

Four New Pseudococculinid Limpets Collected by the Deep-Submersible *Alvin* in the Eastern Pacific

by

JAMES H. McLEAN

Los Angeles County Museum of Natural History, 900 Exposition Boulevard,
Los Angeles, California 90007, USA

Abstract. Four new species of Pseudococculinidae collected with the deep-submersible *Alvin* are described. One species represents a new monotypic genus, *Punctabyssia*, and two represent new subgenera: *Dictyabyssia* (of *Caymanabyssia* Moskalev, 1976) and *Gordabyssia* (of *Amphiplica* Haszprunar 1988). New species are: *Punctabyssia tibbettsi* and *Caymanabyssia (Dictyabyssia) fosteri*, both from the same piece of wood at abyssal depths on the East Pacific Rise Axis near 12°N, and two from abyssal depths on the Gorda Ridge off northern California, *Caymanabyssia (Caymanabyssia) vandoverae* and *Amphiplica (Gordabyssia) gordensis*. The latter is the first member of the family to be recovered from sulfide crust in the hydrothermal-vent habitat. New character states for the radula and protoconch are defined for the new genus *Punctabyssia*.

INTRODUCTION

The cocculiniform limpets include a number of deep-sea families in which there is an association with biogenic substrates (for review see HASZPRUNAR, 1988b). Until recently the only method by which these limpets have been recovered has been by chance trawling of pieces of wood or other biogenic substrates. Records of cocculiniform limpets are so infrequently obtained that many species remain known from a single station. Such a sparsity of records indicates that our knowledge of the distribution of these species is very incomplete and that additional new species are likely to be discovered.

A more direct approach to sampling the widely scattered wood or bone "islands" (TURNER, 1978) is now possible with the deployment of deep-submersible research submarines. The four pseudococculinid limpets described here were collected by using the deep-submersible *Alvin* of the Woods Hole Oceanographic Institution. Although the objective of each dive was the exploration of hydrothermal-vent fields, three of the four species were taken on wood outside the influence of hydrothermal activity.

Two species were found on the same piece of wood recovered from the ridge axis of the East Pacific Rise near 12°N. One represents a monotypic new genus, and the other a new subgenus, which has a congener from abyssal depths near New Zealand.

Two species are added from explorations of the *Alvin* on the Gorda Ridge, one from wood not under the influence

of hydrothermal vents, and another from sulfide crust produced by hydrothermal vents. The latter species represents a new monotypic subgenus and is the first member of the family restricted to the hydrothermal-vent habitat.

Recent work on the systematics and anatomy of the pseudococculinid limpets (MOSKALEV, 1976; HICKMAN, 1983; MARSHALL, 1986; HASZPRUNAR, 1988a; McLEAN, 1988) makes it possible to establish the taxonomic placement of the four new species treated here, and to justify the proposal of new generic and subgeneric taxa.

The new species described here introduce new character states for the family Pseudococculinidae and contribute to the understanding of relationships of genera within the family. The broader implications for classification are summarized in the discussion.

MATERIALS AND METHODS

Limpet specimens were collected on wood or other substrate samples with the mechanical arm of the deep-submersible *Alvin*. Material was preserved on reaching the surface, fixed in buffered formalin, and transferred to 70% alcohol. Sorting was accomplished at Woods Hole Oceanographic Institution, following which the specimens were forwarded to me.

Radulae were extracted from preserved specimens after dissolution of tissues in 10% NaOH, washed in water, air dried, and coated with gold or gold-palladium for examination with SEM. Protoconchs and juvenile shells were

examined with SEM. Protoconch lengths were taken directly from scale indications for the SEM micrographs.

Institutions mentioned in the text are abbreviated as follows: LACM, Los Angeles County Museum of Natural History; USNM, National Museum of Natural History, Washington, D.C.

Suborder Cocculiniformia Haszprunar, 1987

Superfamily LEPETETELLACEA Dall, 1881

Family PSEUDOCOCCULINIDAE Hickman, 1983

Punctabyssia McLean, gen. nov.

Type species: *P. tibbettsi* McLean, sp. nov.

Diagnosis: Shell thin and translucent; protoconch with tightly spaced pits in longitudinal rows; teleoconch sculpture of fine concentric ridges with larger pits in interspaces. Eyes lacking, right cephalic tentacle slightly larger than left; gill leaflets present on right side only; epipodial tentacles a single posterior pair. Rachidian tooth large and quadrangular, uncusped; cusp of first lateral with fine serrations; upper shaft and cusp of second lateral fused with that of first lateral; third and fourth laterals with long beaklike cusps; fifth lateral reduced to stubby base; marginals similar in size.

Remarks: The protoconch sculpture of *Punctabyssia* is unique in having pits in rows. *Punctabyssia* is also unique in the serration on the first lateral and in the fusion between the cusps of the first and second laterals. Punctations on the protoconch are otherwise known only in *Tentaoculus* Moskalev, 1976. As diagnosed by MARSHALL (1986), *Tentaoculus* differs in having the protoconch pits in irregular order, in having a tapered, cusped rachidian, a strongly developed fifth lateral, having eyes, and occurring at bathyal rather than abyssal depths.

Etymology: The name derives from the Latin noun *punctura*, hole, with reference to the punctate sculpture of both protoconch and teleoconch, combined with the word-ending first used by MOSKALEV (1976) for genera related to *Pseudococculina*.

Punctabyssia tibbettsi McLean, sp. nov.

(Figures 1–8)

Description: Shell (Figures 1–3, 6) of medium size for family (maximum length 5.0 mm), translucent; periostracum thin, smooth. Height low, that of holotype 0.26 times that of length. All slopes nearly straight. Outline in dorsal view elongate-oval, anterior end slightly broader than posterior; sides of shell slightly raised relative to ends. Apex slightly anterior to center, at highest point of shell. Shell of most specimens with scattered, shallow eroded areas. Protoconch (Figure 6) lost in all but small specimens under 2 mm in length; protoconch posteriorly directed, length 170 μ m, sculpture of fine pits aligned in rows. Teleoconch

sculpture of fine concentric ridges, ridges sometimes coalescing; interspaces with aligned rows of pits (Figure 6); pits larger than those of protoconch, present at all stages of growth. Radial sculpture lacking. Shell margin sharp, easily chipped; interior transparent, showing exterior pattern of erosion; position of muscle scar not visible in shell interior.

Dimensions: Length 4.7, width 3.5, height 1.2 mm (holotype).

External anatomy (Figures 4, 5) as described for genus.

Radula (Figures 7, 8): Shaft of rachidian tooth broad, laterally constricted near base, upper edge with thick swelling, uncusped. First and second lateral fused at midshaft and having fused cusps. First lateral large, extending well above position of rachidian, its cusp with fine serrations on inner side and beaklike cusp at tip, which derives from second lateral. Fused second lateral with strong lateral projection. Third and fourth laterals with lateral curvature and long beaklike cusps. Fifth lateral reduced to shaft base only. Marginals numerous, with pointed cusps and serrations, similar in size.

Type locality: Along axis of East Pacific Rise near 12°N (11°51'N, 103°50'W), on wood, 2700 m.

Type material: 14 specimens from type locality, collected with deep-submersible *Alvin*, dive No. 2000, 22 March 1988. Holotype LACM 2434, 7 paratypes LACM 2435, 6 paratypes USNM 784764.

Remarks: Although only 2 of the 14 specimens retained the protoconch, the specimens of this species are otherwise in good condition, not showing the nearly complete erosion of the shell that is often characteristic of pseudococculinid as well as cocculinid species. The gill leaflets are so small that they can readily be seen only on one of the paratype specimens; unfortunately they are not apparent in Figure 5.

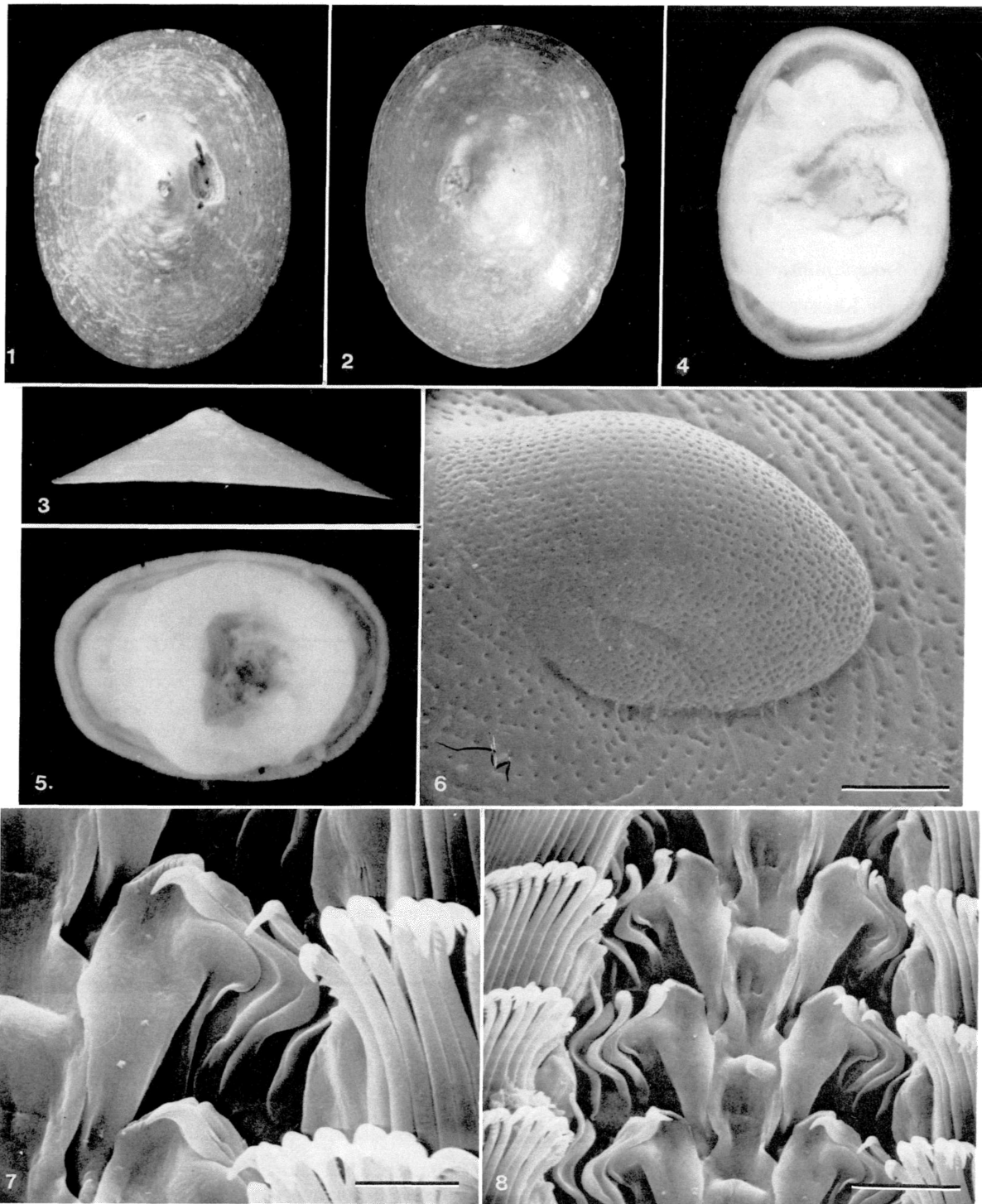
Etymology: The specific name honors Paul Tibbetts, one of the pilots of *Alvin*, marking *Alvin* dive 2000, a major peak in the history of undersea exploration.

Caymanabyssia Moskalev, 1976

Type species: *C. spina* Moskalev, 1976.

Diagnosis: Shell sculpture dominated by pustules superimposed on anastomosing network of surface sculpture; protoconch microsculpture of columnar crystals. Eyes lacking, oral lappets present, several gill leaflets present on right side; single leaflet on left; right cephalic tentacle of same size or slightly larger than left; epipodial tentacles a single posterior pair. Radula degenerate, rachidian and laterals lacking cusps.

Remarks: MARSHALL (1986) allowed a species in *Caymanabyssia* that lacked the conical granules that dominate the teleoconch sculpture of the type species of the genus. The discovery of another species with the same lack of a



Explanation of Figures 1 to 8

Figures 1–8. *Punctabyssia tibetensis* McLean, sp. nov. *Alvin* dive 2000, near 12°N, 2700 m. Anterior at top in vertical views. Figures 1–3. Holotype, LACM 2434. Exterior, interior, and left lateral views. Length 4.7 mm. Figure 4. Dorsal view of holotype body, showing contracted right cephalic tentacle larger than left through mantle skirt. Length 3.0 mm. Figure 5. Ventral view of holotype body, showing posterior pair of epipodial tentacles at right; gill leaflets obscured by foot. Length 3.0 mm. Figure 6. SEM view of protoconch and early teleoconch, oblique view from left side, showing pits on protoconch and teleoconch. Scale bar = 40 μ m. Figure 7. SEM view of half-widths of radular ribbon. Scale bar = 10 μ m. Figure 8. SEM view of nearly full width of radular ribbon. Scale bar = 20 μ m.

major sculptural element warrants the separation of the two species at least at the subgeneric level. Accordingly the subgenus *Dictyabyssia* is described below.

Dictyabyssia McLean, subgen. nov.
(of *Caymanabyssia* Moskalev, 1976)

Type species: *Caymanabyssia sinespina* Marshall, 1986.

Diagnosis: Surface sculpture of anastomosing threads; lacking conical granules. Protoconch (where known) sculptured with minute columnar crystals. External anatomy and radula as in typical subgenus.

Remarks: The need for this subgenus is noted above. Marshall's species is selected as the type species of the new subgenus because it has an intact protoconch, which is missing on specimens of the species described here.

Two species are known in *Dictyabyssia*, the type species and the following new species.

Etymology: The name combines the Greek noun *dictyon*, meaning net, with reference to the anastomosing sculpture, plus the word-ending first used by MOSKALEV (1976) for genera related to *Pseudococculina*.

Caymanabyssia (Dictyabyssia) fosteri McLean,
sp. nov.

(Figures 9–16)

Description: Shell (Figures 9–11, 14, 15) of medium size for family (maximum length 5.7 mm), translucent white, periostracum very thin. Height moderate, that of holotype 0.46 times that of length. All slopes weakly concave. Outline in dorsal view elongate-oval, anterior narrower than posterior; margin of aperture nearly resting in same plane. Apex at $\frac{2}{5}$ shell length from anterior end, at highest point of shell. Protoconch unknown; apical area eroded in all specimens (none smaller than 2.5 mm). Teleoconch sculpture preserved at margin of smallest specimens, consisting of concentric growth irregularities and fine, densely anastomosing surficial threads (Figures 14, 15) visible under high magnification. Radial sculpture lacking. Entire surface of all specimens over 4 mm in length deeply eroded, showing coalescing linear pattern typical in family (Figure 9). Position of muscle scar marked by thick callus deposits in dorsal view (Figure 9), showing the inward expansion of scar characteristic of family. Shell margin sharp, easily chipped. Interior glossy white, outline of muscle scar well marked in mature specimens, anterior pallial attachment scar also marked. Shell interior thickened within to compensate for exterior erosion.

Dimensions: Length 5.7, width 4.2, height 2.6 mm (holotype).

External anatomy (Figures 12, 13) as defined for genus.

Radula (Figure 16): Rachidian tooth quadrangular, outer edges thickened, upper edge thin, uncusped. First lateral tooth elongate and tilted, cusp rows of laterals higher than

that of rachidian. First four laterals with projecting nubs but no overhanging cusps. Fifth lateral reduced to stubby basal portion. Marginal teeth of similar size, with long, beaklike cusps.

Type locality: Along axis of East Pacific Rise near 12°N (11°51'N, 103°50'W), on wood from 2700 m.

Type material: 19 specimens from type locality, collected with deep-submersible *Alvin*, dive No. 2000, 22 March 1988. Holotype LACM 2436, 10 paratypes LACM 2437, 8 paratypes USNM 784765.

Remarks: *Caymanabyssia (Dictyabyssia) fosteri* reaches a much larger size than *C. (D.) sinespina* Marshall, 1986, from New Zealand (5.8 mm, compared to 2.15 mm). In addition, the anastomosing sculpture of the immature specimen of *C. (D.) fosteri* (Figure 15) is much more dense than that illustrated by Marshall for *C. (D.) sinespina*.

Radulae of all species of *Caymanabyssia* s.s. and *C. (Dictyabyssia)* are similar, characterized by MARSHALL (1986) as "degenerate" in lacking cusps on the rachidian and laterals.

Etymology: The specific name honors Dudley Foster, senior pilot of the *Alvin*, on the occasion of the hallmark *Alvin* dive 2000.

Caymanabyssia (Caymanabyssia) vandoverae McLean,
sp. nov.

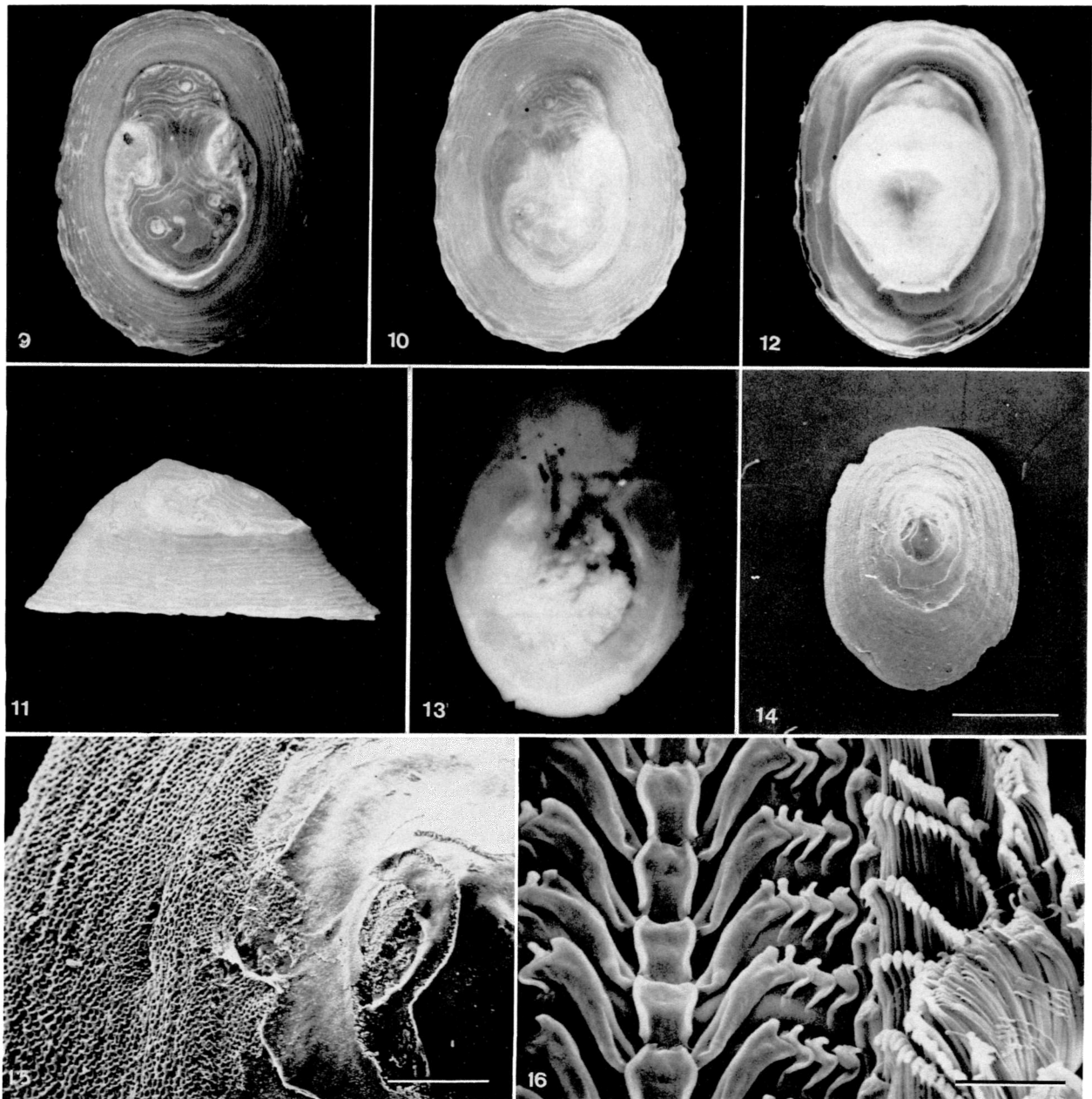
(Figures 17–24)

Description: Shell (Figures 17, 18, 22–24) of small size for family but typical size for genus (maximum length 3.9 mm), translucent white, periostracum very thin. Height low, that of holotype 0.25 times that of length. All slopes slightly convex. Outline in dorsal view elongate-oval, anterior end same width as posterior; sides of shell raised relative to ends. Apex nearly central, at highest point of shell. Protoconch (Figures 22–24) posteriorly directed, length 200 μ m, sculpture of clumped columnar prisms, usually lost in specimens over 3.0 mm in length. Teleoconch sculpture of prominent pustules aligned in curving rows, superimposed on microsculpture of finely anastomosing threads; threads visible only under high magnification. Radial sculpture lacking. Sculpture preserved in large specimens, although scattered erosional pits are present. Interior surface translucent white, revealing position of exterior erosional pits and only faintly indicating position of muscle scar. Shell edge showing position of exterior pustules.

Dimensions: Length 3.6, width 2.7, height 0.9 mm (holotype).

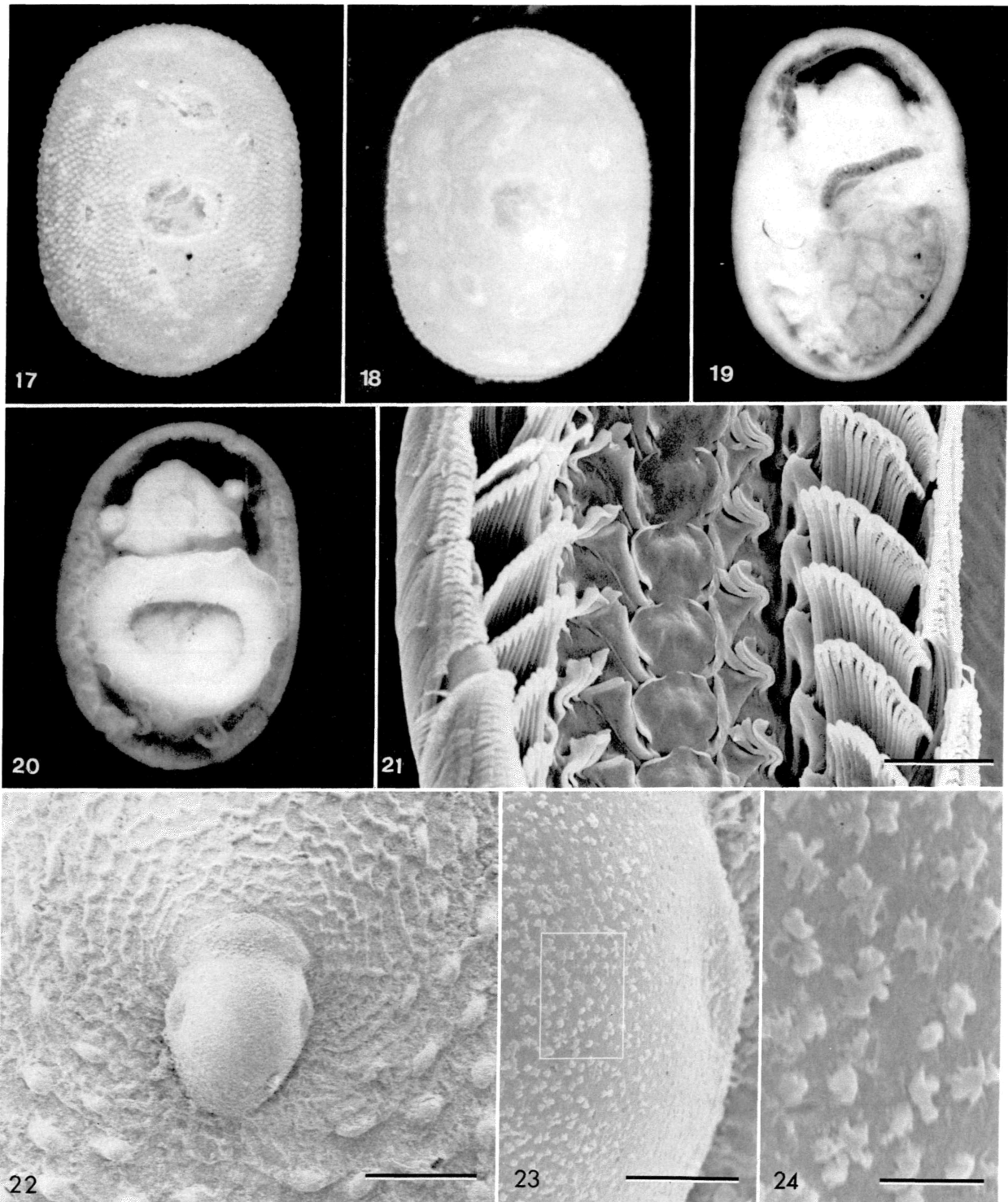
External anatomy (Figures 19, 20) as defined for genus.

Radula (Figure 21): Rachidian plate broad, thin, raised at edges, lacking overhanging cusp. First lateral tooth extending to height of rachidian, with strong lateral projection, lacking cusp. Second, third, and fourth laterals with



Explanation of Figures 9 to 16

Figures 9–16. *Caymanabyssia (Dictyabyssia) fosteri* McLean, sp. nov. *Atvin* dive 2000, near 12°N, 2700 m. Anterior at top in vertical views. Figures 9–11. Holotype, LACM 2436. Exterior, interior, and left lateral views (surface sculpture eroded). Length 5.7 mm. Figure 12. Ventral view of paratype body attached to shell, showing paired posterior epipodial tentacles. Length 5.6 mm. Figure 13. Dorsal view of same specimen detached from shell, showing cephalic tentacles of nearly equal size. Length 3.0 mm. Figure 14. SEM view of juvenile shell with intact surface sculpture, but eroded protoconch. Scale bar = 1 mm. Figure 15. SEM view of surface detail of anastomosing lines in same specimen as in Figure 14, eroded apical area at right. Scale bar = 200 μ m. Figure 16. SEM view of radular ribbon. Scale bar = 40 μ m.



Explanation of Figures 17 to 24

Figures 17–24. *Caymanabyssia* (*Caymanabyssia*) *vandoverae* McLean, sp. nov. Alvin dive 2034, Gorda Ridge, 3362 m. Anterior at top in vertical views. Figures 17, 18. Holotype, LACM 2438. Exterior and interior views. Length 3.9 mm. Figures 19, 20. Dorsal and ventral views of detached body of holotype, showing right cephalic tentacle slightly larger than left. Length 2.2 mm. Figure 21. SEM view of radular ribbon. Scale bar = 40 μ m. Figure 22. SEM view of protoconch and teleoconch surface, showing pustules and anastomosing sculpture of teleoconch. Scale bar = 100 μ m. Figure 23. Detail of protoconch sculpture, showing columnar prisms. Scale bar = 60 μ m. Figure 24. Enlargement of columnar prisms in area outlined by rectangle of Figure 23. Scale bar = 15 μ m.

lateral elbows, lacking cusps. Fifth lateral elongate, with two basal prongs to shaft, cusps lacking. Marginal teeth numerous, long and slender, with sharp cusp and serrations, nearly equal in size.

Type locality: Escanaba Trough, Gorda Ridge (41°00.4'N, 127°29.3'W), on wood, 3362 m.

Type material: 5 specimens from type locality, collected with deep-submersible *Alvin*, dive No. 2034, 4 June 1988. Holotype LACM 2438, 4 paratypes LACM 2439, 1 paratype USNM 784766.

Remarks: *Caymanabyssia vandoverae* is clearly a member of subgenus *Caymanabyssia* in having the sculpture dominated by pustules superimposed on an anastomosing network of surface sculpture, having the protoconch microsculpture of columnar crystals, and having a radula lacking cusps on the rachidian and laterals. The dorsal sperm groove is prominent and may be seen by probing the tentacle in ventral view. The new species is the third member of the genus. Other species are the type species from the Cayman Trough in the Western Atlantic, and *C. rhina* Marshall, 1986, from off White Island, New Zealand. It differs from *C. rhina* in having much more prominent and densely spaced pustules. Moskalev's *C. spina* also has more broadly spaced pustules than *C. vandoverae*.

Etymology: The name honors Dr. Cindy Van Dover, of Woods Hole Oceanographic Institution, who is responsible for the preservation and forwarding of each species described herein.

Amphiplica Haszprunar, 1988

Type species: *A. venezuelensis* McLean, 1988.

Diagnosis: Shell size large for family; white, periostracum thin; protoconch unknown; teleoconch sculpture of sharply raised concentric ridges. Eyes lacking, right tentacle similar in size to left; up to six pairs of secondary subpallial gill leaflets on both sides near anterior end of foot; oral lappets present; epipodial tentacles a single posterior pair. Rachidian tooth prominent, tapered, with beaklike cusp; lateral teeth with sharply pointed cusps; fifth lateral with five short denticles; innermost marginals larger than the rest.

Remarks: The new species described below has the sharply raised concentric sculpture, the secondary gill lamellae on both sides, and the oral lappets (although more weakly developed) of *Amphiplica*, but differs in its smaller size, having a more posterior apex, retaining the protoconch in mature sizes, and radular differences (four strong rather than five weak cusps on the fifth lateral, the second marginal tooth not larger than the others). The three members of *Amphiplica* s.s. (*A. venezuelensis* McLean, 1988, *A. knudseni* McLean, 1988, and *A. concentrica* (Thiele, 1909)) are the largest known members of the family. These three species lose the protoconch at an early age.

These differences are recognized at the subgeneric level.

Gordabyssia McLean, subgen. nov.
(of *Amphiplica* Haszprunar, 1988)

Type species: *Amphiplica (Gordabyssia) gordensis* McLean, sp. nov.

Diagnosis: Shell small, white, periostracum thin; protoconch with subreticulate pattern of anastomosing threads in longitudinal rows; teleoconch sculpture of sharply raised concentric ridges. Eyes lacking, right tentacle similar in size to left; up to six pairs of secondary subpallial gill leaflets on both sides near anterior end of foot; epipodial tentacles a single posterior pair. Rachidian tooth prominent, tapered, cusp beaklike; lateral teeth with sharply pointed cusps; fifth lateral with four pointed cusps; innermost marginals larger than the rest.

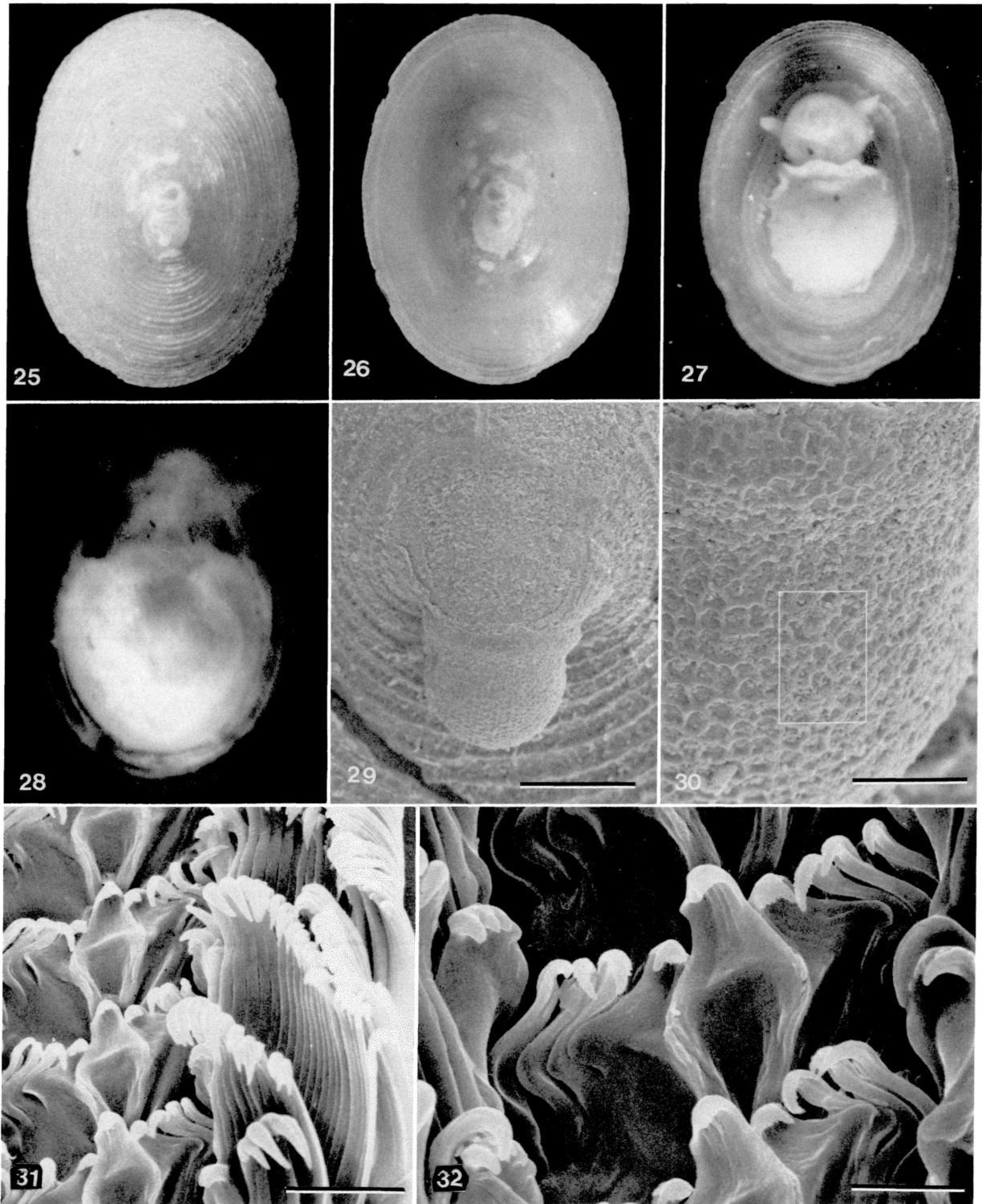
Remarks: Reasons to justify the new subgenus are given above. The new species described here provides a provisional protoconch definition for the genus *Amphiplica* s.s., as the protoconch is unknown in the typical subgenus. Should the protoconch in the typical subgenus prove to be of a different type, the subgenus *Gordabyssia* should be raised to a full genus. Similar protoconch sculpture to that of *Amphiplica (Gordabyssia) gordensis* is known in *Mesopelex* Marshall, 1986, and *Kurilabyssia* Moskalev, 1976, but characters of radula and teleoconch sculpture do not agree.

The new species is the only member of the family to be associated with sulfide crust at hydrothermal vents, albeit having a very limited distribution in the habitat. Specimens were collected from four stations in the Escanaba Trough on the Gorda Ridge, in each case on hard substrates, indicated as sulfide crust on the labels, so it is clear that this is not an association with wood, as in most other pseudococculinids. There seem to be no modifications that correlate with the hydrothermal-vent environment.

Amphiplica (Gordabyssia) gordensis McLean,
sp. nov.

(Figures 25–32)

Description: Shell (Figures 25–27, 29, 30) of medium size for family (maximum length 3.9 mm), translucent; periostracum thin, light brown. Height low, that of holotype 0.28 times that of length. Anterior and lateral slopes convex; posterior slope straight. Outline in dorsal view elongate-oval, anterior end about the same width; shell margin in same plane (sides or ends not raised). Apex posterior to center, at highest point of shell. Shell of most specimens with scattered, shallow eroded areas. Protoconch (Figures 29, 30) retained on most specimens, even on specimens with eroded apical area; protoconch posteriorly directed, length 200 μ m, sculpture of subreticulate pattern of anastomosing threads in longitudinal rows. Teleoconch sculp-



Explanation of Figures 25 to 32

Figures 25–32. *Amphiplica (Gordabyssia) gordensis* McLean, sp. nov. *Alvin* dive 2035, Gorda Ridge, 3305 m. Anterior at top in vertical views. Figures 25, 26. Holotype, LACM 2440. Exterior and interior views. Length 3.9 mm. Figure 27. Ventral view of holotype body attached to shell, showing paired gill leaflets near both sides of foot. Length 3.9 mm. Figure 28. Dorsal view of detached body of holotype. Length 2.1 mm. Figure 29. SEM view of protoconch (with subreticulate sculpture) and teleoconch surface (concentric sculpture). Scale bar = 100 μ m. Figure 30. Enlarged view of subreticulate sculpture of protoconch. Scale bar = 25 μ m. Figure 31. SEM view of radular ribbon. Scale bar = 25 μ m. Figure 32. Enlarged view of central field, showing four cusps on fifth lateral tooth. Scale bar = 12 μ m.

ture of fine, sharp concentric ridges, ridges not coalescing. Radial sculpture of exceedingly fine striae, detectable under high magnification, producing fine swellings on crossing concentric ridges. Shell margin sharp, easily chipped; interior transparent, showing exterior pattern of erosion; position of muscle scar faintly visible in shell interior.

Dimensions: Length 3.9 mm, width 2.8 mm, height 1.1 mm (holotype).

External anatomy (Figures 27, 28) as described for genus and subgenus.

Radula (Figures 31, 32): Rachidian tooth elongate, rising above level of all lateral teeth, having simple beaklike overhanging cusp, central part of shaft laterally expanded. First pair of laterals with strong lateral projection, overhanging cusp with long tip and serrations on inner side; second, third, and fourth laterals similarly shaped, cusps with single pointed tip and serrations on both sides. Fifth lateral tooth massive, with four pointed cusps; marginal teeth with long overhanging cusps, the second, third, fourth and fifth pairs having the longest cusps.

Type locality: Escanaba Trough, Gorda Ridge (41°00.4'N, 127°29.3'W), on sulfide crust, 3305 m.

Type material: 34 specimens from type locality, collected with deep-submersible *Alvin*, dive No. 2035, 5 June 1988. Holotype LACM 2440, 18 paratypes LACM 2441, 15 paratypes USNM 784767.

Additional paratypes were taken at four other *Alvin* dives at the type locality (same coordinates for each dive but different depths and dates): LACM 2441a, 5 specimens, dive 2033, 3356 m, 3 June 1988; LACM 2441b, 4 specimens, dive 2039, 3305 m, 9 June 1988; LACM 2441c, 9 specimens, dive 2040, 3271 m, 10 June 1988; LACM 2441d, 1 specimen, dive 2042, 3271 m, 12 June 1988.

Remarks: This species exhibits considerable variation in shell proportions and in the degree of erosion. A number of specimens were smaller, more elevated and with more compressed sides than the holotype. Most specimens retain the protoconch, even though the surface sculpture on the anterior slope may be eroded.

One other limpet has recently been described from the Escanaba Trough on the Gorda Ridge: *Neoleptopsis gordensis* McLean, 1990. A general report on the hydrothermal-vent fauna of the Escanaba Trough on the Gorda Ridge is given by VAN DOVER *et al.* (1990).

Etymology: The specific name derives from the type locality, the Gorda Ridge.

DISCUSSION

Until now the family Pseudococculinidae has been represented in the Eastern Pacific by a single species, *Yaquinabyssia careyi* McLean, 1988, from the Cascadia Abyssal Plain off Oregon. The four species described here bring the total to five species for the family in the Eastern Pacific.

The use of a deep-submersible research submarine has provided new opportunities to locate and sample "islands" of biogenic origin, a sparse habitat in the deep sea (TURNER, 1978). Further opportunities should be taken whenever possible to sample additional wood falls on dives made by deep-submersibles. The sparsity of records indicates that our knowledge of distribution is minimal and that additional species of Pseudococculinidae may remain to be discovered.

New limits to character states in the family Pseudococculinidae are provided here by the new monotypic genus *Punctabyssia*, which has a unique protoconch with pits aligned in rows and radular tooth elements that show a derived state of fusion between the first and second lateral tooth elements, which in all other genera are separate elements.

The new subgenus *Dictyabyssia* (of *Caymanabyssia*) flags the existence of two species that lack the most prominent sculptural element of typical *Caymanabyssia*.

The new subgenus *Gordabyssia* (of *Amphiplica*) provides an exception to the rule that pseudococculinids are always associated with biogenic substrates. One other cocculiniform family, the Pyropeltidae, described by McLEAN & HASZPRUNAR (1987) occurs in the hydrothermal-vent habitat.

MARSHALL (1986) defined a number of pseudococculinid genera on characters of the radula, protoconch, and external anatomy; HASZPRUNAR (1988a) added anatomical definitions, recognizing a total of 11 genera. Two subfamilies were originally defined by MARSHALL (1986), the Pseudococculininae and Caymanabyssinae, in large part on radular characters. Diagnoses were altered by HASZPRUNAR (1988a:175-176), who questioned the validity of radular characters as a basis for subfamily distinctions and based his own definitions on gill and protoconch characters. However, the utility of a two-fold subdivision is questioned here because the new species *Amphiplica (Gordabyssia) gordensis* has gill characters of Caymanabyssinae and protoconch characters more typical of Pseudococculininae. Accordingly, a subfamily division is not recognized here. Until more is known about how characters combine in this family it may be premature to arrive at a robust classification.

ACKNOWLEDGMENTS

I am especially grateful to Dr. Cindy Van Dover of Woods Hole Oceanographic Institution, who was aboard the expeditions of the *Alvin* when the specimens were collected, for preserving the specimens of each of the four species and forwarding them to me. She has also read the manuscript and provided helpful comments. I thank Cliff Coney for operating the scanning electron microscope at the Center for Electron Microscopy and Microanalysis, University of Southern California, and Bertram C. Draper for the photos of preserved animals. I thank reviewers Carole S.

Hickman, Gerhard Haszprunar, and Bruce A. Marshall for helpful suggestions.

LITERATURE CITED

- HASZPRUNAR, G. 1988a. Anatomy and affinities of pseudococculinid limpets (Mollusca: Archaeogastropoda). *Zoologica Scripta* 17:161-180.
- HASZPRUNAR, G. 1988b. Comparative anatomy of cocculiniform gastropods and its bearing on archaeogastropod systematics. Pp. 7-16. *In*: W. F. Ponder (ed.), *Prosobranch Phylogeny, Proceedings of a Symposium Held at the 9th International Malacological Congress, Edinburgh, 1986*. Malacological Review, Supplement 4.
- HICKMAN, C. S. 1983. Radular patterns, systematics, diversity, and ecology of deep-sea limpets. *The Veliger* 26(2):73-92.
- MARSHALL, B. A. 1986. Recent and Tertiary Cocculinidae and Pseudococculinidae (Mollusca: Gastropoda) from New Zealand and New South Wales. *New Zealand Journal of Zoology* 12:505-546.
- MCLEAN, J. H. 1988. Three new limpets of the family Pseudococculinidae from abyssal depths (Mollusca, Archaeogastropoda). *Zoologica Scripta* 17(2):155-160.
- MCLEAN, J. H. 1990. Neolepetopsidae, a new docoglossate limpet family from hydrothermal vents and its relevance to patellogastropod evolution. *Journal of Zoology, London* 222: 485-528.
- MCLEAN, J. H. & G. HASZPRUNAR. 1987. Pyropeltidae, a new family of cocculiniform limpets from hydrothermal vents. *The Veliger* 30(2):196-205.
- MOSKALEV, L. I. 1976. On the generic classification in Cocculinidae (Gastropoda, Prosobranchia). *Trudy Instituta Okeanologii Imeni P. P. Shirshov Akademii Nauk SSSR* 99:59-70 [in Russian].
- TURNER, R. D. 1978. Wood, mollusks, and deep-sea food chains. *Bulletin of the American Malacological Union*, 1977:13-19.
- VAN DOVER, C. L., J. F. GRASSLE & M. BOUDRIAS. 1990. Hydrothermal-vent fauna of Escanaba Trough (Gorda Ridge). Pp. 285-287. *In* G. R. McMurray (ed.), *Gorda Ridge: A Seafloor Spreading Center in the United States' Exclusive Economic Zone*. Springer-Verlag: New York.