A New *Homalopoma* from Southern California Resembling *Parviturbo acuticostatus:* A Case of Mimicry?

BY

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(2 Plates; 2 Text figures)

FOR THE LAST SEVERAL YEARS the Invertebrate Zoology Section of the Los Angeles County Museum of Natural History has been giving special attention to marine mollusks in the minute to microscopic size range, particularly from subtidal rocky areas where systematic collecting was virtually impossible prior to the advent of SCUBA diving as a collecting method. As a result of these efforts substantial numbers of specimens of many undescribed or poorly known subtidal species are now available and with study may provide answers to many perplexing questions. So it is with the species dealt with in this paper.

Parviturbo acuticostatus (Carpenter, 1864) (family Skeneidae) and *Homalopoma radiatum* (Dall, 1918) (= *Leptothyra paucicostata* var. *fenestrata* Dall, 1919 ex Bartsch MS) (family Turbinidae), two quite unrelated species, have long been confused in the literature, as an examination of their synonymies will attest. This confusion was no doubt contributed to by the inadequacy of the original descriptions but seems to me to be more basic than that. The discovery of a previously unrecognized, though not rare, species of *Homalopoma*, virtually identical in size, shape, color and sculpture with *Parviturbo acuticostatus* may provide a convincing explanation of this confusion. The new species is separable from many specimens of *P. acuticostatus* only on generic and familial characters easily missed if not specifically looked for. This similarity may be the result of mimicry, an interesting adaptation for survival found in a number of species of animals, most notably the insects, but apparently little known in the Mollusca. Although it cannot be stated with certainty whether *P. acuticostatus* or the new *Homalopoma* are exhibiting true mimicry, parallel evolution, or coincidental convergence, the circumstantial evidence provided by shell characters and geographic distribution suggests the first. The new species is also very similar to *H. radiatum*, the species to which it is most closely related, and from which it differs chiefly in quantitative characters.

The first suggestion of the discovery arose when I observed, during routine sorting of specimens from a subtidal Catalina Island station, that *Homalopoma radiatum* and *Parviturbo acuticostatus* appeared to intergrade. The improbability of this spurred a thorough examination of these species in the Museum collection and led to the isolation of 103 specimens of a new species from 32 different stations. The new species had been intermixed and about equally divided between the 72 lots of *Parviturbo acuticostatus* and 56 lots of *Homalopoma radiatum* in the collection, which in itself is suggestive of its similarity to both. Although it is easily separable from *Parviturbo* by qualitative generic characters, a statistical evaluation was necessary to establish objective criteria for separating it from *H. radiatum*. Descriptions and figures of the 3 species are given here to facilitate their correct determination. A statistical comparison of the new species with *H. radiatum*, and the evidence relating to mimicry will be found in the discussion that follows the description of the new species.

I wish to gratefully acknowledge the help and encouragement received from Dr. James H. McLean during the preparation of this paper, from suggesting the name for the new species to reading and criticizing the drafts. I also wish to thank Mr. Bert Draper for taking the photographs of the Los Angeles County Museum specimens and

Dr. McLean for photographing holotypes in the United States National Museum and California Academy of Sciences.

Institutions mentioned in the text and their abbreviations are as follows:

LACM	Los Angeles County Museum of Natural History
LACMIP	Invertebrate Paleontology Section, Los Angeles County Museum of Natural History
CAS	California Academy of Sciences, San Francisco
USNM	United States National Museum (Smithsonian Institution)

Parviturbo acuticostatus (Carpenter, 1864)

(Figures 2, *11 - 18, 24, 25, 27, 28*)

Liotia acuticostata Carpenter, 1864 (July, *fide* DALL, 1909): 159 (lectotype [designated by PALMER, 1958: 146] US NM 16282, Catalina Island, California, 10 - 20 fms.). — CARPENTER, 1864 (August): 612 (list), 652 (description); (reprint 1872: 98, 138).—OLDROYD, 1927, **2** (3): 170 (in part).—STRONG, 1934: 437; plt. 29, figs. 7 - 9.—(not TRYON, 1888, **10**: 109; plt. 36, fig. 1 = *Homalopoma radiatum* (Dall, 1918)).

Fossarus angiolus DALL, 1919: 350 (Holotype USNM 271503, Todos Santos Bay, Baja California). — OLDROYD, 1927, **2** (3): 70.

"*Liotia acuticostata bristolae* Baker, 1929" — STRONG, 1934: 438; plt. 29, figs. 13 - 15 (not BAKER, 1929).

Arene acuticostata (Carpenter, 1864). — BURCH, 1946, #57: 25, 26 (distribution list). — PALMER, 1958: 146; plt. 19, figs. 12, 13 (lectotype).

Parviturbo acuticostatus (Carpenter, 1864). — McLEAN, 1969: 23; fig. 9.6. — McLEAN *in* KEEN, 1971: 343; fig. 121.

Description: Shell small, globose, uniformly white, 3 whorled, narrowly umbilicate; sculpture of 2 spiral cords per whorl visible on the spire, 6 evenly spaced spiral cords on the body whorl plus one on the umbilical wall; axial sculpture of fine, sharp, closely spaced lamellae between the spiral cords on the spire, becoming more or less obsolete on the body whorl of the adult, where they are replaced in many specimens from north of Latitude 29° N in central Baja California by more widely spaced, broad, rounded axial ribs on the upper part of the whorl, forming squarish pits; aperture circular, outer lip thickened and slightly constricted in the adult, interior porcelaneous; operculum chitinous, multispiral, 5 to 6 whorled, light brown.

Dimensions of Adults: height 2.1 - 2.8 mm; modal height 2.6 mm; width 2.1 - 2.9 mm; modal width 2.7 mm.

Distribution: Aumentos Rock, Monterey Peninsula, California (LACM sta. 72-90, 36°38′N; 121°55′12″W) south to Cabo San Lucas, Baja California (LACM sta. 66-12, 22°08′N; 109°54′W) and into the Gulf of California as far as Isla Cerralvo, near La Paz, Baja California (LACM sta. 66-25, 24°10′N; 109°55′W) and including all of the southern California Channel Islands and offshore banks (numerous LACM stations) and Isla Guadalupe, Baja California (LACM sta. 65-42, 29°00′N; 118°02′W, and other stations), intertidal to 100 m on rock and gravel bottoms. Specimens referred to this species by STRONG (1934: 438) under the name *L. a. bristolae* from the Gulf of California are undoubtedly *Parviturbo stearnsi* (Dall, 1918), which differs chiefly in having 3 spiral cords in the early whorls instead of 2 (see McLEAN *in* KEEN, 1971: 345; fig. 124).

Fossil Occurrence: Upper Pliocene: San Diego Formation (LACMIP localities 305 and 305A). Lower Pleistocene: Lomita Marl (LACMIP Localities 64 and 435). Upper Pleistocene: Palos Verdes Sand (LACMIP Localities 66-2, 136 and 4685).

Homalopoma radiatum (Dall, 1918)

(Figures *1*, *3 - 6* and *19 - 23*; Tables 1 - 3)

"*Liotia acuticostata* Carpenter." — TRYON, 1888, 10: 109; plt. 36, fig. 1 (not CARPENTER, 1864).

Liotia acuticostata var. *radiata* DALL, 1918: 8 (Holotype US NM 223291, off South Coronado Island, Baja California).

Leptothyra paucicostata fenestrata DALL, 1919: 358 (ex Bartsch MS; Holotype USNM 193796a, Monterey, California).

Liotia acuticostata radiata Dall, "1919" — DALL, 1921: 173 (list).—OLDROYD, 1927, **2** (3): 170.

Leptothyra paucicostata fenestrata "Bartsch," 1919. — DALL, 1921: 172 (list). — OLDROYD, 1927, **2** (3): 168 (type locality cited incorrectly as "Tiajuana, Lower California").

Liotia acuticostata bristolae BAKER, 1929: 72 (unnecessary replacement name for *L. a. radiata* Dall, 1918). — (not STRONG, 1934: 438; plt. 29, figs. 13 - 15 = *Parviturbo acuticostatus* (Carpenter, 1864)).

Liotia acuticostata supranodosa STRONG, 1934: 438 (ex Carpenter MS; Holotype CAS 5472, San Diego, California).

Homalopoma fenestratum [(Dall)]. — KEEN, 1937: 37 (list).

Homalopoma paucicostatum fenestratum ("Bartsch," 1919). — BURCH, 1946, #57: 23 (distribution list).

Arene acuticostata var. *supranodosa* (Strong, "1933"). — BURCH, 1946, #57: 25 (distribution list).

Arene acuticostata var. *bristolae* (Baker, 1929). — BURCH, 1946, #57: 26 (distribution list).

Homalopoma supranodosum (Strong). — KEEN, 1947: 1

Homalopoma fenestratum (Dall, 1919). — McLEAN, 1969: 24; fig. 10.4.

Homalopoma radiatum (Dall, 1918). — SMITH & CARLTON, 1975: 503 (list).

Description: Shell small, globose, imperforate; color variable from white with minute flecks of pink on the spiral cords to solid pink and brown, with most specimens having easily visible spots or blotches of pink and brown on a white ground; nucleus smooth, one whorled; post nuclear whorls $3\frac{1}{2}$; sculpture of 2 spiral cords visible per whorl on the spire, 7 evenly spaced spiral cords on the body whorl, the 7th (basal) cord usually broader than the 6th; axial sculpture of short rib segments on the upper part of the last 1 to $1\frac{3}{4}$ whorls creates 2 rows of strong quadrilateral pits between the 1st and 3rd spiral cords, weaker pits are occasionally visible below the 3rd spiral cord; aperture circular, outer lip thickened and slightly constricted in adults; interior nacreous, iridescent pink and green in fresh specimens; columella with strong node at base, 2 additional nodes, one at the top of the columella and one on the lower lip are visible on most adult specimens; operculum calcareous, multispiral, 5 - 7 whorled, nucleus central, outer surface granular, translucent white.

Dimensions of Adults: height 2.8 to 3.9 mm; modal height 3.3 mm; width 2.9 to 3.9 mm; modal width 3.4 mm (a statistical summary and analysis of the variation of selected characters will be found in the discussion that follows the description of the new species).

Distribution: Aumentos Rock, Monterey Peninsula, California (LACM sta. 72-90, 36°38′N; 121°55′12″W) south to Sacramento Reef, south of Isla San Geronimo, outer coast of Baja California (LACM sta. 71-91, 29° 43′42″N; 115°45′36″W), including all of the southern California Channel Islands and offshore banks (numerous LACM stations). Subtidal to 100 m, on rock and gravel bottom, rarely intertidal.

Fossil Occurrence: Upper Pliocene: San Diego Formation (LACMIP localities: 305, 305A, 305C, 318, 319, and 323); Fernando Formation (LACMIP Locality 1219). Lower Pleistocene: Lomita Marl (LACMIP Localities 64 and 435).

Taxonomic Discussion: Because of the confusion surrounding the nomenclature of this species and the number of synonyms under which it has been known, I am reinstating the earliest available name for the species, *Homalopoma radiatum* (Dall, 1918), despite the fact that it had been unnecessarily suppressed as a secondary homonym. This new use of the oldest name has already been adopted by Carlton in SMITH & CARLTON (1975).

Liotia acuticostata var. *radiata* Dall, 1918, was suppressed by BAKER (1929: 72) as a junior homonym of *Delphinula radiata* Kiener, 1839 (p. 7; plt. 4, fig. 9). Kiener's taxon is a junior synonym of *Arene cruentata* (Mühlfeld, 1829), a Caribbean species and type species of *Arene* H. & A. Adams. In 1888, TRYON (10: 111) allocated Kiener's taxon to *Liotia* "section" *Arene*, and Baker, noting this, apparently suppressed Dall's name on purely nomenclatural grounds, without realizing that Dall's name applied to *Homalopoma*.

Arene radiata (Kiener, 1839) and *Homalopoma radiatum* (Dall, 1918) are secondary homonyms (originally described in different genera) and are no longer in the same family.

The International Rules of Zoological Nomenclature direct the revival of secondary homonyms rejected after 1960, if the two species in question are no longer believed to be congeneric. However, the Rules offer no directions concerning secondary synonyms rejected before that date, apparently leaving the decision of whether to revive an earlier name to the judgment of individual authors. Despite the current use of a junior synonym, *Homalopoma radiatum* is not so familiar to biologists that reinstatement

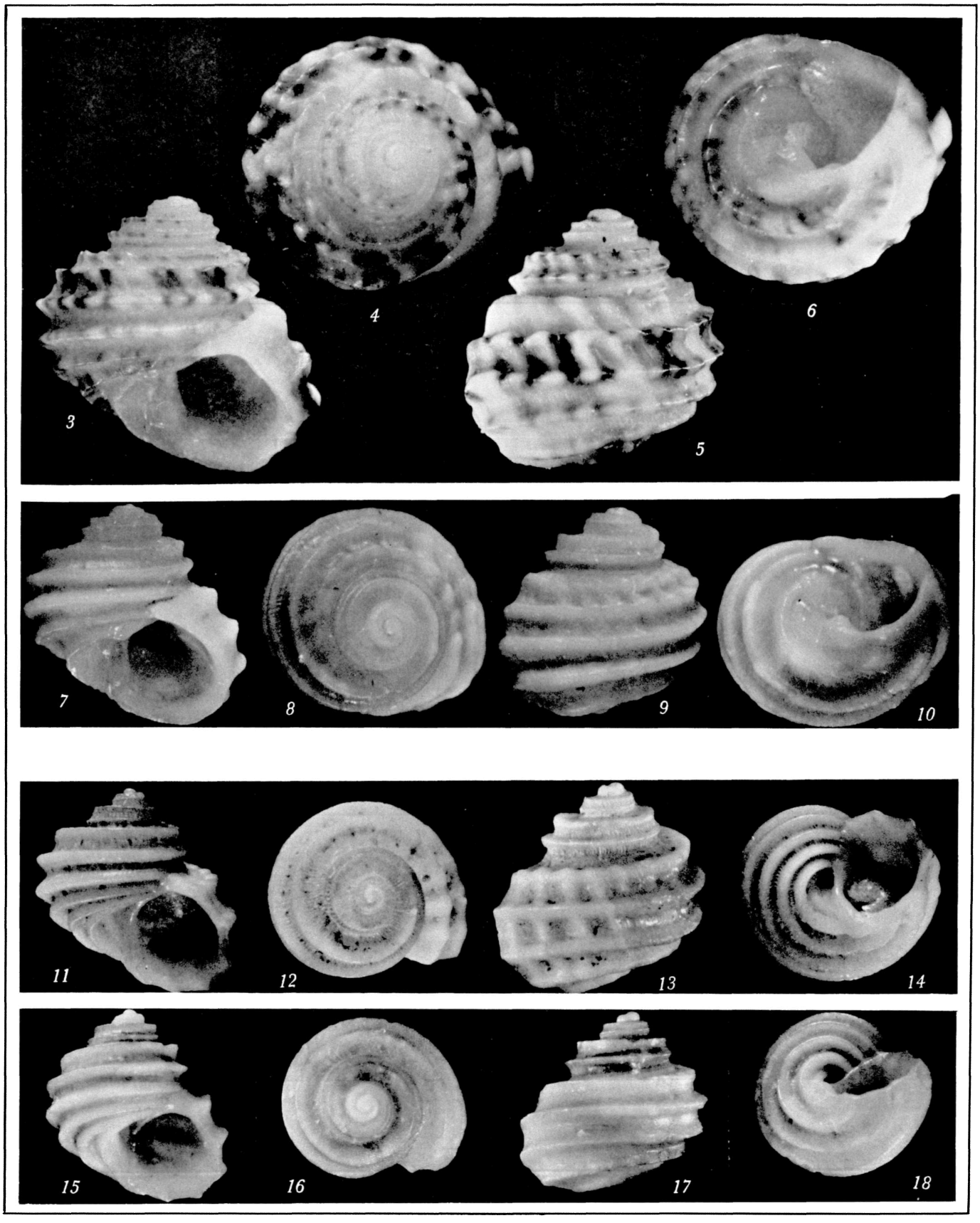
Explanation of Figures *3* to *18*

(All Figures × 15)

Figures *3* to *6*: *Homalopoma radiatum* Dall, 1918. LACM 69-34, Cortez Bank, 66 km SW San Clemente Island, Los Angeles, California (32°26′N; 119°07′30″W), 12 - 27 m on granite cliffs and boulders. Leg. J. H. McLean, October 4 and 5, 1969. Height 3.4 mm; width 3.5 mm

Figures *7* to *10*: *Homalopoma mimicum* LaFollette, spec. nov. Holotype LACM 1765. LACM 71-148; $6\frac{1}{2}$ fm bank, 6.4 km SW Isla San Martin, Baja California (30°25′23″N; 116°08′12″W), 24 - 30 m on volcanic rubble. Leg. J. H. McLean, October 17, 1971. Height 2.6 mm; width 2.7 mm

Figures *11* to *18*: *Parviturbo acuticostatus* (Carpenter, 1864). Figures *11* - *14*: Pitted form. LACM 71-97, Sugarloaf Rock, Descanso Bay, Baja California (32°13′18″N; 116°58′W), 27 to 33 m on talus slope. Leg. J. H. McLean, October 1, 1971. Height 2.5 mm; width 2.5 mm. Figures *15* - *18*: Unpitted form. LACM 66-12, Cabo San Lucas, Baja California (22°52′N; 109°54′W), 7 - 30 m on rocks and coarse sand. Leg. J. H. McLean & P. M. Oringer, April 3 and 4, 1966. Height 2.4 mm; width 2.3 mm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of the original name would be a hardship. I believe that in this case reinstatement of the earliest name will contribute to nomenclatural stability and am therefore taking this action.

Homalopoma ***mimicum*** LaFollette, spec. nov.

(Figures 1, 2, *7 - 10*, and *26*; Tables 1 - 3)

Description of Holotype: Shell small, globose, imperforate, uniformly white; nucleus smooth, one whorled; post-nuclear whorls 3¼, demarcated from the nucleus by the abrupt beginning of spiral sculpture; sculpture of 2 spiral cords visible per whorl on the spire, 7 spiral cords on the body whorl, the 1st subsutural cord emerging on the last ¾ turn; the 1st 6 spiral cords strong and evenly spaced, the 7th (basal) cord much weaker and close to the 6th; axial sculpture of short rib segments appearing near the suture on the last ½ whorl, giving an undulating appearance to the 1st and 2nd spiral cords and forming squarish pits between them, weaker pits visible between the suture and the 1st spiral cord, pitting absent below the 2nd spiral cord; aperture circular, outer lip thickened and somewhat constricted; interior nacreous, iridescent pink and green, the iridescence weakly visible externally between the spiral cords; columella with a strong node near the base, a weaker one above and a 3rd on the lower lip; operculum calcareous, multispiral, 6 whorled, nucleus central, outer surface somewhat granular, translucent white, showing light brown through from the inside.

Dimensions: height 2.6mm; width 2.7mm.

Type Material: Holotype LACM No. 1765; 5 paratypes LACM No. 1766; 1 paratype USNM.

Type Locality: LACM sta. 71-148, 6½ fathom bank, 6.4km SW of Isla San Martin, Baja California (30°25′23″N; 116°08′12″W), 24 - 33m on volcanic rubble, leg. James H. McLean, 17 October 1971 (R/V *Searcher* sta. 222). Holotype and 6 paratype specimens.

Variation: 42 adult specimens varied as follows: Post-nuclear whorls 3 to 3½; spiral sculpture of 7 cords on the body whorl, the 7th (basal) cord varying from obsolete or very weak to equal in strength to the adjacent (6th) spiral cord; axial sculpture of short rib segments near the suture appearing on the final ⅓ to 1 full whorl, forming squarish pits between the 1st and 2nd spiral cords in all specimens, weaker pits between the suture and 1st spiral cord in 50% of the specimens, and much weaker pits between the 2nd and 3rd spiral cords in 10% of the specimens; a prominent node at the base of the columella is present in all specimens, a 2nd node above it, at the point where the 6th spiral cord enters the aperture, and a 3rd node on the lower lip are visible in most fully mature specimens; all specimens show a definite adult stage with the outer lip thickened and somewhat constricted.

Dimensions of 50 adult specimens: Height 2.1 - 2.9 mm; modal height 2.4mm; width 2.2 - 2.9mm; modal width 2.5mm (a statistical summary and analysis of the variation of selected characters will be found in the discussion).

Distribution: Off Point Pinos, Monterey Peninsula, California (LACM sta. 64-14, 36°38′N; 121°58′W) south to Sacramento Reef, south of Isla San Geronimo, outer coast of Baja California (LACM sta. 71-91, 29°43′42″ N; 115°45′36″W), including all of the southern California Channel Islands and offshore banks (numerous LAC M stations). Subtidal to 100m, on rock and gravel bottoms, rarely intertidal.

Fossil Occurrence: Lower Pleistocene: Lomita Marl (LACMIP Locality 435, 136 specimens). Upper Pleistocene: Palos Verdes Sand (LACMIP locality 4685, 1 specimen). The Lomita Marl specimens differ from the Recent ones in being slightly larger on the average and in the 7th (basal) spiral cord being obsolete in all specimens examined.

Discussion: Adults of *Homalopoma* ***mimicum***, the smallest of the eastern Pacific species of the genus, may easily be distinguished from *Parviturbo acuticostatus* by several qualitative characters. Adults of *H.* ***mimicum*** are imperforate, have a node at the base of the columella, a nacreous interior and a calcareous operculum, while *P. acuticostatus* has an umbilicus, lacks the node, has a porcelaneous interior and a chitinous operculum. *Homalopoma* ***mimicum*** lacks the fine axial lamellae between the spiral cords on the juvenile whorls typical of *P. acuticostatus*. Additionally, the squarish pits which characterize *H.* ***mimicum*** are lacking or faint in 20-80% of the specimens of *P. acuticostatus* in their area of range overlap.

The juveniles of *Homalopoma* ***mimicum*** are somewhat more difficult to distinguish as they are umbilicate; the columellar node is much less prominent; and the pitting, characteristic of the adult, may not yet have developed. The absence of axial lamellae, the presence of interior nacre, and the calcareous operculum should enable determination of live collected or well preserved specimens, however.

Homalopoma radiatum may be distinguished from *Parviturbo acuticostatus* by all of the above characters in

addition to being considerably larger and having pink or brown, or both, color markings.

Separation of *Homalopoma* ***mimicum*** from *H. radiatum*, the species to which it is most closely related, may be rather more difficult in some cases. The 4 characters on which I have separated them: size, color pattern, distribution of pitting, and relative strength of the basal spiral cord, all overlap to a limited degree and must be examined in concert to reliably distinguish borderline cases. Fortunately, these characters seem to vary independently so that the probability of a specimen being indeterminate on all 4 characters is extremely small.

A sample of 57 adult specimens of *Homalopoma radiatum* from the LACM collection was statistically analyzed and compared with the 42 adult specimens of *H.* ***mimicum*** on hand. (After the analysis was completed, another 8 adults of the new species were added to the collection. These have been incorporated in the data on size and color only.) All unbroken adult specimens in the selected lots of *H. radiatum* were used for analysis, regardless of condition, so that the data would be as representative of typical museum specimens as possible. The lots used were systematically selected from throughout the range of *H. radiatum*, even though no geographic variation has been observed in either species.

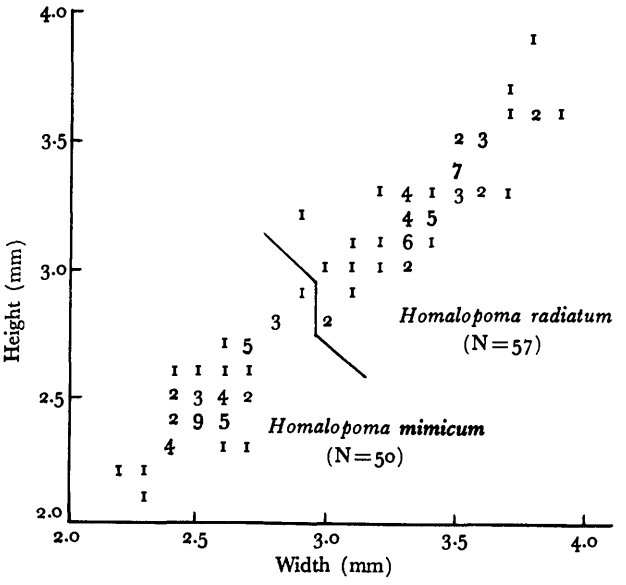

Figure 1

Size Distribution of Adult Specimens of *Homalopoma* ***mimicum*** and *Homalopoma radiatum* by Height and Width

Size: The most obvious difference between the 2 species is size, the modal (most common) height and width for *Homalopoma* ***mimicum*** being 2.4 and 2.5 mm, while *H. radiatum* has a modal height and width of 3.3 and 3.4 mm, 40% higher and more than twice the volume. The size distribution of each species is graphically represented in Figure 1. To simplify presentation, the following calculations are based on the arithmetic mean of height and width for each specimen, which I will call size.

$$\text{size} = \frac{H+W}{2}$$

The mean size for *H.* ***mimicum*** is 2.518 mm with a standard deviation of 0.148 mm; the mean size for *H. radiatum* is 3.334 mm with a standard deviation of 0.208 mm. The difference between the mean sizes of the 2 species is highly significant ($Z = 9.94$), and the standard deviations also differ significantly ($\alpha = 0.01$; $F_{\alpha\ 56,49} = 1.98$). The optimal size dividing point between the 2 species is 2.86 mm (2.29 standard deviations from each mean). Based on this dividing point, the index of predictive association

Explanation of Figures *19* to *28*

(All Figures × 15)

Figures *19*, *20*: *Liotia acuticostata* var. *radiata* Dall, 1918 [= *Homalopoma radiatum* (Dall, 1918)]. Holotype USNM 223291, off South Coronado Island, Baja California. Height 3.4 mm; width 3.5 mm

Figures *21*, *22*: *Leptothyra paucicostata fenestrata* Dall, 1919 [= *Homalopoma radiatum* (Dall, 1918)]. Holotype USNM 193796a, Monterey, California. Height 3.5 mm; width 3.7 mm

Figure *23*: *Liotia acuticostata supranodosa* Strong, 1934 [= *Homalopoma radiatum* (Dall, 1918)]. Holotype CAS 5472, San Diego, California. Height 3.6 mm; width 3.7 mm (Strong, 1938)

Figures *24*, *25*: *Liotia acuticostata* Carpenter, 1864 [=*Parviturbo acuticostatus* (Carpenter, 1864)]. Lectotype USNM 16282, Catalina Island, California, 18 - 36 m. Height 2.8 mm; width 2.7 mm (Carpenter's (August 1864) published dimensions are "Long. 0.12, ... Lat. 0.10, ..." = height 3.0 mm; width 2.5 mm)

Figure *26*: *Homalopoma* ***mimicum*** LaFollette, spec. nov. Paratype LACM 1766, Sta. LACM 71-148. Showing operculum. Height 2.5 width 2.6 mm

Figures *27*, *28*: *Fossarus angiolus* Dall, 1919 [=*Parviturbo acuticostatus* (Carpenter, 1864)]. Holotype USNM 271503, Todos Santos Bay, Baja California. Height 2.5 mm; width 2.2 mm [Dall's (1919) published dimensions are: height 2.25 mm; width 1.75 mm]

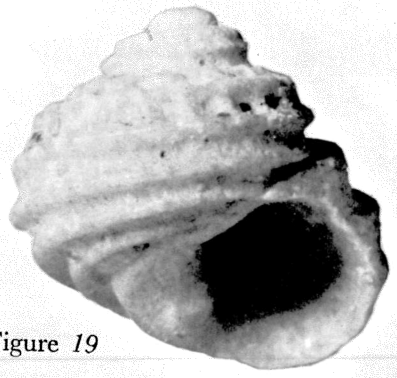

Figure 19

Figure 20

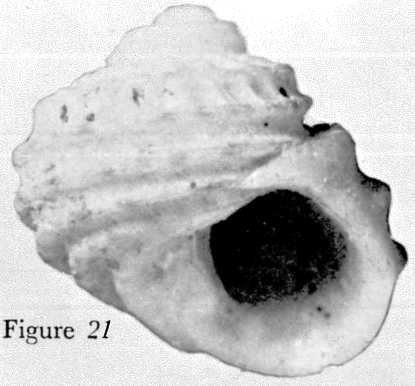

Figure 21

Figure 22

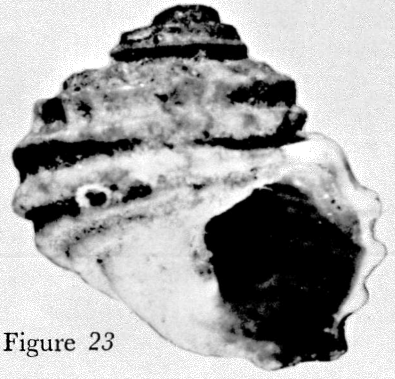

Figure 23

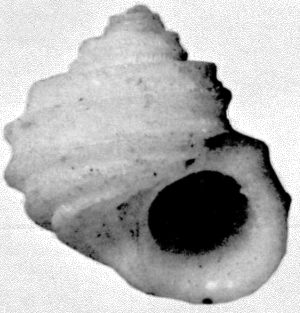

Figure 24

Figure 25

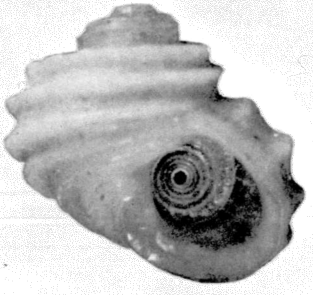

Figure 26

Figure 27

Figure 28

(λ_{y*}) is 0.98, meaning that adult specimens of these species may be correctly distinguished on the basis of size alone with 98% certainty, using 2.86mm as the dividing point. Another way of expressing this is that 98% of adult specimens below 2.86mm in size will be *H. **mimicum*** and 98% of those above will be *H. radiatum*. Similar results were achieved from the standard deviation:

$$1 - [p(Z \leqslant -2.29) + p(Z \geqslant +2.29)] = 0.978.$$

Color: Color is the second obvious difference between the 2 species. *Homalopoma **mimicum*** is uniformly white without any indication of pigmented spots, while all fresh specimens of *H. radiatum* (more than 200 examined) exhibit at least minute flecks of pink on the spiral cords and most have easily seen spots or blotches of pink or brown. One specimen was solid pink and brown. However, all traces of color were lost on several specimens as a result of abrasion or fading, and a fresh pure white specimen may eventually be found as the pink flecks on a few specimens were so small as to be visible only by careful microscopic examination. Table 1 gives the statistical distribution of color variation. The X^2 test of significance on a truncated version of this table indicates that the results are highly significant ($X^2_{df\ 1} = 92.8$). The index of predictive association (λ_{y*}) is 0.92, meaning that there is a 92% probability of correctly determining species on the basis of color alone.

Pitting: Both *Homalopoma **mimicum*** and *H. radiatum* have axial riblets that form squarish pits between the spiral cords on the upper part of the body whorl. These riblets are shorter on *H. **mimicum*** so that pitting below the 2nd spiral cord from the suture, typical of *H. radiatum*, is rare. When it does occur, it is much weaker than between the 1st and 2nd spiral cords. In *H. radiatum* the strength of pitting between the 1st and 2nd, and 2nd and 3rd spiral cords is approximately equal. The distribution of pitting on the specimens examined is summarized in Table 2. A X^2 test of significance on a modified version of this table indicates that the results are highly significant ($X^2_{df\ 2} = 83.1$). The index of predictive association (λ_{y*}) is 0.90, meaning that there is a 90% probability of correctly determining specimens on the basis of the distribution of sculptural pits alone.

Table 1

Distribution of specimens of *Homalopoma **mimicum*** and *Homalopoma radiatum* by variation in color pattern

Species	White (no color)	Minute flecks	Spots	Blotches	Solid or nearly solid	Total
*Homalopoma **mimicum*** (N = 50)	100%	0	0	0	0	100%
Homalopoma radiatum (N = 57)	7%[1]	28%	47%	14%	4%	100%

[1]Specimens worn or faded.

Table 2

Percentage of specimens of *Homalopoma **mimicum*** and *Homalopoma radiatum* showing "pits" between various pairs of spiral cords

Species	Pits present between spiral cords: 1 and 2	2 and 3	3 and 4	4 and 5	5 and 6
*Homalopoma **mimicum*** (N = 42)	100%	10%[1]	0	0	0
Homalopoma radiatum (N = 57)	100%	100%	14%	2%[1]	0

[1]Pitting very weak.

Table 3

Distribution of specimens of *Homalopoma* ***mimicum*** and *Homalopoma radiatum* by relative strength of the seventh spiral cord as compared to the sixth

Species	Much weaker or obsolete	Noticeably weaker	Slightly weaker	Equal	Slightly stronger	Much stronger	Total
Homalopoma ***mimicum*** (N = 42)	39%	35%	16%	10%	0	0	100%
Homalopoma radiatum (N = 57)	0	0	0	2%	28%	70%	100%

Basal Cord: The final character that I analyzed statistically was the relative strength (or width) of the basal cord, the 7th spiral cord from the suture on the body whorl. In comparing it with the adjacent (6th) spiral cord I found that it is typically weaker on adult specimens of *Homalopoma* ***mimicum*** and stronger on *H. radiatum*. The results are presented in Table 3. The X^2 test on a truncated version of the table found the results highly significant ($X^2_{at\ 2} = 96.0$). The index of predictive association ($\lambda_{y|x}$) is 0.98, meaning that specimens may be determined with 98% certainty on the basis of the relative strength of the 7th spiral cord, when all specimens with that cord equal to or weaker than the 6th are considered *H.* ***mimicum*** and those with the 7th spiral cord stronger than the 6th, *H. radiatum*.

Another character that was observed to differ between *Homalopoma* ***mimicum*** and *H. radiatum*, but which was not quantifiable with sufficient precision to make statistical evaluation worthwhile, was the number of whorls of pitting visible on the adult specimens. The pitting usually starts off somewhat falteringly, making the starting point rather difficult to pinpoint. However, *H.* ***mimicum*** usually has less pitting than *H. radiatum*, usually having 1 whorl or less of pitting (most frequently about ¾ whorl) while *H radiatum* normally has 1 whorl or more (most frequently about 1⅓ whorls).

I found that size and color are the easiest characters to use in sorting *Homalopoma* ***mimicum*** and *H. radiatum* when these species are both present in a station, an examination of other characters being necessary only in borderline cases.

One final point that needs discussion is the possibility that *Homalopoma* ***mimicum*** and *H. radiatum* are dimorphs of the same species, sexual or otherwise. The identity of their ranges and the fact that 89% of the stations containing specimens of *H.* ***mimicum*** also contain specimens of *H. radiatum* suggest this possibility; while the extreme fluctuations in the relative proportions of these species in different stations, independent of geographic or bathymetric range, and the fact that only 47% of the stations containing *H. radiatum* also contain *H.* ***mimicum*** suggest that they are different species.

Discussion of Mimicry: There are several bits of evidence that support the hypothesis of mimicry and suggest that if mimicry is taking place, it is *Parviturbo acuticostatus* that is the mimic. There is also some evidence against mimicry.

The range of *Homalopoma* ***mimicum***, as known at present, falls entirely within the northern half of the range of *Parviturbo acuticostatus*. Both have their northern range limit in the Monterey area, *H.* ***mimicum*** extending about 800 km south to Sacramento Reef, about ⅓ of the way down the outer coast of Baja California, while *P. acuticostatus* extends almost another 800 km to the La Paz area.

The presence of pitting between the spiral cords on the upper part of the body whorl, typical of *Homalopoma* ***mimicum***, is a variable character in *Parviturbo acuticostatus*, the pitted form comprising 0 to 84% of the specimens in different portions of the geographic range. The pitted form is totally confined, however, to the area of range overlap with *H.* ***mimicum***. In the southern half of the range of *P. acuticostatus*, south of the southern range limit of *H.* ***mimicum***, no specimens were found that show even the faintest trace of pitting, while in the area of range overlap no sizable sample was found that lacked pitting in at least some specimens. Additionally, the area with the highest incidence of easily visible pitting is in southern California, between 32° and 34° N, the center of the range of *H.* ***mimicum***. The geographic distribution of the pitted form of *P. acuticostatus* and its relative proportion in the various populations is presented in Figure 2. To study this character, I observed only adult and near adult specimens of *P. acuticostatus* and judged the presence of easily visible pitting on whether it could

(← adjacent column)

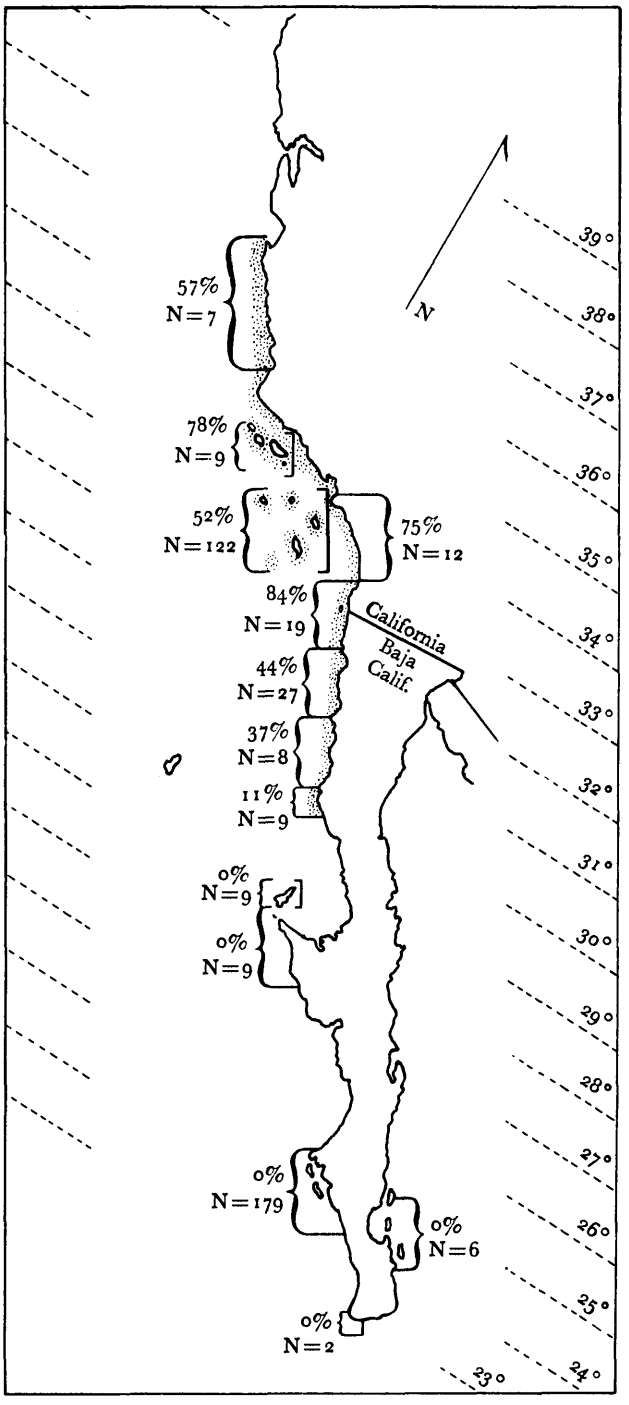

Figure 2

Parviturbo acuticostatus: Percentage of Mature Specimens Showing easily visible pitting. N = number of specimens examined from stations grouped by latitude or islands. Stippling indicates the distribution of *Homalopoma mimicum*

be seen by the naked eye. I chose the character "easily seen pitting" because this most nearly mimics *H.* ***mimicum***, and because almost all specimens from the northern part of the range show at least a gentle undulation of the surface between the suture and the 2nd spiral cord on the body whorl; but this undulation could not be interpreted as a significant imitation of the sculpture of *H.* ***mimicum***.

It was further observed that 86% of the sizable stations containing specimens of *Homalopoma mimicum* also contained specimens of *Parviturbo acuticostatus*. Although this may be explained by the relative omnipresence of *P. acuticostatus* in subtidal gravels, it does at least indicate that they live in close association with one another.

The evidence presented by geographic distribution and ecological association, especially the fact that the range of the pitted form of *Parviturbo acuticostatus* is identical with the range of *Homalopoma mimicum*, strongly suggests mimicry as a possible explanation.

Arguing against the hypothesis of mimicry is the fact that *Parviturbo acuticostatus* is considerably more common than *Homalopoma mimicum* and that the 2 species are not always found together. Many stations containing an abundance of *P. acuticostatus* have not contained *H.* ***mimicum***. The normal situation in mimicry is for the mimicking species to be considerably less numerous than the species mimicked. Otherwise, the selective advantage of the mimicked species, which is to a greater or lesser extent imparted to the mimic, is "drowned out" by the overabundance of the mimic, thus destroying the adaptive advantage gained by the mimicry. One possibility is that the mimicry may have developed at an earlier time when the relative abundance of the species may have been different. The fossil evidence is inconclusive. In the Lomita Marl (Lower Pleistocene) of San Pedro, *H.* ***mimicum*** outnumbers *P. acuticostatus* by better than 4 to 1 (136 specimens to 32), but in the earlier San Diego Formation (Upper Pliocene) *H.* ***mimicum*** has not been found, while *P. acuticostatus* is represented by 13 specimens, 3 with faint axial ribbing.

Probably the best rival hypothesis to mimicry is that the pitting may be adaptive to some characteristic of the habitat to the north of Cedros Island, Baja California, in the area of range overlap of the 2 species. If this is the case, each species may have independently developed parallel characteristics in response to the same ecological conditions.

A final possibility is that the similarities between *Homalopoma* ***mimicum*** and the pitted form of *Parviturbo acuticostatus* in size, shape, color, sculpture, geographic range and habitat may be the result of purely coincidental convergence.

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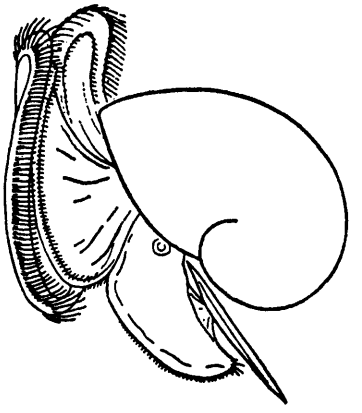

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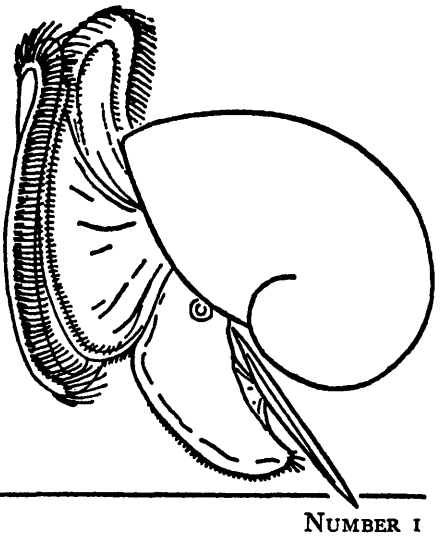

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Note: The various taxa above species are indicated by the use of different type styles as shown by the following examples, and by increasing indentation.

ORDER, Suborder, **DIVISION**, Subdivision, SECTION,
SUPERFAMILY, FAMILY, Subfamily, *Genus*, ***(Subgenus)***
New Taxa

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