

Taxonomic descriptions of cocculinid limpets (Mollusca, Archaeogastropoda): two new species and three rediscovered species

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Taxonomic descriptions of five species treated anatomically in an accompanying paper by Haszprunar are given. Based on a new record from Florida, the type species of *Cocculina*, *C. rathbuni* Dall, 1882, is treated, enabling other genera in the family to be compared anatomically to the type genus. *Cocculina ovata* Schepman, 1908 is recognized from continental shelf depths off the Philippines. Two new species of *Cocculina* are described: *C. baxteri*, from the continental slope, Prince William Sound, Alaska, and *C. cowani*, from the continental slope off the Queen Charlotte Islands, British Columbia. *Coccocrater agassizi* (Dall, 1908) is newly reported and redescribed from the lower continental slope and abyss in the Gulf of Panama.

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Introduction

The long neglected family Cocculinidae has recently been treated by Moskalev (1976), Hickman (1981, 1983, 1984) and Marshall (1986). A more complete understanding of generic relationships within the family has awaited the concurrently published paper by Haszprunar (1987), in which external and internal anatomy for the available genera, including two new genera described by Haszprunar, are treated. The family Pseudococculinidae was separated by Hickman (1983); this action is supported both by Marshall (1986) and Haszprunar (1987).

One stumbling block to an understanding of the family Cocculinidae has been the unavailability of the type species, *Cocculina rathbuni* Dall, 1882, for which anatomical information has been wanting. Original material could not be located in the U.S. National Museum of Natural History or the Museum of Comparative Zoology, Harvard, either by Marshall (1986) or by myself. This occasion is therefore taken to illustrate and discuss a specimen tentatively identified as *C. rathbuni*, received on loan from Dr Paul S. Mikkelsen of the Indian River Coastal Zone Museum, Fort Pierce, Florida.

Although literature accounts have indicated the presence of two species of the family Cocculinidae in the northeastern Pacific, the only species known from this area are the two new species of *Cocculina* here described. One has previously been cited, misidentified as '*Cocculina*' *agassizii* Dall, 1908. The Alaskan '*Cocculina*' *casanica* Dall, 1919 is a synonym of *Lepeta caeca* (Müller, 1776), as discussed by McLean (1966).

Serial sections of each of the species treated here have been examined by Haszprunar (1987). Shells, radulae and, in some cases, external features are also illustrated here.

Abbreviations

CAS	California Academy of Sciences, San Francisco
IRCZM	Indian River Coastal Zone Museum, Fort Pierce, Florida
LACM	Los Angeles County Museum of Natural History, Los Angeles
MNHMP	Muséum National d'Histoire Naturelle, Paris
NMC	National Museum of Canada, Ottawa
NMNZ	National Museum of New Zealand, Wellington
USFC	United States Fisheries Commission (R/V Albatross stations)
USNM	National Museum of Natural History, Washington, DC
ZMA	Zoological Museum, Amsterdam
ZMC	Zoologisk Museum, University of Copenhagen, Copenhagen

Family COCCULINIDAE Dall, 1882

Cocculina Dall, 1882

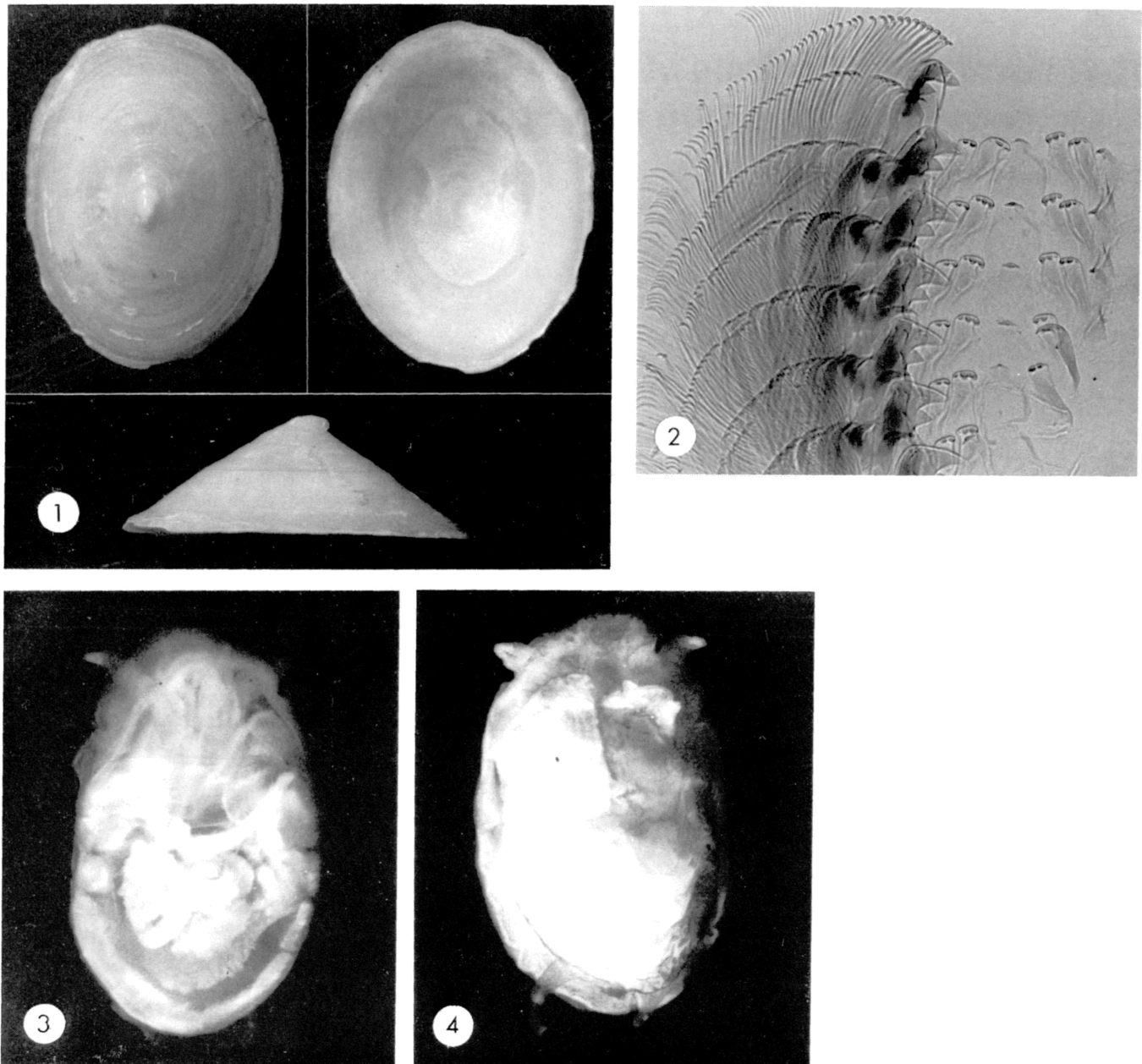
Type species (subsequent designation; Dall 1908). *Cocculina rathbuni* Dall, 1882.

Diagnosis. Shell relatively low, elongate; apex posterior to center; sculpture radial; periostracum fine, smooth. Posterior epipodial tentacles present; gill present; penis at posterior of right oral lappet.

The most important anatomical feature is the location of the penis posterior to the right oral lappet. Further details on the internal and external anatomy of the genus and the following four species are given by Haszprunar (1987).

Cocculina rathbuni Dall, 1882 (Figs. 1–4)

Cocculina rathbuni Dall, 1882, p. 402; Dall 1889, p. 347, pl. 15, figs. 5 [radula], 7 [shell]; Dall 1908, p. 340 [type designation].



Figs. 1–4. *Cocculina rathbuni* Dall. Off Fort Pierce, Florida.—1. Exterior and interior views (anterior at top) and lateral (left side) views. Length 6.2 mm.—2. Light microscope preparation of radula of same specimen. Horizontal width of field 0.20 mm.—3. Dorsal view of body of same specimen (anterior at top), showing no prominent hypobranchial gland in mantle skirt over head; muscle in bundles.—4. Ventral view of body of same specimen, showing posterior epipodial tentacles, cephalic tentacles and cut in foot for extraction of radula.

Type locality. USFC sta. 937, 925 m, about 264 km SE of Martha's Vineyard Island, Massachusetts.

Type material. Type material matching this station number has not been located in the USNM or the Museum of Comparative Zoology, Harvard University, Cambridge, MA. Other original localities were: USFC sta. 388, 730 m, off Barbados, and USFC sta. 195, 919 m, off Martinique. Material from these stations has not been located.

Material studied. One specimen, IRCZM, uncat., 124 m, off Fort Pierce, Florida (27°28.86'N, 79°56.40'W), collected by Paul S. Mikkelsen, 10 April 1981. Dimensions: length 6.2, width 4.6, height 2.2 mm.

Original description. Because of the lack of type material, poor quality of the original illustrations of shell and radula and importance of this species to the definition of the family, the original description of Dall (1882) is quoted in full.

“Shell depressed, white, thin, with sides nearly parallel and their slopes slightly flattened, and with

ends similarly broadly rounded; sculpture of faint closely (but irregularly) set grooves radiating from a smooth apex (which has originally a subspiral nucleus) and crossed by concentric growth lines, which are more or less irregular in different individuals; faint yellowish areas seem to indicate a thin, very closely adherent epidermis; apex prominent, more or less incurved and slightly laterally compressed, usually showing a scar where the embryonic nucleus was attached; inside polished or smooth; length 11.0, width 6.5; altitude 2.75 mm. Another dead specimen is three times larger.

Soft parts: Foot ovate, thin, not very high, somewhat pointed behind; mantle moderately wide with a thickened plain border; behind on each side of

the "tail," between the mantle and foot, is one cylindrical blunt filament; sinus above the head and neck quite deep; gill exactly as in *Acmaea*, small, hardly projecting out of the sinus; head large, end of muzzle semi-lunate, with a strongly marked margin; in the midst of this flat lunate area is a rounded papillose space surrounding the mouth; this organ, if furnished with jaws at all, has them of such soft and cuticular consistency as to show neither under the knife nor under an ordinary dissecting microscope, but it appeared to be without jaws; tentacles moderate, subcylindrical; eyes none; course of the intestine much as in *Patella*, but shorter.

Dentition: Rachidian tooth squarish, rounded in front, nearly flat, about as long as the two inner laterals; inner three laterals slender, with small denticulate cusps, outer or third usually a little longer than the others, but the proportions slightly different in the less mature part of the radula; fourth or major lateral about twice as long as the others and slightly broader than the rachidian tooth, rather strongly cusped, the cusp notched into five or six denticles, and the shaft somewhat curved, the shaft and cusp translucent; uncini numerous (100 or more), slender, slightly twisted and hooked, united on each side on a single continuous base, which is a little longer than the width of the radula between the uncini."

Remarks. The shell of the Fort Pierce specimen (Fig. 1) agrees with the description of Dall (1882). The apex is positioned slightly posterior to center, as illustrated by Dall (1889). The muscle scar was not described by Dall, but this shows clearly in the interior view of the present specimen; it is typical of the pattern throughout the family. The protoconch has a length of 200 μm ; it has a finely pitted surface under the dissecting microscope.

Nothing in Dall's description of the soft parts conflicts with the Fort Pierce specimen. His comparison of the gill with that of *Acmaea* was superficial. The gill in the present specimen is visible through the mantle skirt in dorsal view. Dall did not look closely enough to detect the penis, but the present specimen shows a prominent penis within the mantle groove, forked at the tip, originating posterior to the oral lappet. There is no large hypobranchial gland in the mantle skirt (compare with Fig. 13, which shows a large hypobranchial gland).

The radula of the Fort Pierce specimen had been extracted and mounted for light microscopy by P. Mikelsen (Fig. 2). Dall described the rachidian tooth as "squarish, rounded in front," and his later illustration (Dall 1889, pl. 25, fig. 5) does not show the projecting and tapered tip of the present specimen. This difference is the only discrepancy between Dall's description and the present specimen, but Dall's specimen was larger and the morphology of the rachidian could change with age or the portion of the ribbon examined by Dall may have suffered enough wear to obliterate the tapered cusp. Other notes by Dall about the radula agree with the present specimen.

Although the locality of the present specimen off the east coast of south-central Florida is considerably to the

south of Martha's Vineyard, the bottom temperatures would not be so disparate. Whether *C. rathbuni* occurs also at Barbados and Martinique is uncertain, as these localities are not on contiguous continental shelf.

The lack of clear correspondence between the original material and the Florida specimen regarding the shape of the rachidian tooth and the locality and depth make the identification somewhat tentative, subject to further review.

Cocculina ovata Schepman, 1908 (Figs. 5–9)

Cocculina ovata Schepman, 1908, p. 19, pl. 1, fig. 7 [shell], pl. 8, fig. 10 [radula].

Type locality. Saleh Bay, north coast of Sumbawa Island, Indonesia, Siboga sta. 312, 274 m.

Type material. ZMA, holotype and two paratypes.

Material studied. Numerous lots and specimens in MNHNP, from Musorstom-1 (March 1976) and Musorstom-3 (June 1985) expeditions to the Philippines. Figured specimens from 187–210 m, off SW Luzon, Philippine Islands (14°00'N; 120°19'E).

Description. Shell (Fig. 5) moderately large for family (length of figured specimen 8.3 mm) thin, not eroded, white under thin, barely perceptible periostracum. Shell height relatively low; height of figured specimen 0.36 times length. Anterior slope slightly convex; lateral and posterior slopes straight to slightly concave. Outline (in dorsal view) oval; anterior end slightly broader than posterior; sides nearly parallel; anterior and posterior ends raised relative to sides. Apex nearly central, at maximum height of shell; protoconch projecting posteriorly. Protoconch sculpture finely pitted under dissecting microscope; protoconch length 200 μm . Sculpture of numerous fine, rounded, undulating radial threads, with interspaces twice as broad as threads, and more prominent, irregularly spaced concentric growth lines. Shell margin sharp; muscle scar not prominent, anterior tips slightly swollen; expansion of anterior pallial line seeming to make entire muscle scar ring-shaped.

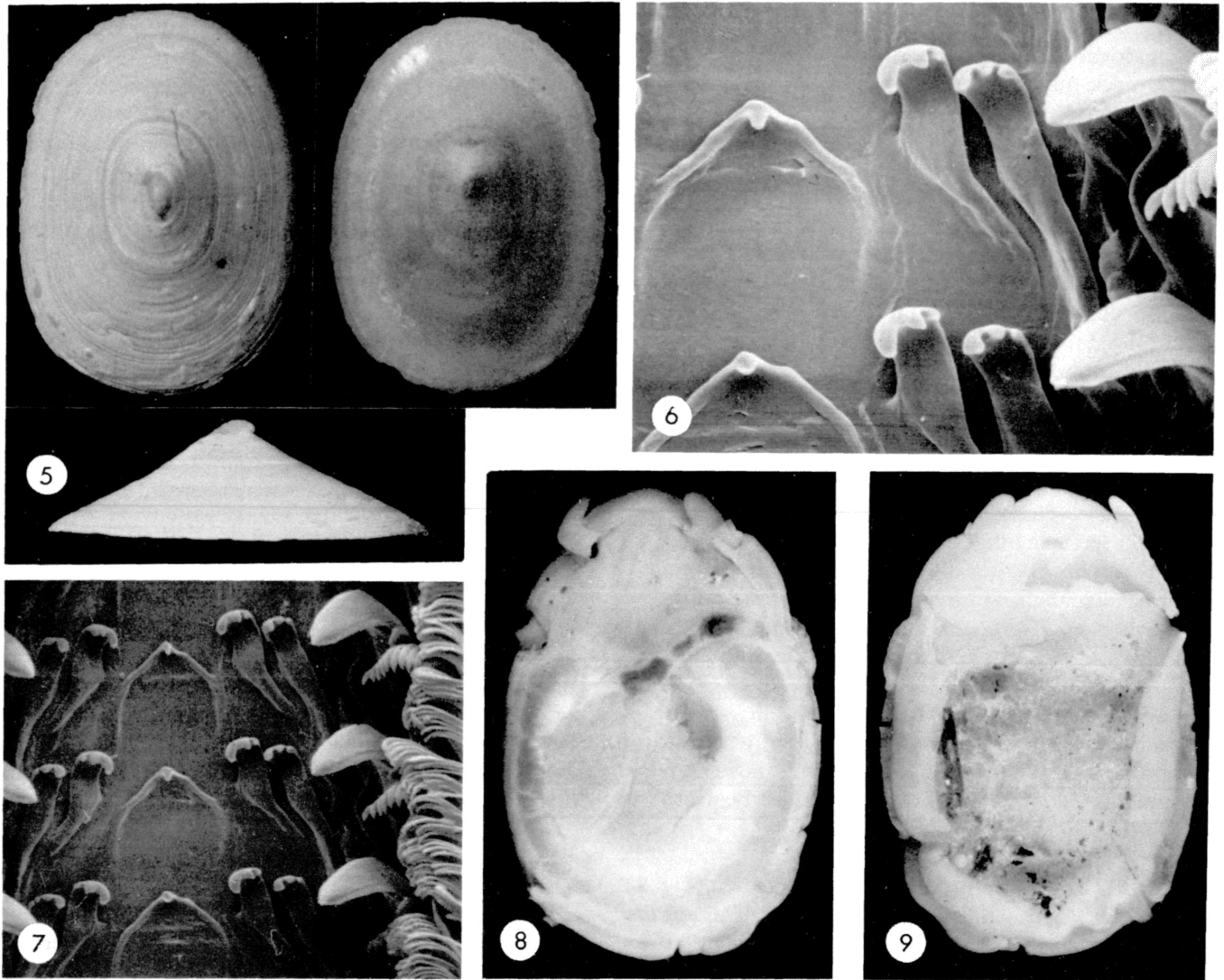
Radula (Figs. 6, 7): rachidian plate broad, outer edges thickened, tapering to a small spur-shaped tip; first and second inner laterals robust and strongly cusped, third inner lateral poorly developed; outer lateral with strong main cusp and reduced secondary cusp; marginals numerous.

External anatomy (Figs. 8, 9): hypobranchial gland not prominent; epipodial tentacles present; gill present; penis at posterior end of oral lappet (see Haszprunar 1987).

Dimensions: length 8.3, width 5.9, height 2.7 mm (figured specimen).

Remarks. Although Indo-Pacific cocculinid species are in need of review, the identity of the present material with *Cocculina ovata* Schepman is certain. Size and dimensions agree with Schepman's account and the morphology of the rachidian tooth is a perfect match for Schepman's drawing, unlike that of any other previously figured member of the family.

This species has shell characters that are similar to those of *Cocculina rathbuni*, the type species of *Cocculina*. Both have moderately large, uneroded white shells that are low in profile with subcentral apex and fine, smooth radial



Figs. 5–9. *Cocculina ovata* Schepman. Off SW Luzon, Philippine Islands.—5. Exterior and interior views (anterior at top) and lateral (left side) views. Length 8.3 mm.—6. SEM view of radula. Horizontal width of field 0.095 mm.—7. Same preparation. Horizontal width of field 0.075 mm.—8. Dorsal view of body of another specimen (anterior at top), mantle skirt stripped away over head. Length 6.2 mm. Showing cephalic tentacles, muscle in bundles and dark rectum extending to right.—9. Ventral view of body of same specimen, showing posterior tentacles and oral lappets on both sides of mouth.

sculpture. *Cocculina ovata* differs from the specimen of *C. rathbuni* (Fig. 1) in having more closely spaced and more undulating radials and in having the ends raised relative to the sides. Both species are known from moderate depths, but occur on opposite sides of the world. *Cocculina ovata* has the low profile, raised ends, subcentral apex and fine, smooth radial sculpture of *Paracocculina laevis* (Thiele 1903), but that species has more compressed sides, in addition to the anatomical differences that place it in a different genus (Haszprunar 1987).

Cocculina cowani sp.n. (Figs. 10–13)

Cocculina sp.; Hickman 1981, fig. 16 [radula].

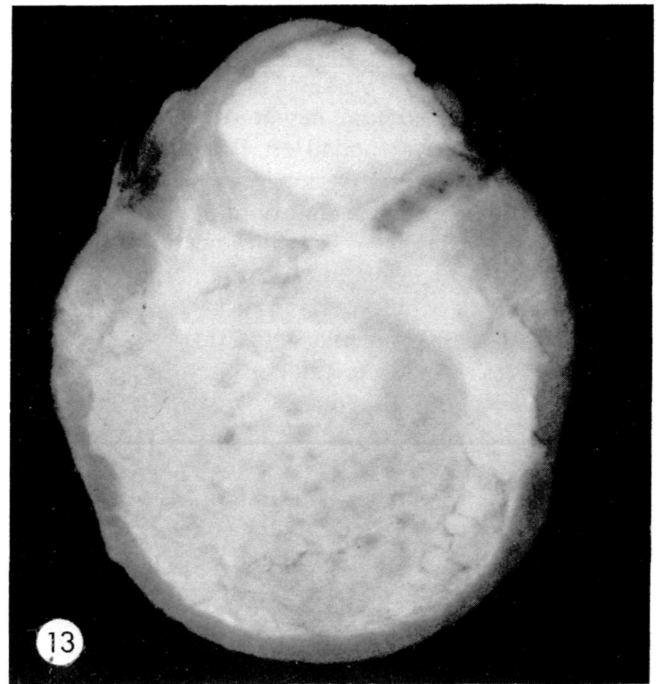
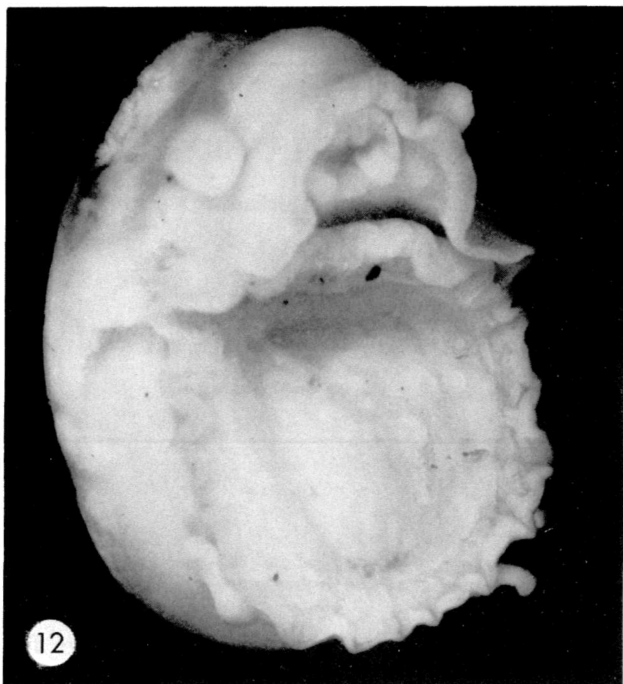
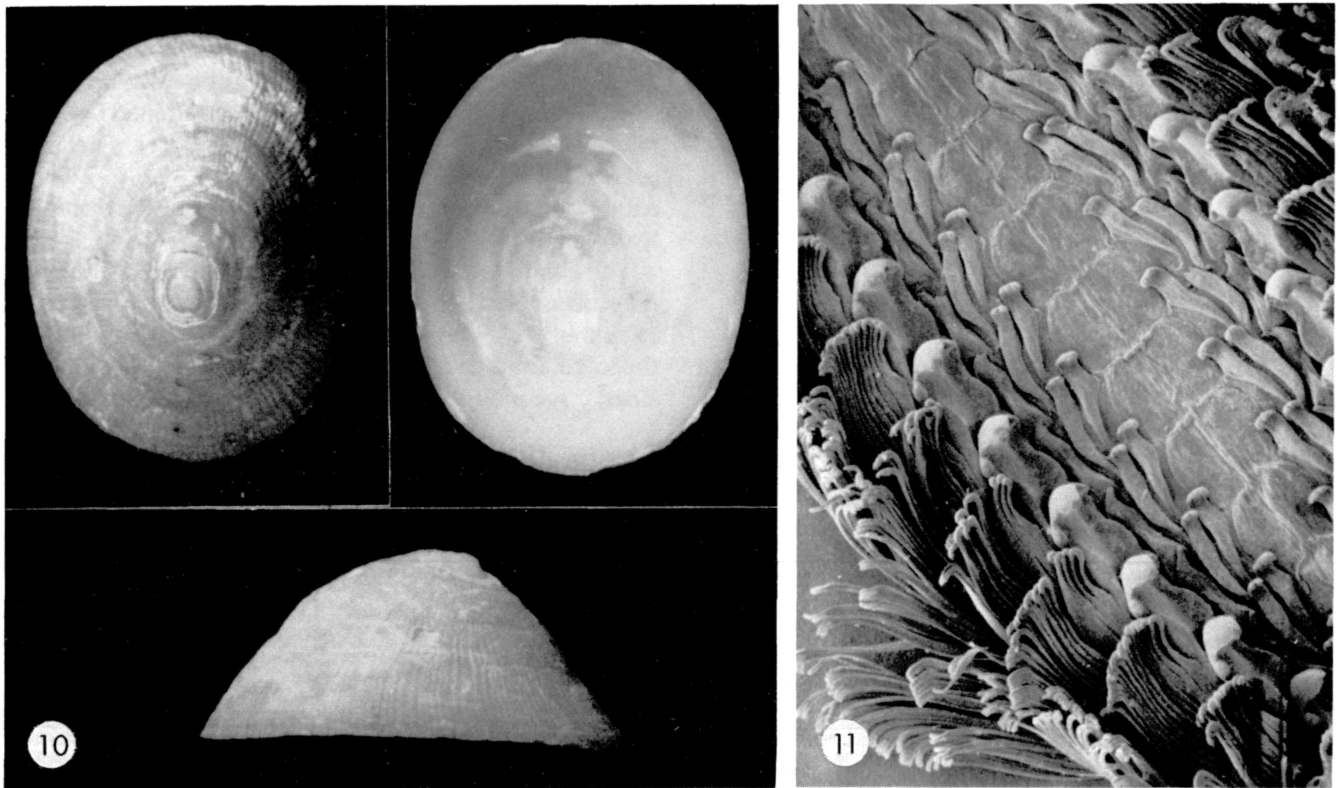
Type locality. On wood from 1370 m depth off W side of Moresby Island, Queen Charlotte Islands, British Columbia (52°30.5'N, 131°55.0'W).

Type material. 15 specimens from the type locality, dredged by R/V G. B. Reed, Fisheries Research Board of Canada sta. 1966–70, October 1966. Holotype NMC 86716, 4 paratypes NMC 86717, 4 paratypes LACM 2066, 2 paratypes USNM 784751, 2 paratypes CAS 050120, 2 paratypes NMNZ 34207.

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Description. Shell (Fig. 10) medium sized for family (maximum length 7.4 mm), white, with pale brown periostracum. Height moderate, that of holotype 0.48 times length. Anterior slope convex; lateral slopes slightly convex; posterior slope nearly straight. Outline (in dorsal view) oval; anterior end slightly broader than posterior. Apex posterior to center, slightly below maximum height of shell, 2/5 shell length from posterior end, slightly to left of midline. Protoconch bulbous, length 150 μ m; sculpture not apparent under dissecting microscope. Teleoconch sculpture of numerous radial ribs of varying breadth; ribs defined by incised grooves; radial sculpture crossed by growth lines, producing beads. All radial ribs curving slightly to left (relative to apex) with growth. Shell margin sharp; interior white, slightly transparent; muscle scar faintly marked; apical area thickened within.

Radula (Fig. 11): rachidian plate broad, faintly cusped; first and second inner laterals robust, with three divided cusps; third inner lateral with narrow tip; outer lateral massive, with large primary cusp and smaller secondary cusps on inner and outer sides.



Figs. 10–13. *Cocculina cowani* sp.n.—10. Exterior and interior (anterior at top) and lateral (left side) views of holotype. Length 5.8 mm.—11. SEM view of radula of paratype. Horizontal width of field 0.35.—12. Right lateral-ventral view of body of paratype; mantle skirt and gill on right side stripped away over head. Length 3.7 mm. Showing equal cephalic tentacles, oral lappets on both sides of mouth, thin edge of foot and two posterior epipodial tentacles.—13. Dorsal view of same specimen, anterior at top, showing white hypobranchial gland in mantle skirt over head and dark rectum extending to right. The shell muscle is the dark zone at posterior and lateral edges; oval muscle bundles are apparent and the left and right anterior terminations are broad. The light colored testis region of the gonad is adjacent to the anterior end of the shell muscle on the right; the digestive gland and ovary occupy the dorsal posterior.

External anatomy (Figs. 12, 13): hypobranchial gland prominent; epipodial tentacles present; gill present; penis a large swelling posterior to tip of right oral lappet.

Dimensions: length 5.8, width 4.5, height 2.8 mm (holotype); length 7.4, width 5.8, height 3.4 mm (largest paratype, LACM).

Comparisons. *Cocculina cowani* differs from other species of the family in having the curved radial riblets. It has some resemblance to '*Cocculina*' *japonica* Dall, 1907 from the Sea of Japan, for which the generic assignment is unknown. That species is larger (8.2 mm in length), more elevated and has a posteriorly projecting apex.

Remarks. Except for the holotype, shells of the larger specimens in the type lot are partially covered with the calcareous tubes of a serpulid polychaete. Some specimens still had pieces of wood attached to the foot.

Etymology. The species is named after Dr Ian McTaggart Cowan, of Victoria, British Columbia, who originally brought this species to my attention.

***Cocculina baxteri* sp.n.** (Figs. 14–18)

'*Cocculina agassizii*'; Dall 1921, p. 172 [British Columbian record only]; McLean in Keen 1971, fig. 173 [upper figure only]. Not *C. agassizii* Dall, 1908, p. 340.

Type locality. On wood, 424–430 m, Prince William Sound, Alaska (60°42.6'N, 148°04.0'W).

Type material. 123 specimens collected in *Bankia* channels and tunnels drilled in spruce log, collected by Rae Baxter, R/V *Oregon* cruise 78-1, 26 April 1978. Holotype LACM 2067, 78 paratypes LACM 2068, 10 paratypes CAS 050120, 10 paratypes NMC 86718, 10 paratypes USNM 784752, 5 paratypes NMNZ 34200.

Referred material. One specimen (Fig. 15), USNM 226123, USFC sta. 4201, 265 m, Queen Charlotte Sound, off Fort Rupert, Vancouver Island, British Columbia.

Description. Shell (Fig. 14) small for genus (maximum length 4.9 mm), white, with pale brown periostracum. Relatively high; height of holotype 0.53 times length. Anterior slope convex; lateral slopes slightly convex; posterior slope slightly concave. Outline (in dorsal view) elongate oval; anterior end markedly broader than posterior. Apex posterior, 1/8 shell length from posterior end, lower than maximum height of shell; apical tip strongly projecting down and to left. Protoconch bulbous, length 150 µm, sculpture not apparent (under dissecting microscope). Teleoconch sculpture of numerous, faintly raised radial ribs; width of ribs approximately equal to interspaces; concentric sculpture not apparent. Shell margin sharp; interior white; muscle scar not evident; apical area thickened to fill projecting apical tip.

Radula (Figs. 16, 17): rachidian plate broad, faintly cusped and having two longitudinal ridges; first and second inner laterals robust and cusped; third inner lateral uncusped; outer lateral with large primary cusp, an outer secondary cusp and two inner secondary cusps; marginals numerous.

External anatomy (Fig. 18): epipodial tentacles and gill present; penis thick, posterior to right oral lappet; hypobranchial gland not prominent.

Dimensions: length 4.9, width 3.5, height 2.6 mm (holotype).

Comparisons. This species is smaller and more elevated than *Cocculina cowani* sp.n. It differs from *Cococrater agassizii* (Dall, 1908), from the Gulf of Panama (Figs. 19, 22), in having the apex markedly deflected to the left. The radula of *C. baxteri* differs from that of *C. cowani* in having the rachidian plate narrower and in having two rather than one secondary cusp on the inner side of the massive outer lateral.

Remarks. The shell of the British Columbian specimen identified by Dall (1921) as '*Cocculina*' *agassizii* (Fig. 15) has the sculpture and proportions, including the leftward deflected apex, of *C. baxteri*; its identity is therefore

reasonably certain. This specimen is similar in size to those of the type lot. The shell is badly eroded and thickened from within; it appears to be an older shell, suggesting that maximum size had been attained by specimens in the type lot. What appear to be dark patches of periostracum on the figure of this shell (and to a lesser extent on the holotype) are the remains of a hydractinian hydrozoan.

The condition of the massive outer lateral of *C. baxteri* may be unusual in having two inner secondary cusps. Hickman (1983) reported that the massive outer lateral in the cocculinid radula has a "large primary cusp and a smaller secondary cusp on either side".

Etymology. Named after Rae Baxter, of Bethel, Alaska, who collected the type lot.

***Cococrater* Haszprunar, 1987**

Type species. *Cocculina radiata* Thiele, 1903, in Martens & Thiele (1903).

Remarks. *Cococrater* was proposed by Haszprunar (1987) for species having a pair of posterior epipodial tentacles and the enlarged right cephalic tentacle serving as the penis. Further details about the internal and external anatomy in the genus and the following species are given by Haszprunar (1987).

***Cococrater agassizii* (Dall, 1908)** (Figs. 19–22)

Cocculina agassizii Dall, 1908, p. 340; McLean in Keen 1971, p. 361, fig. 173 [lower figure only].

Cocculina sp. D; Hickman 1983, p. 82, fig. 17 [radula, cited from Galathea sta. 276; error for sta. 726].

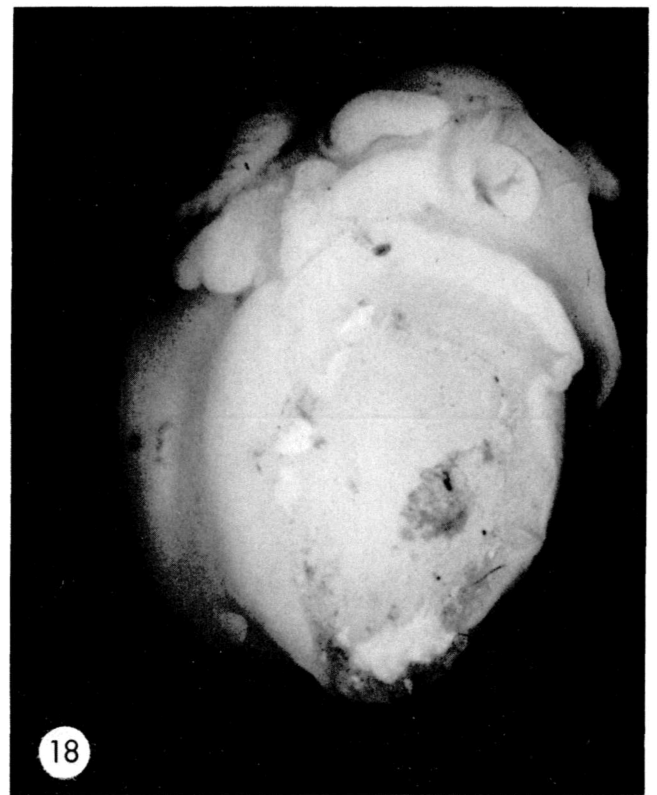
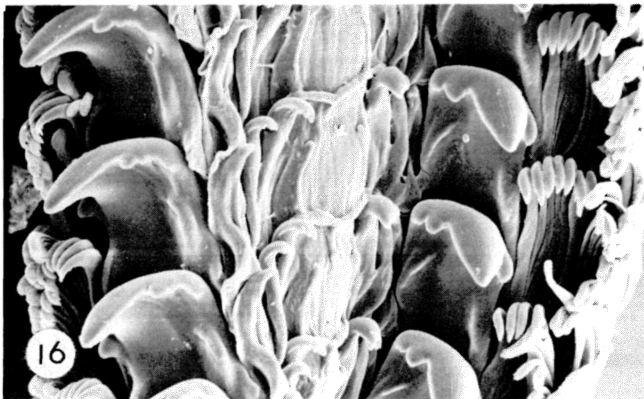
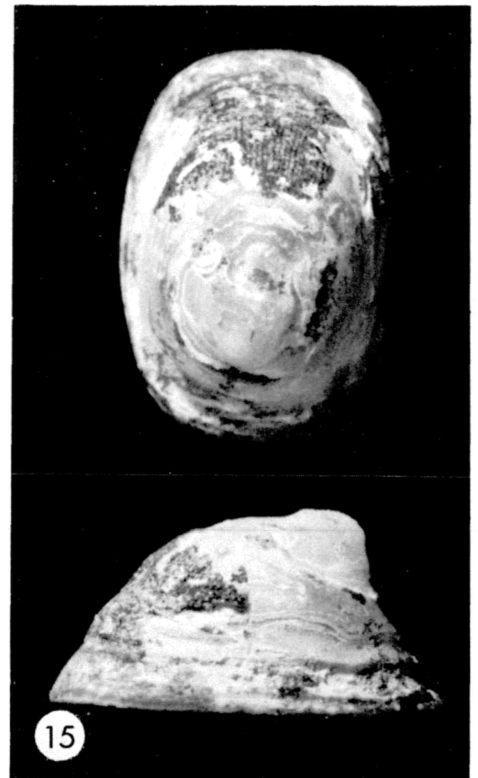
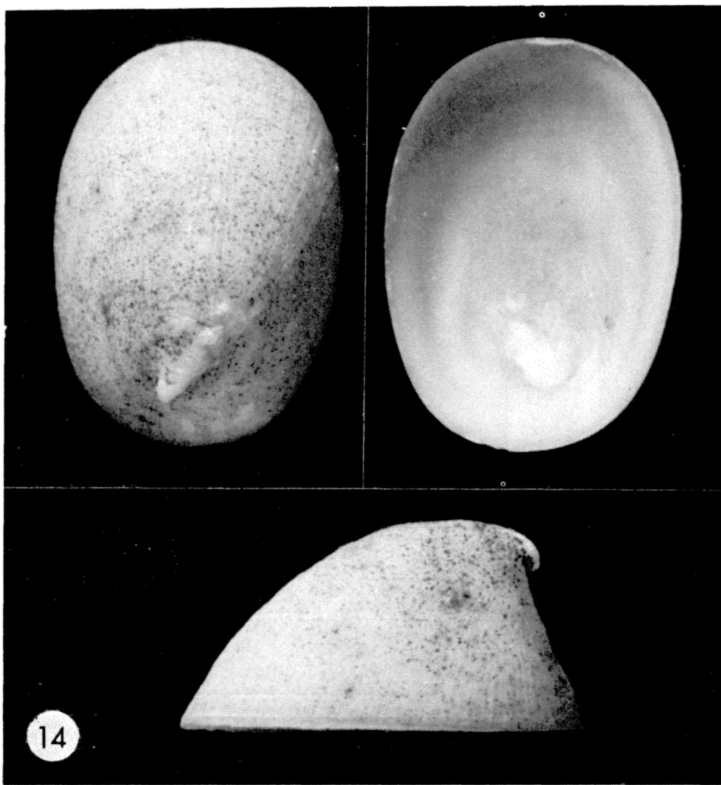
Type locality. 1015 m, Gulf of Panama (6°55'N; 81°42.5'W).

Type material. Holotype (Fig. 18), USNM 110660, USFC sta. 4360 (dry shell with dry animal).

Material studied. 4 specimens (Fig. 15), ZMC, Galathea sta. 726, 3710 m, Gulf of Panama (5°49'N, 78°52'W), 13 May 1952 (3 intact specimens in alcohol and 1 broken dry shell); of these specimens one wet preserved body from which the radula was extracted remains; one body was used by Hickman for radular preparation; one body was sectioned by Haszprunar).

An additional specimen from this station represents another species of cocculinid; the apical area is uneroded and the periostracal ridges are lacking; the specimen is not treated further, as the soft parts are missing.

Description. Shell (Figs. 19, 22) of moderate size for family (maximum length 6.9 mm), thick; apical area eroded to chalky white; shell surface near margin protected by thick brown periostracum. Relatively high, height of holotype 0.57 times length. Outline in dorsal view oval; anterior end narrower than posterior. Anterior slope convex; posterior and lateral slopes straight to slightly convex. Protoconch unknown; apical area of all specimens deeply eroded; apical position mid-dorsal at highest point of shell, slightly posterior to center; apical tip directed posteriorly. Uneroded sculpture of strongly raised periostracal ridges; concentric sculpture not evident. Shell margin sharp, interior white, thickened at apex and clearly defining muscle scar. Tips of muscle scar slightly expanded; anterior pallial line narrow, well defined.

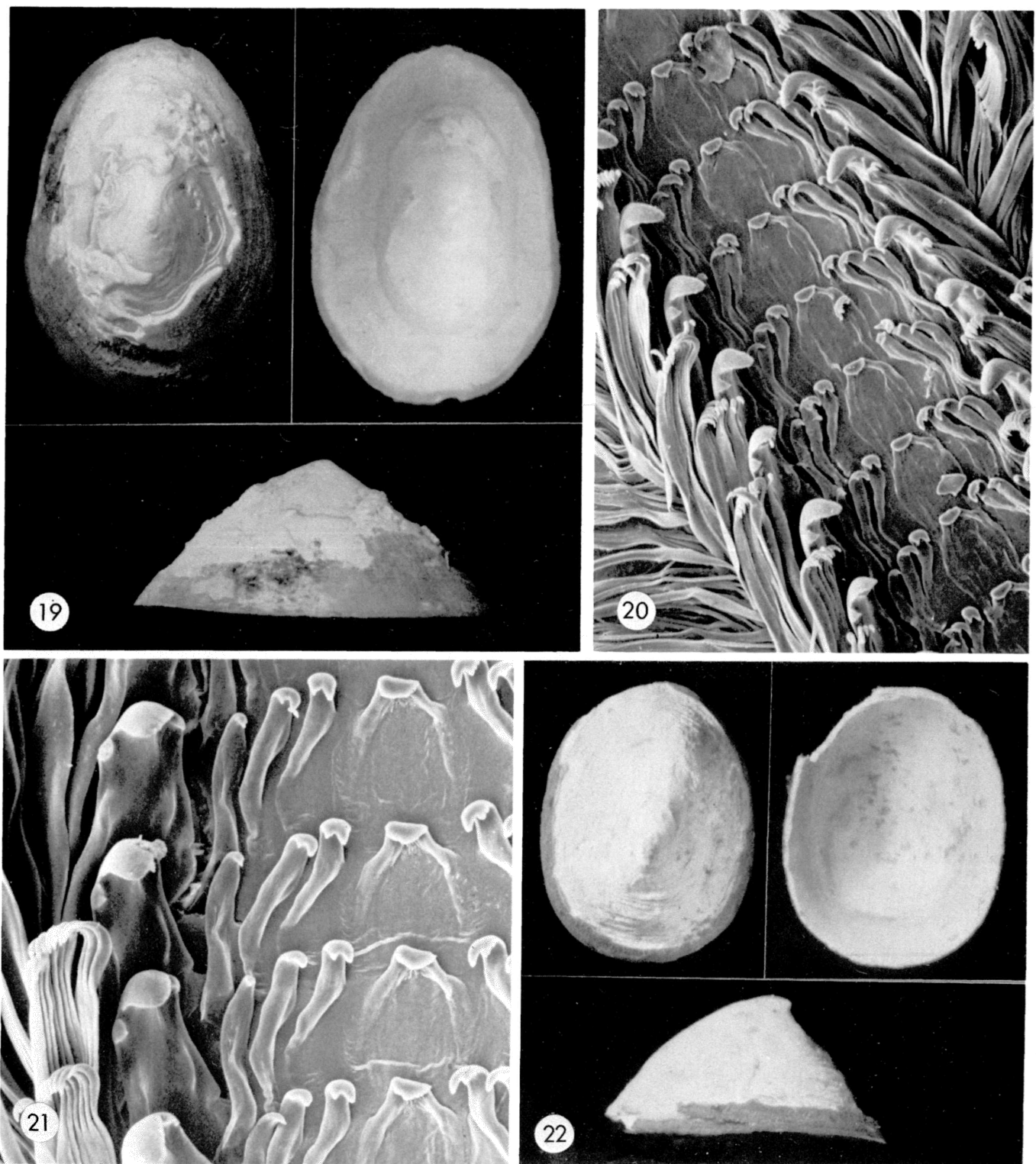


Figs. 14–18. *Cocculina baxteri* sp.n.—14. Exterior and interior (anterior at top) and lateral (left side) views of holotype. Length 4.9 mm.—15. Exterior (anterior at top) and left side views of British Columbian specimen (USNM 226123). Length 4.5 mm.—16. SEM view of radula of paratype. Horizontal width of field 0.30 mm.—17. Same preparation. Horizontal width of field 0.20 mm.—18. Right lateral-ventral view of body of paratype, mantle skirt stripped away over head. Length 2.9 mm. Showing cephalic tentacles, oral lappets extending lateral to both sides of mouth, thick cephalic tentacles above oral lappets, gill on right side dorsal to cephalic tentacle and penis with thick base ventral to gill. The left epipodial tentacle of this specimen has a side branch, the only example of this noted.

Radula (Figs. 20, 21): rachidian tooth elongate, its simple overhanging cusp with strong lateral props that define edges of shaft; three inner lateral teeth with slender shafts and coarsely divided cusps; outer lateral with large main cusp and smaller distal cusp; marginals numerous.

External anatomy: see Haszprunar (1987).

Dimensions: length 3.5, width 2.5, height 2.0 mm (holotype); length 6.9, width 4.8, height 3.0 mm (Fig. 19, largest of 4 specimens cited above).



Figs. 19–22. *Cococrater agassizii* (Dall).—19. Exterior and interior (anterior at top) and lateral (left side) views of shell from 3710 m, Gulf of Panama. Length 6.9 mm.—20. SEM view of radular ribbon of specimen from same lot. Horizontal width of field 0.30 mm.—21. Same preparation. Horizontal width of field 0.10 mm.—22. Exterior and interior (anterior at top) and lateral (left side) views of holotype. Length 3.5 mm.

Comparisons. The only other species known to have the generic characters of *Cococrater* is the type species *Cococrater radiata* (Thiele 1903), which differs markedly in having a low profile and fine, smooth radial sculpture. The only other described cocculinid from the equatorial eastern Pacific is the much larger '*Cocculina*' *nassa* Dall, 1908, for which the anatomy and generic assignment remain unknown.

Remarks. The present material is larger than the holotype (maximum length 6.9 compared to length 3.5), but is identified as *C. agassizii* because it comes from the same faunal area and shares with the holotype the following features: extreme erosion and pitting of the apical region, the elevated profile with apex posterior to center and the dark brown periostracum with strong radial ridges.

Acknowledgements

I am indebted to Gerhard Haszprunar for making it possible to assign the species to genera based upon anatomical characters. I thank Paul S. Mikkelsen of the Harbor Branch Foundation, Inc., Fort Pierce, Florida, for loan of the specimen of *Cocculina rathbuni*. Material of *C. ovata* was loaned by Philippe Bouchet of the MNHNP. Material of *C. cowani* was provided by Ian M. Cowan, of Victoria, British Columbia, and Frank R. Bernard of the Fisheries Research Board of Canada, Nanaimo, British Columbia, that of *C. baxteri* by Rae Baxter of the Alaska Department of Fish and Game, Bethel, Alaska. Serial sections of *C. cowani* and *C. baxteri* were made by Jo-Carol Ramsaran of the LACM Malacology Section. Photographs of the limpet bodies were made by LACM volunteer Bertram C. Draper. SEM micrographs of radulae of *C. cowani* and *Cocccrater agassizi* were made by Carole S. Hickman, University of California, Berkeley, those for *C. baxteri* by Bruce Marshall of the NMNZ, those for *C. ovata* at the University of Southern California, Los Angeles. Both G. Haszprunar and B. Marshall made their papers on cocculinids available to me prior to publication; I thank them for commentary on the manuscript.

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