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TROPICAL EASTERN PACIFIC LIMPETS OF THE FAMILY ACMAEIDAE (MOLLUSCA, ARCHAEOGASTROPODA): GENERIC CRITERIA AND DESCRIPTIONS OF SIX NEW SPECIES FROM THE MAINLAND AND THE GALÁPAGOS ISLANDS

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ABSTRACT: We define genera on conservative shell structure characters and on qualitative radular characters. *Lottia*, previously considered monotypic, is expanded to include Panamic species with a secondary gill (branchial cordon) formerly assigned to *Scurria*. *Scurria* has a similar gill, but the shell structure differs. The new species *Notoacmea ubiquita* from Mexico and *N. pumila* from Ecuador are small-shelled allopatric species with radular teeth modified for feeding on coralline algae. Two new species of *Notoacmea* (*N. rothi* and *N. immaculata*), endemic to the Galápagos Islands, constitute a species pair differing chiefly in radular features: the radular teeth of *N. immaculata* are adapted for feeding on calcareous algae; those of *N. rothi* for noncalcareous algae. A pair of endemic new species of *Lottia* from the Galápagos Islands (*L. mimica* and *L. smithi*) also differ mainly in radular characters. *Lottia mimica* is a noncalcareous-alga feeder and *L. smithi* is a calcareous-alga feeder. These four endemic species are the principal acmaeid limpets of the Galápagos. Two mainland species, *Notoacmea filosa* and *Lottia mesoleuca*, are known only sporadically from the Galápagos Islands.

INTRODUCTION

The last comprehensive, illustrated review of the Acmaeidae of the tropical eastern Pacific was given by McLean (1971). At the time of preparation of that account, two of the species described herein—*Notoacmea ubiquita* and *Lottia mimica*—were recognized as new but were not described. The generic placement of these two species was puzzling because they had previously unknown combinations of radular, shell, and gill characters.

Further study of generic relationships has now provided a basis for the convincing allocation of these species. Although a full review of generic

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criteria in the family is beyond the scope of this paper, we include some discussion pertaining to the Panamic species. A major distinction has become apparent between *Lottia* Sowerby, 1834, and *Scurria* Gray, 1847, two genera having a secondary gill (accessory gill lappets on the mantle margin). These two genera are redefined here, the name *Lottia* thus being made available for use for some tropical species previously considered to belong to *Scurria*.

A closer examination of the acmaeids of the Galápagos Islands has resulted in the recognition of four new endemic species, representing two species pairs wherein the principal differences are in radular tooth morphology. The shell characters of each pair are insufficiently distinct to permit reliable identification by shell alone. Radular characters in the Acmaeidae have been found by all workers to be species-specific. In no species has ontogenetic or situs variation in radulae been found. Similar shell morphologies have been reported, however, in both congeneric and noncongeneric species of Acmaeidae (McLean 1966; Lindberg 1979). We therefore consider each radular morphotype to represent a separate species. Because the shell characters of each pair are insufficiently distinct to permit reliable identification, both species are discussed in a combined discussion section following their formal descriptions.

Abbreviations are as follows: AHF, Allan Hancock Foundation, University of Southern California, Los Angeles (collection on loan to LACM); AMNH, Department of Invertebrates, American Museum of Natural History, New York; ANSP, Department of Malacology, Academy of Natural Sciences, Philadelphia; CAS, Department of Invertebrate Zoology, California Academy of Sciences, San Francisco; LACM, Section of Malacology, Natural History Museum of Los Angeles County, Los Angeles; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge; SU, Stanford University, Stanford (collection on loan to CAS); USNM, Division of Mollusks, U.S. National Museum of Natural History, Washington, D.C.

Generic Criteria for the Panamic Acmaeidae

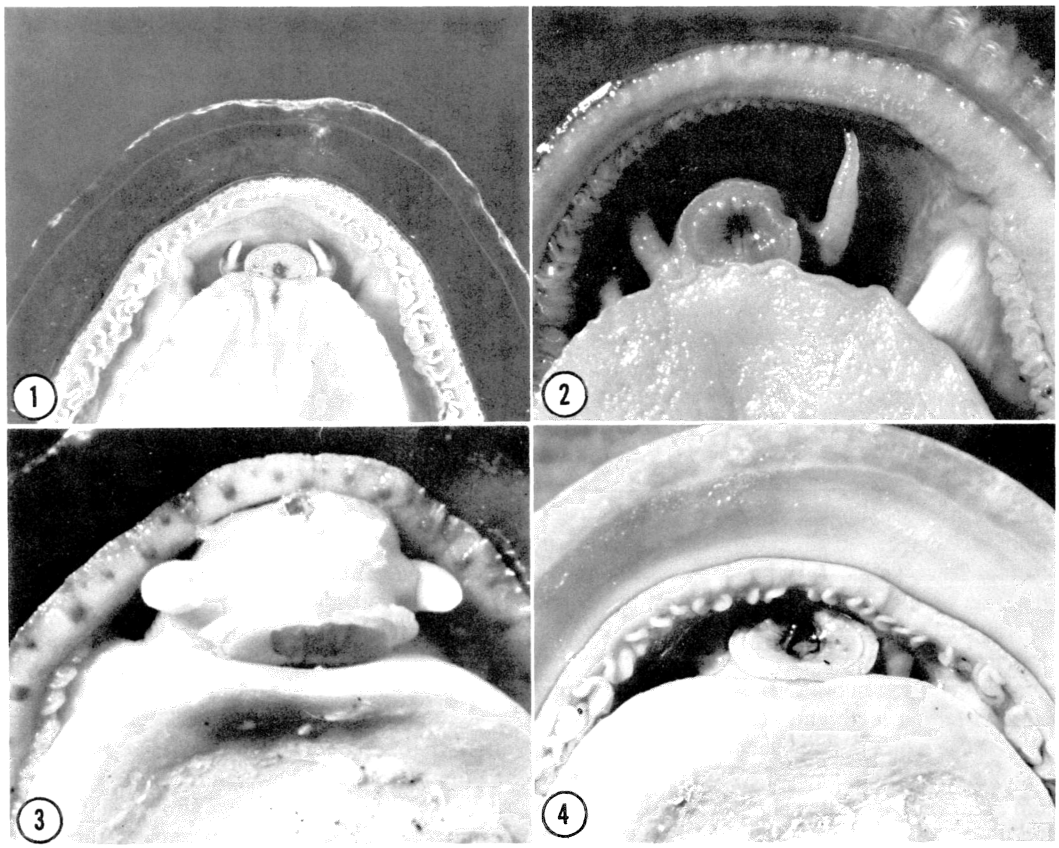
Generic assignments in McLean's (1971) review were based on shell sculpture, presence or absence of the secondary gill, and whether marginal radular teeth are represented by two pairs of fully developed teeth, a single pair of rudimentary teeth (uncini), or are absent altogether. We now realize that a system based on these three characters alone is not adequate.

Christiaens (1975) proposed a generic classification of the Acmaeidae in which tooth shape and configuration were especially emphasized. He felt some genera had three pairs of lateral teeth and some two, the latter group having a bicuspid second lateral tooth. We maintain that all acmaeids have three pairs of lateral teeth. We fail to see how the third lateral tooth can be interpreted as part of the second, because in all acmaeid radulae we have examined, we find that the ventral plates of the radular ribbon have three lateral plate components, one corresponding to each lateral tooth. We believe that the reduction of the outermost tooth that occurs in some species is a result of dietary specialization. Relation of diet to tooth shape was discussed by McLean (1966), and we are now aware of similar tooth shape and configuration in species of diverse genera. We do not consider lateral tooth shape to be useful as a generic character.

We continue to maintain full generic separation of species groups in which the marginal teeth have three possible expressions: (1) two pairs of fully functional marginals (*Patelloida* Quoy and Gaimard, 1834); (2) a single pair of marginal remnants or uncini (*Collisella* Dall, 1871; *Lottia* Sowerby, 1834; *Scurria* Gray, 1847); and (3) no marginals or uncini (*Acmaea* Eschscholtz, 1833; *Notoacmea* Iredale, 1915; *Problacmaea* Golikov and Kussakin, 1972; *Rhodopetala* Dall, 1921; and *Tectura* Gray, 1847). We therefore disagree with Christiaens's ranking of *Notoacmea* as a subgenus of *Collisella*.

Recent work by Lindberg (1976, 1978) has employed shell structure characters first used for patellacean limpets by MacClintock (1967). We believe that the relationships suggested by shell structure are conservative and are basic to a modern classification of the family.

We are now inclined to define genera using shell structure, branchial characters, radula basal plate structure, and the three possibilities for marginal teeth listed above, recognizing that shell sculpture characters are convergent in all genera and that lateral tooth shape is likewise



FIGURES 1–4. Ventral views of preserved specimens of *Lottia* and *Scurria* species showing secondary gill in relation to head. FIGURE 1. *Lottia gigantea*, Isla de Guadalupe, Mexico (LACM 55618). FIGURE 2. *Lottia mesoleuca*, Bahía Tenacatita, Jalisco, Mexico (LACM 66-55). FIGURE 3. *Lottia mimica* new species, paratype, Academy Bay, Isla Santa Cruz, Galápagos Islands, Ecuador (LACM 1926). FIGURE 4. *Scurria scurra*, Punta El Lacho, Santiago Province, Chile (LACM 75-32).

convergent and widely variable interspecifically (although not intraspecifically).[1]

Acmaea and *Notoacmea* differ in lateral plate morphology. In *Acmaea* the lateral plates are similar in size and shape and are arranged in a posteriorly diverging V-configuration. In *Notoacmea* the lateral plates are unequal in size and shape—the first and second lateral plates tend to lie in the same line and the third lateral plates are always lateral and slightly posterior to the second lateral plates.

Acmaea and *Tectura* also differ in lateral plate morphology. In both genera dentition consists of three pairs of equal-sized and equal-shaped lateral teeth; however, in *Tectura* the lateral plates that support these teeth are complex and similar in shape and position to those found in the genus *Collisella*.

All species of *Acmaea* are known to feed on coralline algae and have blunt, equal-sized teeth. Some of the tropical eastern Pacific and Caribbean species of *Notoacmea* are now known to have teeth similarly blunt and of equal size. These species may also be coralline alga feeders. Three of the four new species of *Notoacmea* described in this paper (*N. ubiquita*, *N. pumila*, and *N. immaculata*) have blunt equal-sized lateral teeth. The other new species of *Notoacmea*, *N. rothi*, has the outermost lateral tooth

[1] In his discussion of *Notoacmea fascicularis* (Menke, 1851) McLean (1971:327) alluded to two different radular types within that species, suggesting that a "complex involving more than one species" was a possibility. Lindberg will report separately on the two species of the *N. fascicularis* complex.

greatly reduced and the first two pairs more elongate, which is the pattern characteristic of most temperate and tropical species of *Notoacmea*.

Similar modification of the lateral teeth for feeding on coralline algae is known in some tropical species of *Collisella*. Eastern Pacific species of this uncinate genus with lateral teeth so modified are: *C. atrata* (Carpenter, 1857), *C. discors* (Philippi, 1849), *C. mitella* (Menke, 1847), and *C. pediculus* (Philippi, 1846).

Two generic names have been used for acmaeid limpets in which there is a secondary gill (branchial cordon) in addition to the normal acmaeid ctenidium: *Lottia* Sowerby, 1834 (type-species *L. gigantea* Sowerby, 1834), and *Scurria* Gray, 1847 (type-species *Patella scurra* Lesson, 1830). *Lottia* has usually been considered monotypic, with the single Californian species *L. gigantea*. It has been diagnosed (Dall 1871) as having a secondary gill incomplete or interrupted in front of the head, whereas in *Scurria* the gill is complete or continuous. The radular dentition in both genera consists of three pairs of lateral teeth and one pair of uncini.

We have examined the secondary gill in living and preserved specimens of *L. gigantea* and find that many specimens have a greatly reduced but distinct gill in front of the head (Fig. 1). The secondary gill of a tropical eastern Pacific species usually assigned to *Scurria, S. mesoleuca* (Menke, 1851), is normally much less prominent in front of the head than along the sides (Fig. 2). The secondary gill of *Lottia mimica,* new species (Fig. 3), is also much reduced in front of the head. The secondary gill of *Scurria scurra* (Fig. 4) is complete over the head, but it is also somewhat reduced in prominence in this region. We therefore do not regard the reduction of the secondary gill near the head as a useful generic character.

MacClintock (1967) found that *Scurria* in the Peruvian faunal province differ in shell structure from other eastern Pacific species with the secondary gill. The Peruvian *Scurria* species are in MacClintock's shell structure "group 3," whereas *Lottia gigantea* and the two species placed by McLean (1971) in *Scurria* (*S. mesoleuca* and *S. stipulata* (Reeve, 1855)) are in shell structure "group 1" (along with most other species of *Collisella* and *Notoacmea*). Because we believe that shell structure is more conservative than branchial characters, and we place even less emphasis on shell sculpture and coloration, we infer that the Panamic acmaeids previously assigned to *Scurria* are more closely related to *L. gigantea* than to *Scurria*. The two Panamic species plus *L. mimica* and *L. smithi* described in this paper are therefore assigned to *Lottia*. *Lottia* is redefined to include uncinate species in shell structure "group 1," with a secondary gill that is usually reduced but not necessarily absent over the head.

New Species of Acmaeidae from the Tropical Eastern Pacific

Notoacmea ubiquita new species

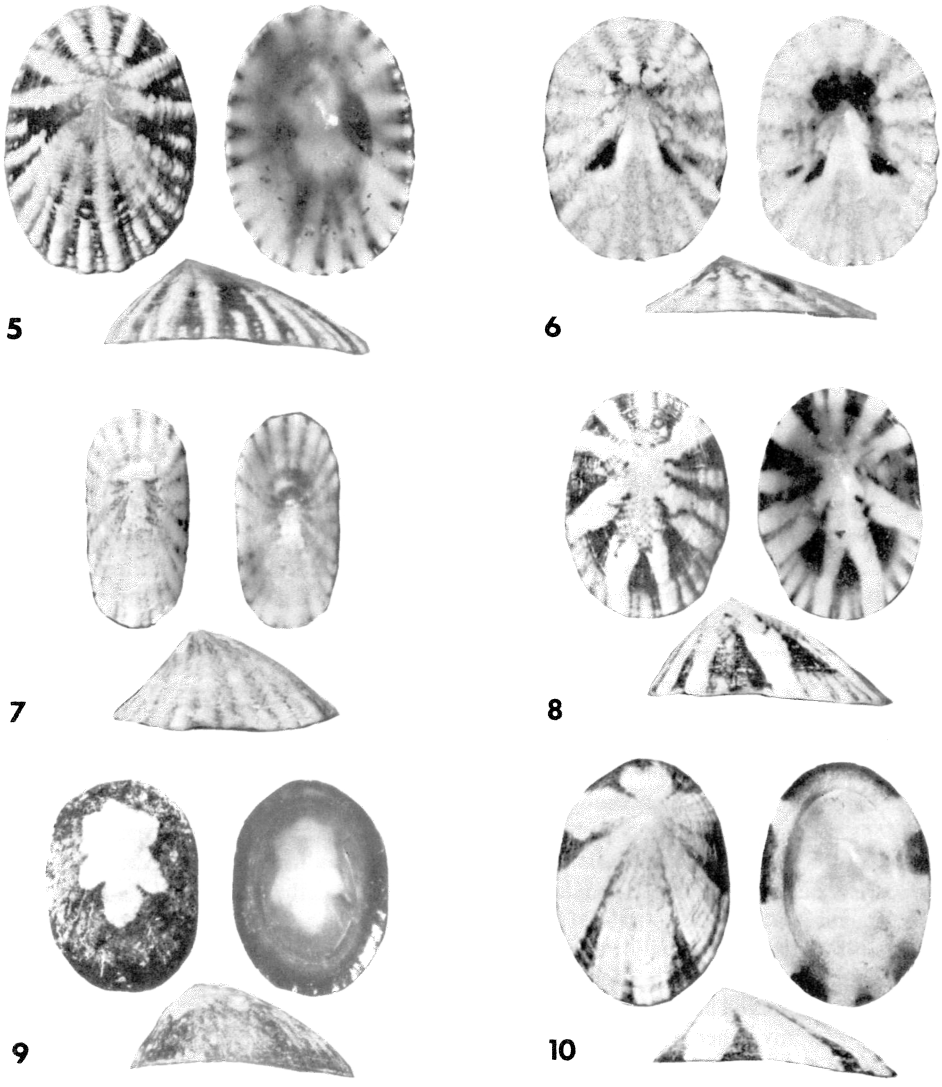
(Figures 5–7, 23, 29)

There are two situs forms of this species, a laterally compressed form and an oval form. A description for each follows.

Shell (oval form) (Figs. 5, 6): Relatively small (maximum length 12 mm), profile of medium height; apex anterior to center; all slopes convex; large shells frequently with a flattened area posterior to apex; sides of shell somewhat parallel. Sculpture of rounded radial ribs, with weaker secondary ribs beginning below apex; ribs extending slightly beyond the shell edge, crenulating the aperture; concentric sculpture of well-defined but nearly microscopic, sharply raised ridges. Exterior translucent white with red-brown markings on early shell, the markings becoming darker, reticulate, and limited to rib-interspaces with growth; ribs white, overlain with dark brown radial markings that may be concentrated into lateral rays. Interior margin white with dark markings that correspond to exterior interspaces; intermediate area white; central area with yellow stain, exterior markings visible through shell.

Shell (compressed form) (Fig. 7): Lateral profile high, ends raised relative to sides; all slopes convex; some specimens compressed in early stage, changing abruptly to oval form. Sculpture and coloration as in oval form.

Radula (Figs. 23, 29): First pair of lateral teeth closely set at anterior edge of ribbon segment, medial edges convex, lateral edges straight to slightly concave, cusps rounded, blunt; second pair of lateral teeth posterior and lateral to first pair, medial and lateral edges convex, cusps rounded, blunt; third lateral teeth lateral to sec-



FIGURES 5–10. FIGURE 5. *Notoacmea ubiquita* new species. Holotype, LACM 1917. Santiago Peninsula, Colima, Mexico. Length 11.7 mm. FIGURE 6. *Notoacmea ubiquita*. LACM 54773. Guaymas, Sonora, Mexico. Length 6.9 mm. FIGURE 7. *Notoacmea ubiquita*. LACM 54773. Guaymas, Sonora, Mexico. Length 5.4 mm. FIGURE 8. *Notoacmea pumila* new species. Holotype, LACM 1919. Punta Ancon, Ecuador. Length 4.7 mm. FIGURE 9. *Notoacmea pumila*. Paratype, LACM 1920. Punta Ancon, Ecuador. Length 3.6 mm. FIGURE 10. *Notoacmea pumila*. LACM 72-17. Bahía Jobo, Costa Rica. Length 5.6 mm.

ond pair, medial edges concave, lateral edges straight, extending to edges of ventral plates, cusps blunt. Marginal teeth lacking. First lateral plates overlap anterior ribbon segment, posterolateral edges concave; second lateral plates irregular, posterior edges convex; third lateral plates lobate with lateral lobes extending to edges of ventral plates; second and third lateral plates separated by a partial suture. Ventral plates closely set with both anterior and posterior processes.

Animal: Pigmentation lacking, snout with oral lappets.

HOLOTYPE DIMENSIONS.—Length 11.7, width 8.1, height 3.6 mm.

TYPE-LOCALITY.—Mexico: Colima; Manzanillo, Santiago Peninsula, Playa Las Hadas (19°05′57″N, 103°19′36″W) (LACM 63-10), inter-

tidal zone to 5 m. *Leg.* J. H. McLean and C. Tenney, 21–24 Mar. 1963, 3 specimens.

TYPE-MATERIAL.—Holotype (oval form), LACM 1917; 2 paratypes, LACM 1918 (both oval and compressed forms). The holotype is the largest specimen examined.

DISTRIBUTION.—Baja California Sur, Mexico, from Punta Pequeña (26°14'N) (LACM 71-6) to Bahía Magdalena and Cabo San Lucas, north in the Gulf of California to Puertecitos (30°25'N) (LACM 65-34) and Guaymas, south to Bahía Tangola Tangola, Oaxaca (15°45'N) (AHF 215).

MATERIAL EXAMINED.—58 lots, approximately 350 specimens, 3 radula preparations.

ETYMOLOGY.—The name is based on the Latin adverb *ubique* (everywhere). The species is indeed ubiquitous—shells, at least, have been recovered from sediment residues taken by divers from nearly all LACM station localities throughout the range.

DISCUSSION.—Although *Notoacmea ubiquita* has been known for many years, it was not described earlier because of uncertainties about its generic position. Its shell shape and sculpture suggested *Collisella,* and its lack of uncini and subtidal habitat suggested *Acmaea.* We are now satisfied to place it in *Notoacmea* because of the basal plate configuration. Although most species of *Notoacmea* are finely ribbed, the rather more prominent ribbing of *N. ubiquita* is not as strong as occurs in many species of *Collisella.*

Notoacmea ubiquita is the only Panamic acmaeid with an oval form and a laterally compressed form. *Notoacmea ubiquita* has broader, stronger ribs than any other tropical species of *Notoacmea.* On the basis of shell characters, it is more similar to some of the Panamic *Collisella,* which differ in having an uncinate radula. The fine brown concentric markings of the early stages do not occur in any other species. *Collisella turveri* (Hertlein and Strong, 1951) differs in having broader, more projecting ribs. *Collisella acutapex* (Berry, 1960) has a higher shell profile with sharper, more prominent ribbing, and its pattern of brown lines is more coalescing. *Collisella mitella* (Menke, 1847) also has white ribs, but its ribs are more numerous and the interspaces are dark colored. *Patelloida semirubida* (Dall, 1914) has sharper radial and concentric sculpture, with red rather than brown markings; its radula is also markedly different, having two pairs of marginal teeth per ribbon segment.

Large lots show a complete series of possible shell shapes between the elevated narrow forms with raised ends and the low oval forms. Some shells have an early compressed phase, with later growth stages like the oval form; some relatively large shells are angulate at the sides, giving the shell a flat-topped appearance. Color variation is relatively minor; one color variant characteristic of specimens from Jalisco is ordinary in early stages, changing to solid maroon at later stages. Largest shells seen are from Jalisco and Colima; specimens from localities in the Gulf of California attain about two-thirds the size of southern specimens.

Notoacmea ubiquita has features in common with two more northern species, *Collisella triangularis* (Carpenter, 1864) and *Tectura rosacea* (Carpenter, 1864), both of which differ in lacking the radial ribbing. All three species have laterally compressed forms, are primarily subtidal, and have equal-sized lateral teeth adapted for feeding on calcareous algae. In *C. triangularis* the compressed form predominates, whereas in *T. rosacea* the oval form is more abundant, but in both species the compressed forms occur on branching coralline algae and the oval forms occur on crustose coralline algae, and all intermediate conditions are known. Although we have not directly observed the compressed form of *N. ubiquita* on branching coralline algae, it probably so occurs, judging from its ability to change from compressed to oval during growth, which implies a change of situs.

Notoacmea pumila new species

(Figures 8–10, 24, 30)

Shell (Figs. 8–10): Small (maximum length 7 mm); profile medium-high; apex anterior to center; anterior slope straight to convex, lateral slopes convex; usually encrusted with coralline algae. Sculpture of fine, sharp radial ribs originating below apex, secondary ribs arising in the interspaces, not reaching thickness of primary ribs. Aperture oval, not crenulate. Color pattern independent of ribbing: most frequently white near apex, gray at margin, with 6 to 10 white rays in a stellate pattern, some rays not reaching margin; some specimens with fine brown lines bordering white rays and fine brown lines that

produce a concentric network. Interior translucent white, showing the exterior pattern.

Radula (Figs. 24, 30): First pair of lateral teeth closely set at anterior edge of ribbon segment, medial edges convex, lateral edges concave, cusps rounded. Second pair of lateral teeth posterior to first pair, medial edges convex, lateral edges straight, cusps rounded. Third pair of lateral teeth positioned posterior and lateral to second pair, medial edges convex, lateral edges straight to slightly concave. Third laterals broader than second laterals, with lateral extensions to edges of ventral plates; cusps rounded. Marginal teeth lacking. First lateral plates irregular, anterior portions overlapping anterior ribbon segments; second lateral plates elongate, ovoid; third lateral plates triangular, with convex posterior edge. Ventral plates with strong anterior and posterior processes. Lateral portions with strong sutures parallel to edges.

Animal: Pigmentation lacking, oral fringe simple.

HOLOTYPE DIMENSIONS.—Length 4.7, width 3.3, height 2.0 mm.

TYPE-LOCALITY.—Ecuador: Santa Elena Peninsula; Punta Ancon, north and south sides (2°20'S, 80°54'W), intertidal zone. *Leg.* J. H. McLean and D. Shasky, 6–7 Mar. 1970 (LACM 70-11, 70-12), 72 LACM specimens, 12 Shasky specimens.

TYPE-MATERIAL.—Holotype, LACM 1919, paratypes, LACM 1920; paratypes have also been deposited in the collections of CAS and USNM, and in Shasky collection (Redlands, California).

DISTRIBUTION.—El Velero, Nicaragua (12°01'N) (LACM 74-86), south to Ecuador (type-locality). There are numerous dead specimens from Bahía Salinas, Costa Rica (11°02'N, 85°45'W) (LACM 72-17, 72-19); two specimens only from Panama at San Carlos (8°29'N, 79°57'W) (LACM 75-55), and a number of localities in Ecuador collected by D. Shasky.

MATERIAL EXAMINED.—19 lots, approximately 200 specimens, 3 radula preparations.

ETYMOLOGY.—The name is a Latin adjective, *pumilus,* meaning small or dwarfish—fitting for this, the smallest tropical eastern Pacific member of the family.

DISCUSSION.—*Notoacmea pumila* could be confused only with two other relatively small forms, *N. ubiquita* new species and *Patelloida semirubida*. It differs from the first in having much sharper ribbing and not being compressed. Although both *N. pumila* and *P. semirubida* have fine sharp radial ribs, *N. pumila* lacks the sharp concentric sculpture and pink markings of *P. semirubida*.

The radula of *N. pumila* is similar to that of two new species described herein, *N. ubiquita* and *N. immaculata*. It differs from both by having a complete rather than partial suture between the second and third lateral plates and having strong ventral plate sutures parallel to the lateral edges. The ventral plates of *N. pumila* have anterior and posterior processes which *N. immaculata* lacks, and the third lateral plates are triangular rather than biformed as in *N. immaculata* and *N. ubiquita*. The radula of *N. pumila* differs from that of *P. semirubida* by lacking marginal teeth.

Large lots show similar color patterns both in the material from Costa Rica and from stations in Ecuador. A small percentage of specimens change with growth from dark rayed to solid dark (see Fig. 9); fewer specimens are rayed only with brown linear markings and fine brown reticulate markings. Shell proportions vary only slightly.

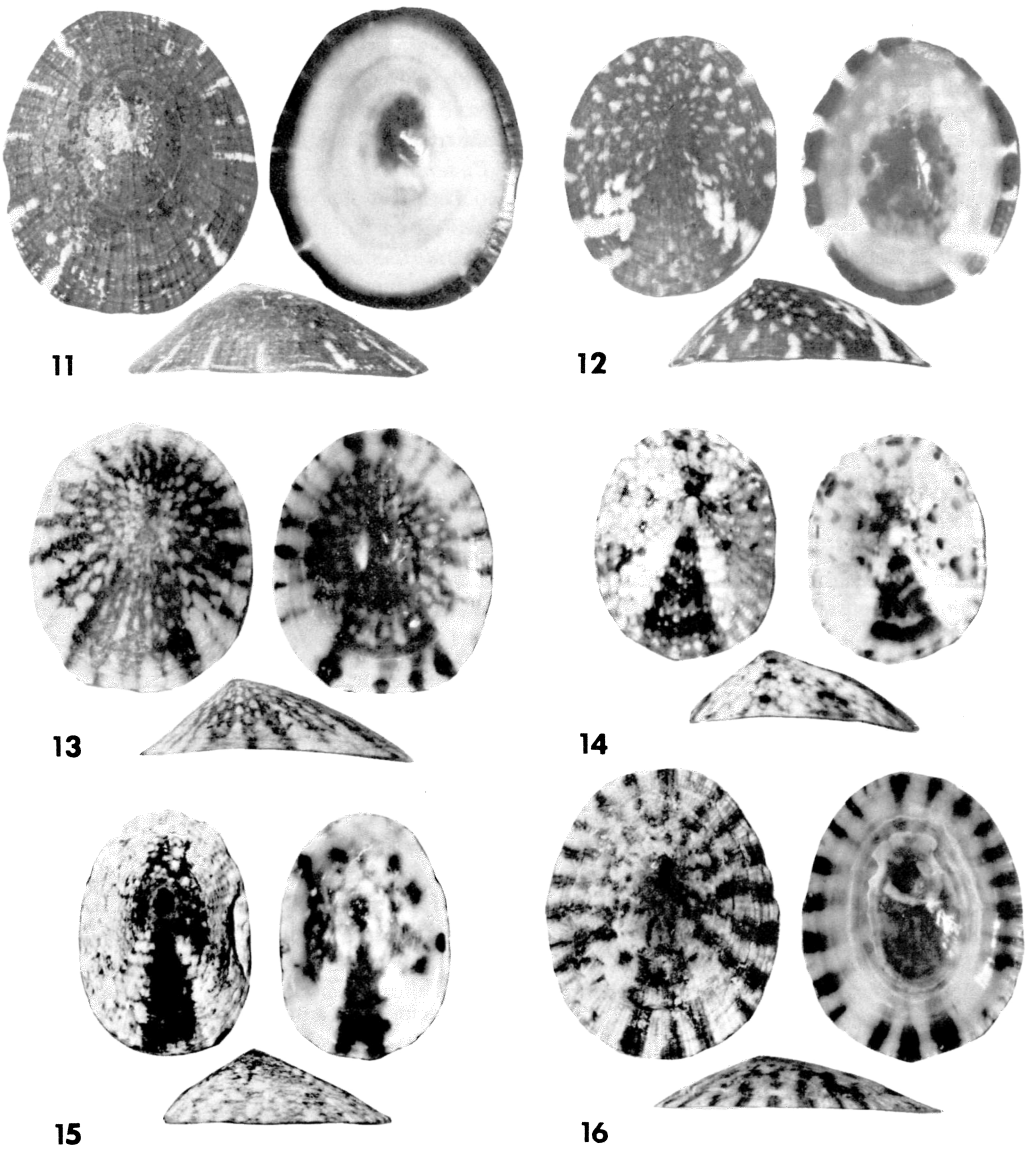
Notoacmea pumila undoubtedly feeds on coralline algae—the lateral teeth are blunt and of equal size. Living specimens have been collected in the low intertidal zone and the species probably also occurs in the immediate subtidal zone on coralline-encrusted rocks.

Notoacmea rothi new species

(Figures 11–13, 25, 31)

Shell (Figs. 11–13): Size medium (maximum length 20 mm), height medium; apex anterior to center; all slopes convex, aperture ovoid. Sculpture of unequal riblets and concentric growth lines; one to three secondary riblets between each two primary riblets. Exterior dark gray with scattered white markings; apical pattern tessellate; white markings often aligned in lateral rays that define a broad, dark posterior ray. Interior margin broad, dark, streaked with white corresponding to exterior pattern; intermediate area blue-white; central area blue-white with brown stain.

Radula (Figs. 25, 31): First pair of lateral teeth closely set at anterior edge of ribbon segment, medial edges convex, lateral edges slightly con-



FIGURES 11–16. *Notoacmea* from the Galápagos Islands. FIGURE 11. *Notoacmea rothi* new species. Holotype, LACM 1921. Wreck Bay, Isla San Cristóbal. Length 16.8 mm. FIGURE 12. *Notoacmea rothi*. LACM 54774. East side, Isla Fernandina. Length 11.5 mm. FIGURE 13. *Notoacmea rothi*. LACM 54777. Bahía Cartago, Isla Isabela. Length 8.8 mm. FIGURE 14. *Notoacmea immaculata* new species. Holotype, LACM 1923. Isla Baltra. Length 5.6 mm. FIGURE 15. *Notoacmea immaculata*. AHF 173-34. Isla Baltra. Length 7.8 mm. FIGURE 16. *Notoacmea filosa* (Carpenter, 1865). LACM 54775. Isla San Cristóbal. Length 15.5 mm.

cave, rounding to pointed cusps. Second pair of lateral teeth lateral to first pair, both edges convex, broad, with pronounced pointed cusps; third lateral teeth lateral to second pair, reduced, medial edges convex, lateral edges straight, cusps angular. Marginal teeth lacking. First lateral plates subrectangular; second lateral plates rounded, separated from third lateral plates by partial suture; third lateral plates biformed, posterior section rounded, lateral section pointed, extending to lateral edges of ventral plates. Ventral plates closely set,

subrectangular, with weak anterolateral extensions.

Animal: Body pigmentation lacking; snout with oral lappets.

HOLOTYPE DIMENSIONS.—Length 16.8, width 14.0, height 4.8 mm.

TYPE-LOCALITY.—Ecuador: Galápagos Islands; Isla San Cristóbal, Wreck Bay (0°54′S, 89°36′W). *Leg.* J. DeRoy, 12 May 1968, 4 specimens.

TYPE-MATERIAL.—Holotype, LACM 1921 (shell and radular slide), 1 paratype, LACM 1922; paratypes also deposited in the collections of CAS and USNM.

DISTRIBUTION.—Galápagos Islands; Isla Fernandina (ANSP 152554), Isla Isabela (SU 239), Isla Rabida (LACM 71-69), Isla Bartolomé (AMNH 163290), Isla Santa Cruz (ANSP 154889), Isla Baltra (AMNH 163263), Isla Santa María (CAS 23025), Isla Santa Fé (AHF 48-33), Isla Española (USNM 102359), Isla San Cristóbal (MCZ 205068).

MATERIAL EXAMINED.—40 lots, 435 specimens, 9 radula preparations.

ETYMOLOGY.—We are pleased to name the species in honor of Barry Roth of the California Academy of Sciences in recognition of his work in molluscan systematics.

Notoacmea immaculata new species
(Figures 14, 15, 26, 32)

Shell (Figs. 14–15): Small (maximum length 12 mm), thin, diaphanous, height medium. Apex anterior to center, anteriorly directed; all slopes convex. Aperture ovoid; sides straight, sides elevated. Sculpture of faint gray, broad riblets and concentric growth lines. Exterior light gray, mottled with yellow-brown, brown, and white; darker markings concentrated into broad posterior ray bordered with white. Interior margin broad, dull, marked with exterior pattern; intermediate area translucent, glossy white; exterior pattern readily visible through shell; central area glossy, translucent, marked with sparse yellow streaks, central stain lacking.

Radula (Figs. 26, 32): First pair of lateral teeth closely set at anterior edge of ribbon segment, medial edges convex, lateral edges straight to slightly concave, tapering to rounded cusps; second pair of lateral teeth posterior and slightly lateral to first pair, both edges convex, tapering to rounded cusps. First and second lateral teeth approximately equal in width. Third pair of lateral teeth posterior and lateral to second pair, medial edges convex, lateral edges elongate, straight to slightly concave, extending to edges of ventral plates, cusps rounded. Marginal teeth lacking. First lateral plates ovoid; second lateral plates rounded posteriorly, separated from third lateral plates by partial suture; third lateral plates lobate. Ventral plates closely set, subrectangular with strong anterior sutures.

Animal: Body pigmentation lacking; snout with oral lappets.

HOLOTYPE DIMENSIONS.—Length 5.6, width 4.3, height 1.4 mm.

TYPE-LOCALITY.—Ecuador: Galápagos Islands; Isla Baltra (0°26′S, 90°17′W), Caleta del Norte, 0–3 m. *Leg.* ANTON BRUUN, cr. 18B, sta. 791, 21 Sep. 1966, 1 specimen.

TYPE-MATERIAL.—Holotype, LACM 1923 (shell and radula slide), 1 paratype, CAS 15920 (shell and radula slide). Paratype from Isla Santa Cruz, Academy Bay.

DISTRIBUTION.—Galápagos Islands; Isla Fernandina (LACM 62-196), Isla Isabela (LACM 71-70), Isla Bartolomé (AMNH 163290), Isla Santa Cruz (ANSP 154889), Isla Baltra (LACM 66-206), Isla San Cristóbal (ANSP 153328).

MATERIAL EXAMINED.—14 lots, 63 specimens, 5 radula preparations.

ETYMOLOGY.—The name is a Latin adjective, *immaculatus* (unstained), referring to the lack of a central stain in the area within the myostracum.

DISCUSSION.—The radular difference that is the chief basis of the separation of the two species is unmistakable and qualitative: in *N. rothi* the third lateral teeth are reduced (Fig. 25) and in *N. immaculata* the third lateral teeth are large (Fig. 26). The lateral plate morphologies are correspondingly different. In *N. rothi* the second and third lateral plates are approximately equal in size, and the lateral edges of the third lateral plates form small pointed projections. In *N. immaculata* the third lateral plates are larger than the second lateral plates and the lateral projections are rounded.

The shells of *N. rothi* and *N. immaculata* have similar overall proportions and sculpture. The color pattern consists of radiating and scattered whitish tessellations, with the greatest concentration of white tessellations in two latero-posterior rays, the posterior area between

the two rays having the least amount of tessellate flecking so that it may appear to be a single, uniformly dark posterior ray. Those specimens confirmed on radular examination to have the tooth pattern of *N. rothi* have the dark gray-green ground color predominating, whereas those identified as *N. immaculata* have a light gray or white ground color. The largest specimens examined have proven to be *N. rothi*; the largest specimen verified as *N. immaculata* is 12 mm in length. The large specimens of *N. rothi* have a dark interior stain, which is generally lacking in *N. immaculata*. One small, stunted specimen verified as *N. immaculata* (LACM 71-48) shows a slight trace of brown interior stain. It is possible that the brown stain is indicative of the attainment of size rather than a species-specific character. Too few specimens verified as *N. immaculata* are available to enable us to be certain that any shell characters may be used as proof of identity.

Of the mainland acmaeid species, the *Notoacmea rothi–immaculata* complex resembles *Notoacmea filosa* (Carpenter, 1865) (Fig. 6), which has similar shell characters. They differ from *N. filosa* in the following ways: *N. rothi–immaculata* has a profile of medium height; *N. filosa* has a low profile. In *N. rothi–immaculata* the interspaces are broader than the riblets; in *N. filosa* the riblets are more numerous and the interspaces approximately equal in width to the riblets. *Notoacmea filosa* has a color pattern of radiating dark and lighter rays, often interrupted, but not tessellated in circular or oval patterns. The tessellate markings are characteristic of *N. rothi–immaculata*. The dark posterior ray of *N. rothi–immaculata* is not a feature of *N. filosa*.

Although the configuration of the lateral teeth of *N. filosa* has little in common with that of *N. immaculata*, there is a similarity between *N. filosa* and *N. rothi*. However, the shape of the second lateral teeth differs: in *N. filosa* the second lateral teeth are triangular; in *N. rothi* the second lateral teeth are broad with convex edges.

No detailed observations on the habitat of either species are available to us. We know from collection data on museum specimens that *N. rothi* occurs intertidally. Specimens are relatively free of encrustations except for some coralline algae and spirorbid worm tubes. The edges of the apertures are smooth and oval, not molded to fit a habitual site of attachment, suggesting that the normal habitat is likely to be on the undersides of stones in tidepools. Station data for the holotype of *N. immaculata* indicate a depth of 0 to 3 m. The absence of specimens in the intertidal collections of J. DeRoy suggests that *N. immaculata* is essentially a subtidal species.

The elongated teeth of *N. rothi* are similar to those of such temperate species as *Collisella pelta* (Rathke, 1833), *Notoacmea persona* (Rathke, 1833), and *Lottia gigantea*. All have pointed cusps on the first and second laterals and reduced third laterals. These temperate species are known to feed upon sessile diatoms and noncalcareous algae in the middle and high intertidal zones, so we infer that *N. rothi* does also.

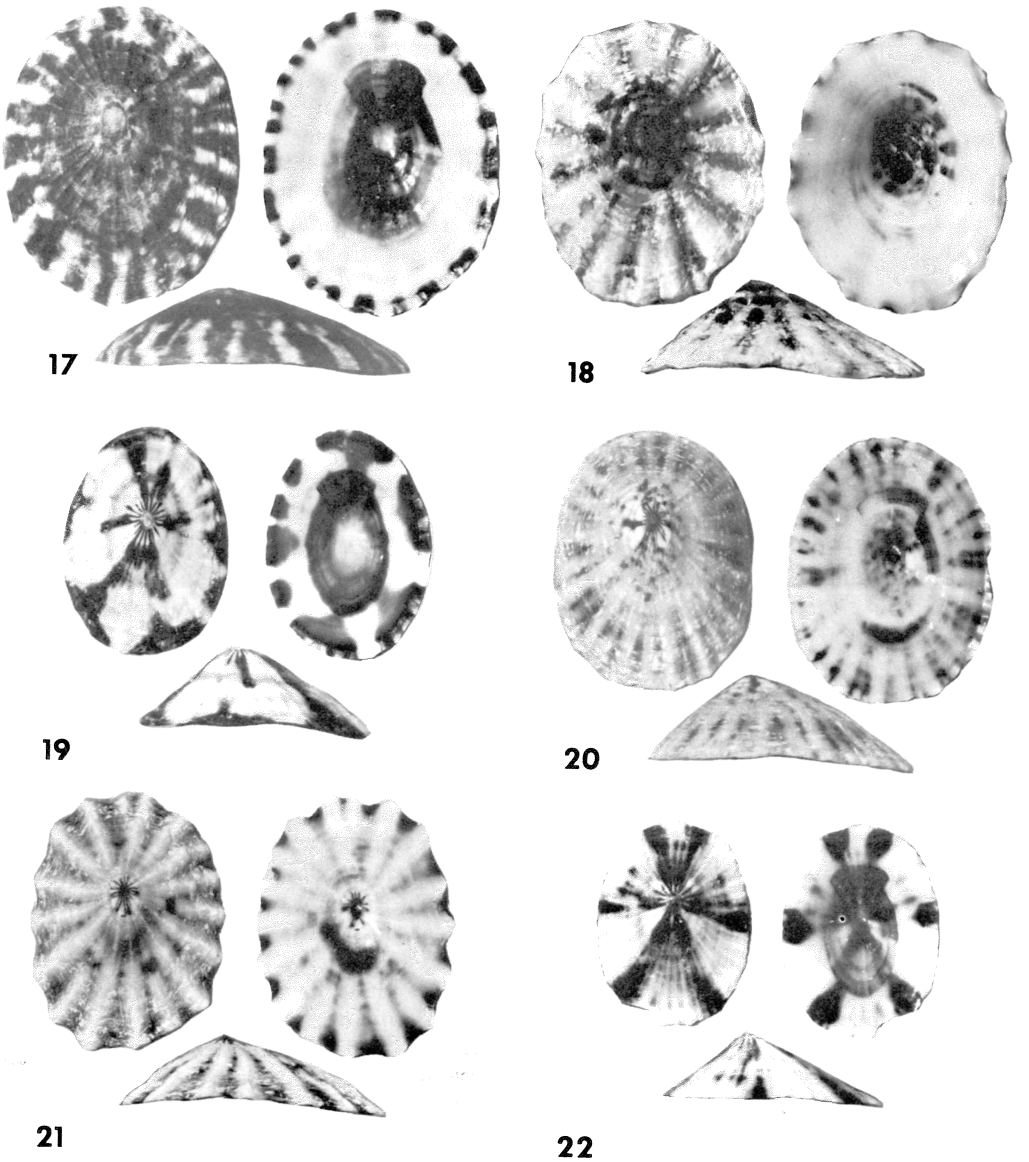
The short blunt teeth of *N. immaculata* are similar to those of species known to feed on coralline algae. The presumed subtidal occurrence of *N. immaculata* is in accordance with the abundant subtidal occurrence of coralline algae.

Lottia mimica new species

(Figures 17–19, 27, 33)

Shell (Figs. 17–19): Size medium (maximum length 25 mm), height medium; apex anterior to center; all slopes convex. Aperture ovoid, lateral edges somewhat parallel. Sculpture of raised angular ribs with one or two secondary ribs between each pair of primary ribs; ribs extending slightly, crenulating the margin. Exterior gray-brown with white radial markings that may or may not correspond to ribs. Apex white, with fine, dark radial lines typically concentrated in rays. Interior margin dark, with white markings corresponding to exterior color pattern; intermediate area blue-white; central area stained with dark brown; apical region white; exterior markings visible through shell.

Radula (Figs. 27, 33): First pair of lateral teeth closely set at anterior edge of ribbon segment, medial edges convex, lateral edges straight, cusps pointed. Second pair of lateral teeth positioned posterior to and slightly lateral to first pair, medial edges convex, lateral edges slightly convex, cusps pointed. Third lateral teeth lateral to second pair, medial edges strongly convex, lateral edges concave, cusps pointed. All lateral teeth approximately equal in width. Marginal



FIGURES 17–22. New species of *Lottia* from the Galápagos Islands. All from Academy Bay, Isla Santa Cruz. FIGURE 17. *Lottia mimica* new species. Holotype, LACM 1925. Length 16.2 mm. FIGURE 18. *Lottia mimica*. Paratype, LACM 1926. Length 14.8 mm. FIGURE 19. *Lottia mimica*. Paratype, LACM 1926. Length 9.6 mm. FIGURE 20. *Lottia smithi* new species. Holotype, LACM 1927. Length 12.4 mm. FIGURE 21. *Lottia smithi*. Paratype, LACM 1928. Length 12.9 mm. FIGURE 22. *Lottia smithi*. Paratype, LACM 1928. Length 7.5 mm.

teeth small, narrow, extending over ventral plates in vicinity of third pair of lateral teeth. First lateral plates square, slightly overlapping anterior ribbon segments; second lateral plates rounded, separated from third lateral plates by partial suture; third lateral plates irregular, with prominent lateral extensions extending to edges of ventral plates. Ventral plates closely set, with broad, rounded anterior process, lateral edges concave, posterior process weak.

Animal: Base of every second or third mantle tentacle with dark red-brown pigmentation;

snout with oral lappets; secondary gill complete but reduced in front of head, composed of lappets (approximately 14 per mm); every other lappet reduced, less than one-half the size of the larger ones.

HOLOTYPE DIMENSIONS.—Length 16.2, width 12.4, height 4.2 mm.

TYPE-LOCALITY.—Ecuador: Galápagos Islands; Isla Santa Cruz (0°38'S, 90°23'W), Academy Bay, Coamaño Island, intertidal zone. *Leg.* J. DeRoy, Oct. 1967.

TYPE-MATERIAL.—Holotype, LACM 1925 (shell and radula slide), 17 paratypes, LACM 1926, paratypes also deposited in the collections of CAS and USNM. Paratypes collected at several stations in Academy Bay by J. DeRoy between 1967 and 1969.

DISTRIBUTION.—Galápagos Islands; Isla Fernandina (AMNH 163363), Isla Isabela (AHF 74-33), Isla Bartolomé (AMNH 163290), Isla Santa Fé (AMNH 163362), Isla Española (AHF 359-35), and Isla San Cristóbal (CAS 23103).

MATERIAL EXAMINED.—33 lots, 198 specimens, 23 radula preparations.

ETYMOLOGY.—The name *mimica* is a Latin adjective, imitative, indicative of the difficulty of distinguishing the two members of the *Lottia* pair by their external appearance.

Lottia smithi new species
(Figures 20–22, 28, 34)

Shell (Figs. 20–22): Size medium (maximum length 25 mm), height medium; apex positioned in anterior third of shell; all slopes convex. Aperture ovoid. Sculpture of rounded primary ribs, secondary ribs of equal strength but beginning below apex. Primary and secondary ribs white, interspaces brown; apex white, with fine dark radial lines gathered into rays; interior margin dull yellow with irregular brown markings that correspond to exterior interspaces; intermediate area and central areas white; interior of myostracum bordered by yellow-brown halo. Exterior markings visible through shell.

Radula (Figs. 28, 34): First pair of lateral teeth closely set at anterior edge of ribbon segment, both edges convex, rounding to blunt cusps; second pair of lateral teeth posterior and slightly lateral to first pair, both edges convex, rounding to blunt cusps. Third pair of lateral teeth positioned lateral and posterior to second pair, both edges convex, rounding to blunt cusps. Marginal teeth small, narrow, overlapping ventral plates just anterior of third pair of lateral teeth. First lateral plates ovoid, slightly overlapping anterior ribbon segment; second lateral plates distinctly smaller than other lateral plates, medial edges rounded, separated from third lateral plates by a partial suture. Posterior edge of third lateral plates concave, with lateral extensions terminating in strongly hooked edges. Ventral plates closely set with strong posterior process; anterior process also present. Lateral edges in vicinity of marginal teeth concave; anterior sutures parallel with anterior edges of ventral plates.

Animal: Mantle tentacle pigmentation sometimes present; snout with oral lappets; secondary gill complete, but reduced in front of head, composed of lappets (approximately 11 per mm).

HOLOTYPE DIMENSIONS.—Length 12.4 mm, width 9.7 mm, height 4.5 mm.

TYPE-LOCALITY.—Ecuador: Galápagos Islands; Isla Santa Cruz (0°38'S, 90°23'W), Academy Bay, Punta Nuñez, intertidal zone. *Leg.* J. DeRoy, 13 Oct. 1969.

TYPE-MATERIAL.—Holotype, LACM 1927 (shell and radula slide), 9 paratypes, LACM 1928; paratypes also deposited in the collections of CAS and USNM. All type-material from Isla Santa Cruz, Academy Bay.

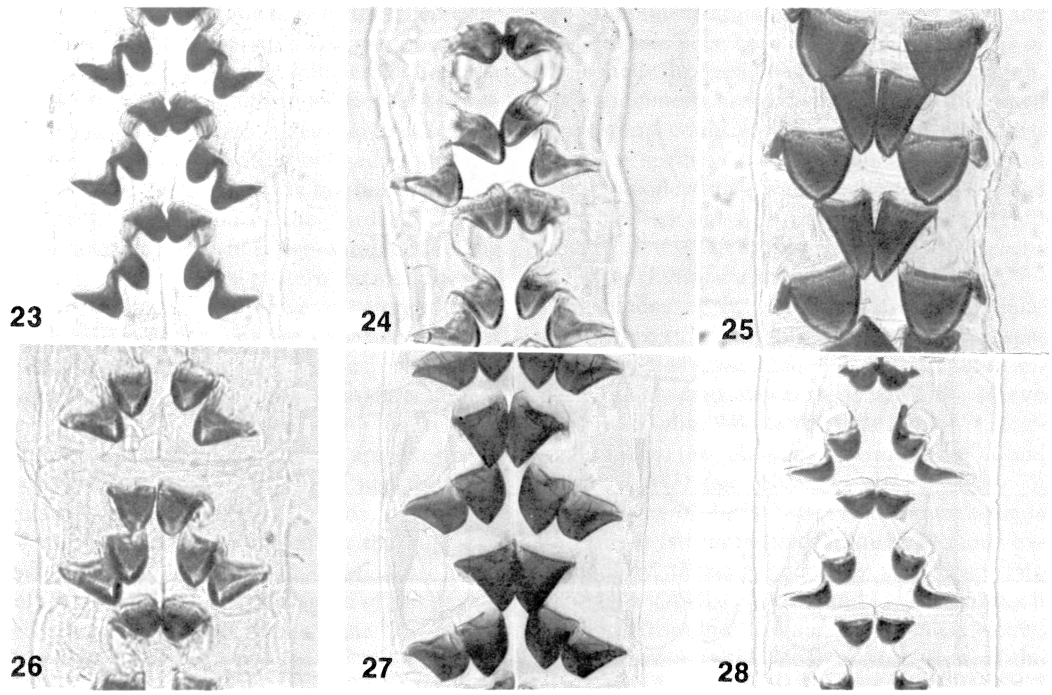
DISTRIBUTION.—Galápagos Islands; Isla Fernandina (LACM 72-196), Isla Isabela (CAS 27221), Isla Bartolomé (AMNH 163290), Isla Santa Cruz (LACM 28839), Isla Santa María (ANSP 153370), Isla San Cristóbal (ANSP 153328).

MATERIAL EXAMINED.—15 lots, 70 specimens, 14 radula preparations.

ETYMOLOGY.—We are pleased to name this species in honor of the late Allyn G. Smith of the California Academy of Sciences in recognition of his work with eastern Pacific mollusks, including those of the Galápagos Islands.

DISCUSSION.—The radular difference that separates *L. mimica* and *L. smithi* is readily apparent. In *L. mimica* the lateral teeth are pointed distally; in *L. smithi* they are rounded. The third lateral teeth of *L. mimica* are of the same width as the second; in *L. smithi* the third lateral teeth are much broader than the second. *Lottia mimica* lacks the strong posterior process on the ventral plates that is present in *L. smithi*.

In addition to radular difference, there is

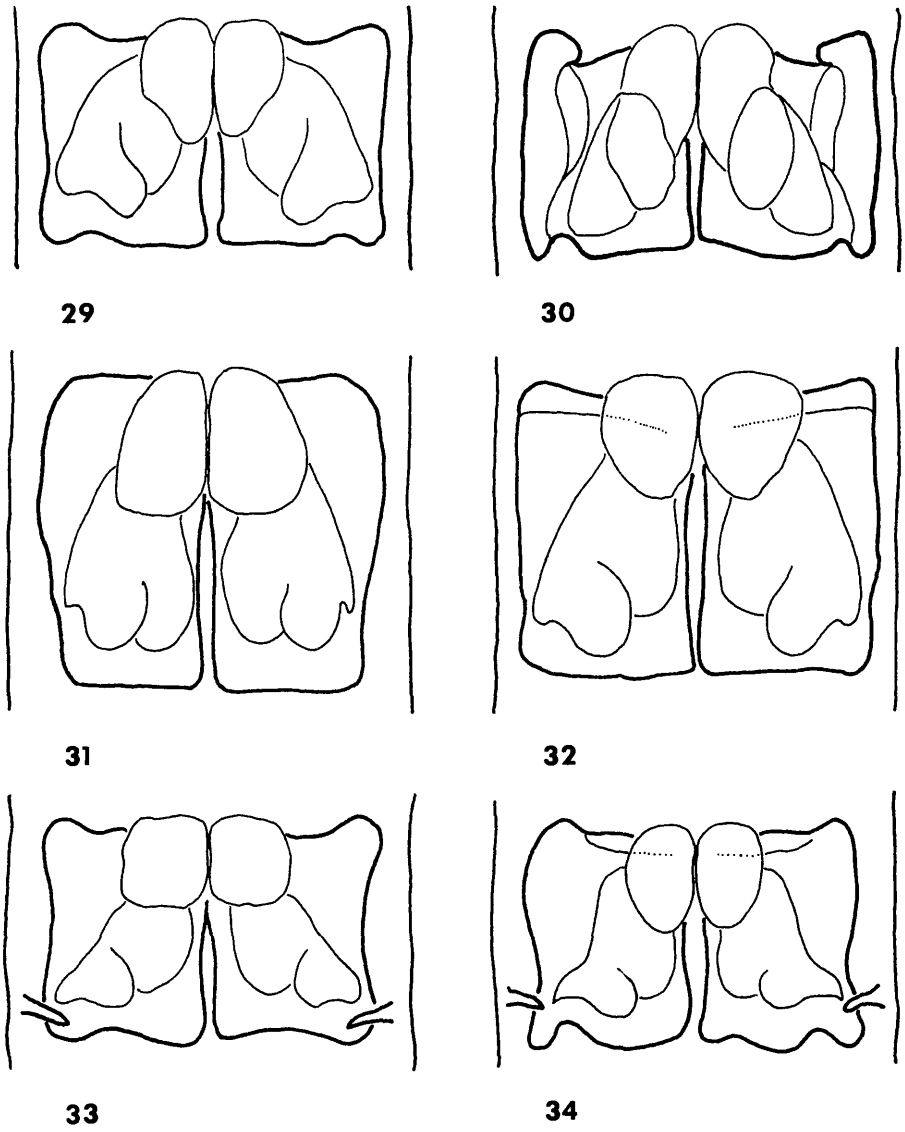


FIGURES 23–28. Radular dentition. FIGURE 23. *Notoacmea ubiquita* new species. FIGURE 24. *Notoacmea pumila* new species. FIGURE 25. *Notoacmea rothi* new species. FIGURE 26. *Notoacmea immaculata* new species. FIGURE 27. *Lottia mimica* new species. FIGURE 28. *Lottia smithi* new species. Anterior towards top of page.

another significant anatomical difference: in *L. mimica* the mantle tentacles are darkly pigmented (Fig. 3) in much the same way as in *L. gigantea* (Fig. 1). This pigmentation is weakly developed or entirely lacking in *L. smithi*. This distinction could prove useful in future field studies because it provides a reliable, nonfatal method of species determination.

Shells of *L. mimica* and *L. smithi* are essentially indistinguishable and are characterized by moderately strong radial ribs, variable in the number reaching the margin. Some specimens of both species have relatively few primary and secondary ribs, and these ribs project, crenulating the margin (Figs. 18, 21). In others the secondary ribs are more numerous and the primary ribs less prominent. In these specimens the ribs project only slightly and the shell margin is relatively even (Figs. 17, 19, 20, 22). The normal pattern on the apical region of juvenile shells is identical in both species (Figs. 19–22). The apical tip is dark colored with a pattern of thin, dark lines, concentrated in six bundles in the 1, 3, 5, 7, 9, and 11 o'clock positions. In most specimens this pattern changes abruptly to one in which rib surfaces are lighter colored and the interspaces darker, often showing concentric variations in intensity. In a few specimens of both species (Figs. 19, 22), the juvenile pattern changes to a solid 6-rayed pattern in the adult. The holotype of *L. mimica* is unusual; in the early stage it is uniformly dark, changing abruptly to a rayed pattern in which the lighter rays do not necessarily correspond to the ribs. Four specimens of the type lot of *L. mimica,* including the holotype, are predominantly dark colored; none in the type lot of *L. smithi* may be so described. The range of variability of *L. mimica* is therefore somewhat broader than that of *L. smithi*.

The peculiar markings in the juvenile shell of *L. mimica–smithi* as well as its particular adult pattern are unlike those of any other acmaeid species. The extreme specimens with few ribs are similar to *Collisella pediculus,* although that species has fewer, more prominent ribs. *Colli-*



FIGURES 29–34. Radular basal plates. FIGURE 29. *Notoacmea ubiquita* new species. FIGURE 30. *Notoacmea pumila* new species. FIGURE 31. *Notoacmea rothi* new species. FIGURE 32. *Notoacmea immaculata* new species. FIGURE 33. *Lottia mimica* new species. FIGURE 34. *Lottia smithi* new species. Anterior towards top of page.

sella mitella has a greater number of ribs and has a more uniform color pattern, with lighter ribs and darker interspaces.

There is no particular similarity to the large, dark brown shells of *Lottia gigantea* or the blue-green shells of *L. mesoleuca* and *L. stipulata*, but that is not surprising in view of the lack of consistent shell characters within all acmaeid genera.

We have no information about the habitat of either *L. mimica* or *L. smithi*. The original collecting information supplied by J. DeRoy indicates that they were collected on rocks exposed to heavy surf. All of the shells in both type lots were heavily encrusted with coralline algae, as are those of the Panamic species of *Collisella* that live under exposed surf conditions, such as *C. pediculus*. Limpets in this habitat have an

habitual site of attachment with the shell edge molded to fit the home site. The margins of *L. mimica* and *L. smithi* are sufficiently irregular to suggest that they conform to specific sites.

The short, blunt, equal-sized radular teeth of *L. smithi* are well adapted for feeding on coralline algae. The shape of the lateral teeth, particularly the expansion of the third laterals, is similar to that found in other coralline-feeding *Collisella* of the tropical eastern Pacific. The lateral teeth of *L. mimica*, however, are not those of a coralline feeder, nor are they like those of most of the diatom-feeding species of *Notoacmea* or *Collisella*, in which the third lateral teeth are reduced. The medium length teeth with pointed cusps, all equally large, are like those of many of the Peruvian *Scurria* and the Californian *Notoacmea insessa* (Hinds, 1842). The last species is known to feed on the stipes of brown algae. The teeth of *L. mimica* are most likely adapted for feeding on some of the fleshy, encrusting, but noncalcareous algae.

Limpets of the *L. mimica–smithi* type are present in late Pleistocene deposits on Isla San Salvador (Hertlein and Strong 1939). The range of variation in the fossil specimens is similar to that seen in Recent specimens of both *L. mimica* and *L. smithi*. However, specific identifications are not possible from the shells alone.

Acmaeidae of the Galápagos Islands

The Galápagos Islands, or Archipiélago de Colón, are located approximately 800 km west of Cabo San Lorenzo, Ecuador. The fifteen islands and numerous islets extend from 1°40′N to 1°36′S and from 89°17′W to 90°01′W. The islands have been the subject of numerous scientific explorations (see Slevin 1959) and are renowned for their unique fauna and flora. The marine molluscan fauna comprises tropical eastern Pacific elements, endemics, and a few forms from the Indo-Pacific faunal region (Emerson 1978).

Some nine different taxa of acmaeid limpets have been reported from the Galápagos Islands since 1855 (Reeve 1855; Carpenter 1864; Wimmer 1880; Stearns 1893; Pilsbry and Vanatta 1902; Dall 1909; Schwengel 1938; Hertlein and Strong 1955; Keen 1958; McLean 1971). None of the species reported have been recognized as endemics, having been considered instead as vagrants from the Californian, Panamic, and Peruvian molluscan faunal provinces. Many of the records have been based on beachworn shells or small shells dredged dead and in poor condition. Such specimens are difficult to refer to known species and could hardly be recognized as distinct new species. After examining a number of museum collections, we are able to confirm the presence of only two previously reported species at the Galápagos Islands, *Notoacmea filosa* and *Lottia mesoleuca*.

Specimens of *L. mesoleuca* from the Galápagos were originally misidentified as the Australian species *Patelloida striata* Quoy and Gaimard, 1834, and were so treated by Reeve (1855:pl. 33, fig. 99) (as "*Patella striata*"), Carpenter (1864) (as "*Acmaea striata* Reeve"), and Stearns (1893) (as "*Acmaea striata* Reeve"). Occurrences of *L. mesoleuca* at the Galápagos are rare. It is represented in the collections examined by three specimens: two from Isla Genovesa (AHF 782-38) and a single beach specimen from the "Galapagos" (ANSP 39189). Isla Genovesa is the most northeastern of the islands, and it is conceivable that the species may be established there and not elsewhere in the archipelago.

Notoacmea filosa is also rare in collections. It is represented by only two museum lots, one from Isla Santa Cruz (AMNH 177320) and one from Isla San Cristóbal (LACM 54775) (Fig. 16) collected in 1929. Further information about the occurrence of these two species at the Galápagos Islands is desirable. Considering that recent collecting efforts have not produced these species, we only provisionally list them in the Galápagos Islands fauna.

We consider all other records of Acmaeidae from the Galápagos Islands to be misidentifications of the four new species described herein. Because separation of members of the species pairs is based on radular characters, it is not possible to list species-specific synonymies for each member.

In both species pairs, additional characters segregate with the radular morphotypes. In the *Notoacmea* siblings, there are differences in shell size and coloration associated with the radular types. In the *Lottia* pair, there are no significant differences in shell size, sculpture, or coloration; however, there are differences in mantle pigmentation and secondary gill morphology. We interpret these separate character

states as evidence against a simple radular polymorphism and instead recognize the pairs as separate species. There is also evidence that the habitat differs in the *Notoacmea* pair but not in the *Lottia* pair.

Whether speciation of the two pairs of sibling species was sympatric or allopatric is unknown. However, we hope that future workers will pursue this problem in the field and the laboratory. Electrophoretic analysis could prove productive.

Acknowledgments

We are indebted to Jacqueline DeRoy of Isla Santa Cruz, Galápagos Islands, who furnished preserved specimens of the new species from those islands. Donald R. Shasky of Redlands, California, loaned pertinent specimens from his collection. Courtesies were extended to Lindberg on his museum visits by George M. Davis (ANSP), William K. Emerson (AMNH), Welton L. Lee (CAS), Joseph Rosewater and Kathy Lamb (USNM), Barry Roth (CAS), and Ruth Turner (MCZ). Barry Roth also made available the late Leo G. Hertlein's unpublished notes on the Galápagos molluscan fauna. Bertram C. Draper, Los Angeles, made the prints of shell specimens, and Sally Walker, University of California, Santa Cruz, prepared the line drawing. We thank Eugene V. Coan, Myra Keen, and Barry Roth for reading the manuscript and offering helpful suggestions.

Resumen

La definición de género está basada en las características conservativas de la estructura de la concha y también en las características cualitativas de la rádula. La *Lottia*, que anteriormente se había considerado monotípica, se extende a incluir las especies panámicas con la agalla secundaria (un cordón branquial), que anteriormente se había atribuido a la *Scurria*. La *Scurria* tiene la agalla semejante, pero la estructura de la concha se diferencia. Las nuevas especies *Notoacmea ubiquita* de México y *N. pumila* de Ecuador tienen las conchas pequeñas y son especies alopátricas con los dientes radulares que están modificados para alimentarse de la alga coralina. Dos nuevas especies de *Notoacmea* (*N. rothi* y *N. immaculata*), que son endémicas a las Islas Galápagos, constituyen un par de especies que se diferencian principalmente por los rasgos de la rádula: los dientes radulares de *N. immaculata* están adoptados para alimentarse de la alga calcárea; los dientes radulares de *N. rothi*, para alimentarse de la alga no calcárea. Un par de nuevas especies de *Lottia* endémicas a las Islas Galápagos (*L. mimica* y *L. smithi*) también se diferencian principalmente por las características radulares. La *Lottia mimica* se alimenta de la alga y es no calcárea; y la *L. smithi* se alimenta de alga y es calcárea. Estas cuatro especies endémicas son las principales lapas acmaeidas de las Islas Galápagos. Dos especies de la tierra firme, *Notoacmea filosa* y *Lottia mesoleuca*, se han observado no más esporadicamente en las Islas Galápagos.

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