplica (Gordabyssia) gordensis*, described by McLean (1991) from hydrothermal vents of the Gorda Ridge; and the family Cocculinidae, reported here in the whale-fall habitat with the description of *Cocculina craigsmithi*. These strong reducing habitats are more extreme extensions of the reducing habitats provided by the biogenic substrates utilized by other families of cocculiniform limpets.

Sulfide is a component in the decay of all biogenic substrates, so it is logical that three cocculiniform limpet families have made inroads into stronger reducing habitats in the deep-sea. Marshall (1987) supposed that all cocculiniform limpets feed on bacteria that are associated with their biogenic substrates, rather than directly on the substrate. It is likely that the limpets feed on the free-living bacteria that are present in both habitats. Although Marshall (1987) noted that *Osteopelta* was concentrated on areas of the whale bone that exude the most oil, this may also be the site of strongest bacterial growth. No home scars were noted by Marshall, nor do any of the limpets treated here produce home scars, another indication that the limpets are not feeding directly on whale bone or whale oil.

*Pyropelta* species have been collected from all four whale-falls recorded here, one of which, off Point Sur, had all three species present (Table 2). Colonization by a particular species is evidently a chance happening dependent on time and bottom currents. Like submerged logs, whale falls represent 'islands' of suitable substrate (Turner, 1978) that over time will be colonized by an increasing number of species. The colonization of the Santa Catalina Basin whale fall by *Pyropelta* may have taken place in the year after the first visit of *Alvin*, as it was not recorded from the first visit, although its absence could have been due to small sample size.

Smith *et al.* (1989) estimated the frequency of whale falls in the northeastern Pacific, arriving at figures on the order of 500 per year, one per 300 $km^2$, spaced at 9 km. They hypothesized that whale skeletons might serve as 'stepping stones' for the dispersal of animals that depend on chemosynthesis. Tunnicliffe & Juniper (1990) noted that the truly endemic vent animals are not present at whale-fall sites, although they did not mention the unique case of *Pyropelta*. The significance of the whale-fall habitat in the dispersal of the majority of vent animals remains to be demonstrated, although it is certain that the habitat has been present throughout the Cenozoic and to some extent in the Mesozoic. Squires *et al.* (1991), reported Oligocene deposits containing whale bone from the north shore of the Olympic Peninsula, Washington, noting the presence of bivalve mollusks known from sulfide reducing habitats and made the comparison with the results from the Catalina Basin whale-fall. Martill *et al.* (1991) suggested that other large marine vertebrates of the Mesozoic would have filled the same role in providing habitats for invertebrates dependent upon reducing environments.

*Pyropelta* is unique in being reported from both the whale-fall habitat and the hydrothermal-vent habitat, but not yet reported from the cold-seep habitat. *Calyptogena* remains the only genus known from all three habitats. Suitable habitats for *Pyropelta* on whale bone are much more closely spaced along continental margins in the deep sea than are the vent habitats.

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