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THORACIC CIRRIPIEDIA OF THE SAN DIEGO FORMATION,
SAN DIEGO COUNTY, CALIFORNIA

By VICTOR A. ZULLO

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DOROTHY M. HALMOS
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THORACIC CIRRIPIEDIA OF THE SAN DIEGO FORMATION, SAN DIEGO COUNTY, CALIFORNIA

By VICTOR A. ZULLO¹

ABSTRACT: The cirriped fauna of the Pliocene San Diego Formation, San Diego County, California, includes six species of *Balanus* Da Costa and one each of *Cetolepas* gen. nov., *Coronula* Lamarck, and *Lepas* Linnaeus. Three species, *Balanus* (*Balanus*) *kanakoffi*, *B.* (*Megabalanus*) *wilsoni*, and *Cetolepas* *hertleini* are new and known only from the San Diego Formation. The single lepadid scutum represents the first fossil record of Lepadomorpha from the margins of the eastern Pacific Basin. The *Coronula* appears to be *C. barbara* Darwin, known previously from the Pliocene and Early Pleistocene of Europe. *Cetolepas* *hertleini* affords a clue to the derivation of *Tubicinella* Lamarck from *Coronula*.

This warm temperate to subtropical fauna is composed of a mixture of extinct and living species and is transitional between California Miocene faunas characterized by extinct species and Pleistocene faunas dominated by living species.

INTRODUCTION

This paper is part of a series (Hertlein and Grant, 1944, 1960) dealing with the geology and paleontology of the San Diego Formation of San Diego County, California, that is being developed under the aegis of Dr. Leo G. Hertlein, California Academy of Sciences. The bulk of the material used in this study was collected by Mr. George P. Kanakoff, former Curator of Invertebrate Paleontology, Los Angeles County Museum of Natural History, and the present Curator, Dr. Edward C. Wilson, and is supplemented by specimens from the collection of the California Academy of Sciences.

Altogether, nine species, of which three are new, representing four genera, of which one is new, are recognized. However, this account does not include all of the species that were evidently present during the deposition of the sediments of the San Diego Formation, for a few isolated opercular valves and disarticulated compartmental plates could not be identified with recognized taxa.

It is difficult to characterize the cirriped fauna of the San Diego Formation, either geographically or historically, primarily because of the present lack of data on fossil barnacle faunas of the Pacific Coast. Of the nine species indicated by the collection, three, including one of a new genus, are new and not known from other deposits. Two, *Balanus* *gregarius* (Conrad) and *B.*

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proinus Woodring, are extinct species that were apparently widespread in shallow Pliocene seas of southern California and endemic to the Pacific Coast of North America. A third extinct species, tentatively identified with the whale barnacle *Coronula barbara* Darwin, is otherwise known only from the Pliocene and Early Pleistocene of Europe. Two of the remaining species appear to represent the extant Pacific Coast barnacles *Balanus nubilus* Darwin and *B. pacificus* Pilsbry. The *Lepas* sp. is similar to an extant cosmopolitan species usually found attached to floating seaweed and debris.

Comparison of this fauna with one of similar size and age from the San Joaquin Basin to the north (unpublished data based on UCMP collections) indicates little similarity between them. Two species, *Balanus gregarius* and *B. proinus*, are common to both faunas, but the remaining San Joaquin species appear to be endemic to the basin. The Pliocene barnacles of the geographically closer Santa Maria District are poorly known, and the two species reported (the *B. aquila* Pilsby and *B. hesperius proinus* of Woodring, in Woodring and Bramlette, 1950) are the same species that tenuously link the San Diego fauna to that of the San Joaquin Basin.

In a broad sense, the barnacle fauna of the San Diego Formation suggests warm temperate to tropical conditions, and is compositionally transitional between that of the Pacific Coast Miocene, whose species are largely extinct, and that of the Pleistocene, which is composed primarily of extant species. On the other hand, surprisingly little information is afforded by the fauna, with the possible exception of the new whale barnacle, regarding the evolution of extant Pacific Coast species.

In order to facilitate identification of the species reported herein, keys to scuta, terga, and shells have been prepared, and are to be found immediately following the section on systematic descriptions. Caution must be exercised in the use of these keys, for they are applicable only to the barnacles of the San Diego Formation, and although the common barnacles of the formation can be recognized from the keys, note must be made of the fact that other species are evidently present and may be better represented in future collections.

The following abbreviations are employed herein to designate those institutions whose collections were examined: CAS, California Academy of Sciences, San Francisco; LACM, Los Angeles County Museum of Natural History, Los Angeles, Section of Invertebrate Paleontology; SDSNH, Natural History Museum, San Diego; UCMP, University of California Museum of Paleontology, Berkeley.

AGE OF THE SAN DIEGO FORMATION

The San Diego Formation has been considered of Middle Pliocene ("Etchegoin") age in terms of Pacific Coast marine chronology. However, in recent years the temporal extent of the Pliocene on the Pacific Coast has been significantly reduced with the establishment of the Pliocene-Pleistocene

boundary at the base of the Calabrian in Italy (circa 3.5 million years Before Present) and the recognition of the Hemphillian-Clarendonian Boundary as the boundary between Pliocene and Miocene (circa 10 m.y. B.P.). This time span reduction coupled with paleontological evidence presently being obtained from a review of the Late Cenozoic of the Pacific Coast suggests that a two- rather than threefold division of the Pliocene is more realistic. On this basis, the San Diego Formation would be regarded as Late Pliocene in age and is treated accordingly herein.

DESCRIPTION OF BARNACLE LOCALITIES
IN THE SAN DIEGO FORMATION

Los Angeles County Museum of Natural History

107. Clay and gravel quarry at end of Arroyo Drive, City of San Diego, California. The 40 to 50-foot high cut contains oyster and pecten beds about 20 to 30 feet above road level and scattered large concretions throughout. G. P. Kanakoff, coll., May 12, 1947.
122. Shore bluff at the end of Loring Street, Pacific Beach, California. San Diego Formation exposed from 0 to 20 feet above sea level is overlain by fossiliferous, coarse grained, red sand of Late Pleistocene age. G. P. Kanakoff, coll.
180. On east side of 2200 block of La Jolla Boulevard at intersection with Tiras Street, ?Pacific Beach, California. G. P. Kanakoff, coll., January 28, 1950.
305. 2400 feet east and 1350 feet south of the northwest corner of Section 8, T. 19 S, R. 2 W, San Bernardino Base and Meridian, San Ysidro quadrangle, 1943 ed. (=CAS Loc. 34814). G. P. Kanakoff, coll.
- 305A. West side of next gulley east of LACM Loc. 305 at the same elevation. Fossils in float slump and consolidated boulders, silt, and sandstone, and silt in place (=CAS Loc. 36555). G. P. Kanakoff and W. K. Emerson, coll., December, 1957.
- 305C. Exposure at base of hill 100 feet west and 440 feet south of the northeast corner of Section 8, T. 19 S, R. 2 W, San Bernardino Base and Meridian, San Ysidro quadrangle, 1953 ed., G. P. Kanakoff, coll.
319. Exactly between U.S.-Mexico boundary fence and Mr. Ericson's (the manager) house; 27 feet above road level on shoulder of second hill. G. P. Kanakoff, coll.
323. Under bridge between Fifth Street and the Radio Station, about 160 feet from fence and about 350 feet from Radio Station. J. Arndt, coll., February, 1961.

485. Marine invertebrates and shark teeth collected from an estimated 20-foot thickness of mostly unconsolidated, yellow, medium to coarse grained sand on 30° bulldozed slope north of Market Street and east of Euclid Avenue, City of San Diego. Intersection of projection of arrows on edges of northwest quarter of map marked "2.6 mi. to U.S. 101" and "0.6 mi. to U.S. 80" on 7.5' National California quadrangle, 1953 ed. E. C. Wilson, coll., December 10 and 24, 1967.
492. Southwest corner of intersection of Home and Fairmont Avenues, City of San Diego. J. Arndt, coll., June, 1957.
493. East side of Wabash Canyon, below Juniper Street, City of San Diego. C. Anderson and E. P. Chace, coll., 1961.

California Academy of Sciences

1405. Street cut 0.2 miles southwest of Alamo Drive and Center Street, City of San Diego.
33218. Near intersection of Maple and Haller Streets, City of San Diego. L. L. Mills, coll., January, 1951.

San Diego Museum of Natural History

- L-2451. Same locality as LACM 485, E. C. Wilson, coll., July 31, 1967.

SYSTEMATIC DESCRIPTIONS

Suborder LEPADOMORPHA Pilsbry, 1916

Family LEPADIDAE Darwin, 1851

Genus **Lepas** Linnaeus, 1758

Lepas sp.

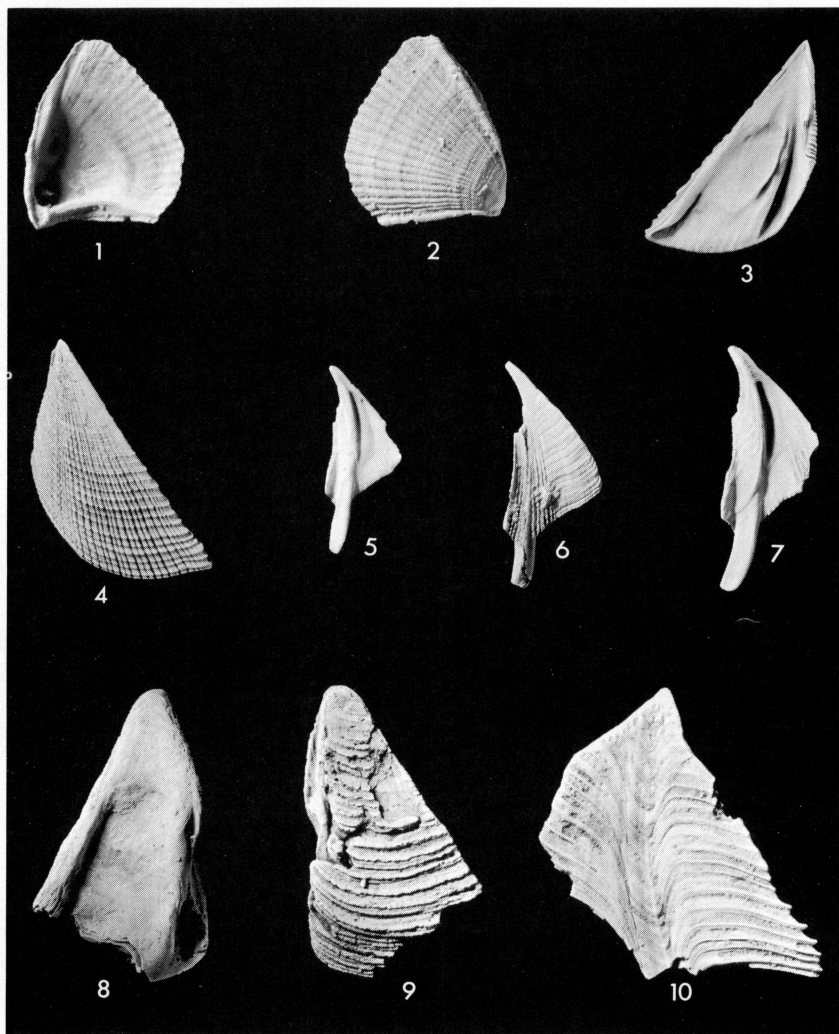
Figs. 1-2

Occurrence: LACM Loc. 305A.

Range: Late Pliocene, San Diego Formation.

Remarks: The single scutum available represents the only fossil lepadomorph to be recorded from the margins of the eastern Pacific Basin. As previously noted by Withers (1953, p. 354), the "*Lepas injudicata*" of Pilsbry (1919, p. 188, pl. 67, fig. 5) described from the Miocene of the Panama Canal Zone is in fact the broken half of a pelecypod shell, probably of the venerid *Chione* (*Lirophora*) *mactropsis* (Conrad).

Extant species of *Lepas* are difficult enough to identify from well preserved material, and at present are best differentiated by the number of filamentary appendages present at the base of the first cirrus. The fossil scutum is quite distinctive, but in itself does not provide sufficient criteria for specific



Figures 1-10. 1-2, opercular valves of *Lepas*, sp., (1-2), interior and exterior of scutum, Hypotype LACM 1196, LACM Locality 305A, height of valve 4 mm. 3-7, opercular valves of *Balanus gregarius* (Conrad), LACM Locality 485. (3) interior of scutum, Hypotype LACM 1197, height 22 mm; (4) exterior of scutum, Hypotype LACM 1198, height 22 mm; (5) interior of tergum showing purple color patch on carinal side, Hypotype LACM 1199, height 18 mm; (6) exterior of tergum, Hypotype LACM 1200, height 21 mm; (7) interior of tergum, Hypotype LACM 1201, height 23.5 mm. 8-10, opercular valves of *Balanus nubilus* Darwin, LACM Locality 305. (8-9) interior and exterior of scutum, Hypotype LACM 1203, height 27 mm; (10) exterior of tergum, Hypotype LACM 1204, height 14.5 mm.

identification. Among extant species that possess strong radial sculpture, it approaches the scutum of *L. pectinata* Spengler, especially in the narrowness of the margin on the occludent side of the ridge extending from umbo to apex.

Suborder **BALANOMORPHA** Pilsbry, 1916

Family **BALANIDAE** Leach, 1817

Genus **Balanus** Da Costa, 1778

Subgenus **Balanus**

Balanus gregarius (Conrad, 1856)

Figs. 3-7, 45

Tamiosoma gregaria Conrad, 1856, p. 315; 1857a, p. 72, pl. 4, fig. 18; Gabb, 1869, p. 61, pl. 18, figs. 22a-d; Dall, 1902, p. 5.

Balanus estrellanus Conrad, 1857b, p. 195, pl. 8, fig. 1; 1877, p. 156.

Radiolites gregaria Conrad, 1864, p. 214.

Balanus H. estrellanus Conrad, 1876, p. 273.

Balanus gregarius (Conrad). Pilsbry, 1916, p. 126, pl. 28, figs. 1-3, pl. 29; Zullo, 1964, p. 360; Durham and Addicott, 1965, p. 14, pl. 1, figs. 2, 3, 6, 8 (not pl. 2, figs. 4, 7).

Balanus (Tamiosoma) cf. B. (T.) gregarius (Conrad). Woodring, in Woodring, Stewart, and Richards, 1940, p. 96, pl. 36, figs. 2-5, 8, 9.

Balanus concavus concavus Bronn. Ross, 1962, p. 14, figs. 6, 7.

Occurrence: LACM Locs. 107, 305, 305C, 319, 323, 485, 492, 493; CAS Locs. 1405, 33218; SDSNH Loc. L-2451.

Range: Early Miocene through Late Pliocene, central and southern California; Pliocene, Baja California.

Remarks: *Balanus gregarius* is the most widespread and abundant barnacle in collections from the San Diego Formation. Opercular valves of this species, and especially scuta, are common at LACM Locs. 305 and 485, together with shells and isolated compartmental plates. Several complete specimens with opercular valves in life position were obtained from LACM Loc. 485. Scuta were also found at LACM Locs. 319 and 323 and CAS Loc. 1405. Large shells with the distinctive vesiculose basis of *B. gregarius* were collected at LACM Locs. 107, 492, and 493, and at CAS Loc. 33218.

Balanus gregarius, in the broad sense, is a common fossil encountered in Miocene and Pliocene deposits of the San Francisco Bay Area, Salinas Valley, and San Joaquin Valley in California, and in Pliocene rocks at Rosario in Baja California. As indicated by the preceding synonymy, there has been considerable confusion regarding its identification and affinities. Conrad

(1856, 1857a, 1864), who originally described *B. gregarius* from its distinctive vesiculose basis, considered it to be a rudistid pelecypod. Later, Conrad (1876) and Dall (1902) recognized its relationship to the genus *Balanus*, but did not have the opercular valves available to them. The valves were first described by Woodring, in Woodring et al. (1940), but because the delicate beaks of the terga were missing in the specimens examined, Woodring (*op. cit.*) was led to conclude that *B. gregarius* was closely related to *B. concavus* Bronn. The marked similarity of the scuta of *B. gregarius* to those of various subspecies of *B. concavus* was also responsible for Ross' (1962) record of *B. concavus concavus* on the basis of a scutum from the Pliocene of Rosario, Baja California. The reassignment of this scutum to *B. gregarius* is supported by the occurrence in the same deposit (UCMP Loc. 4300) of undoubted *B. gregarius* whose scuta are identical in form to that figured by Ross (*op. cit.*).

When well preserved, intact opercular valves of *B. gregarius* are available, the marked resemblance of this species to the extant Pacific Coast species *B. aquila* Pilsbry becomes immediately apparent. The resemblance is so great as to suggest that the two species are conspecific (Zullo, 1964), but a more detailed study of fossil populations, their variation, and their comparison with living *B. aquila* is needed before any conclusions can be drawn.

***Balanus kanakoffi* sp. n.**

Figs. 11-22

Diagnosis: *Balanus* s.s. with conic, strongly ribbed or plicate shell and small, untoothed, subtriangular orifice; sutures between carinolaterals and carina linear and often obscured externally in older specimens; scutum with prominent growth ridges cut by deep longitudinal striae, giving a marked cancellate appearance to the exterior; beaked tergum with broad, basally truncate spur and open spur furrow.

Description: Shell conic, with small, subtriangular, untoothed orifice; parietes strongly and regularly ribbed or plicate, often preserving light, irregularly spaced, transverse color bands corresponding to growth increments against a darker background; parietal tubes large, rectangular, without transverse septa, but solidly filled in upper half; one or two secondary septa occasionally present on outer lamella between major parietal septa; radii narrow, solid, thick, with slightly oblique summits; sutural edges of radii coarsely denticulate; alae thin, with horizontal summits and sharp, non-denticulate sutural edges; sheath one-half height of shell, lower edge dependent; interior of parietes below sheath with conspicuous, square ribs corresponding to parietal septa; basis thick with large, radiating, non-septate tubes.

Scutum thick, slightly concave externally between apex and base; exterior ornamented by high, sharp, regularly spaced growth ridges crossed by broad, deeply incised radial striae, forming a lattice structure with nodes on the

growth ridges and thin vertical pillars in the inter-ridge areas between striae; tergal border reflexed 90°; adductor ridge absent, or at best defined as the raised lower lip of the large, deep, oval adductor muscle pit located in the upper half of the valve; articular ridge confined to upper half of tergal margin, reflexed over shallow articular furrow; depressor muscle pit lenticular, deep, extending from basal margin to base of articular ridge.

Tergum thin, narrow, beaked; width of basal margin equal to one-half height of valve; spur long, broad, situated close to basiscutal angle, and occupying about three-fifths the width of basal margin and one-fourth the total height of valve; juncture of spur with basal margin angular on scutal side, broadly curved on carinal side; articular ridge low, inconspicuous, erect; articular furrow broad, shallow; depressor muscle crests, numerous, conspicuous.

Occurrence and Type Disposition: LACM Locs. 305 (type locality), 305A, 305C; Holotype LACM 1209; Paratypes LACM 1205-1211; Paratypes CAS 13162-13165.

Range: Late Pliocene, San Diego Formation.

Remarks: *Balanus kanakoffi* differs most markedly from other species of the subgenus *Balanus* in the linear and often obscure nature of the suture between the carina and carinolaterals. It has its greatest affinities with the *B. calidus* Pilsbry—*B. spongicola* Brown—*B. trigonus* Darwin group. Although sharing certain characteristics with each of the above mentioned species, *B. kanakoffi* is readily distinguished from them in total aspect, which combines a strongly ribbed or plicate shell with a markedly cancellate scutum and a beaked tergum having a broad, basally truncate spur.

The scutum resembles that of *B. spongicola* in external sculpture, but differs in the shorter articular ridge and the larger depressor muscle pit. The tergum of *B. kanakoffi* is similar to that of *B. trigonus*, but can be recognized by the greater development of the beak and the longer, narrower spur whose juncture with the basal margin on the carinal side is not angular.

Although the shells are easily separated, the opercular valves of *B. kanakoffi* are somewhat similar to those of the extant Gulf of California species, *B. eyerdami* Henry. However, the latter differs in having a channel entering the base of the prominent beak on the inner surface, a more elongate and basally pointed tergal spur, and a larger, but less defined pit for the depressor muscle on the scutum.

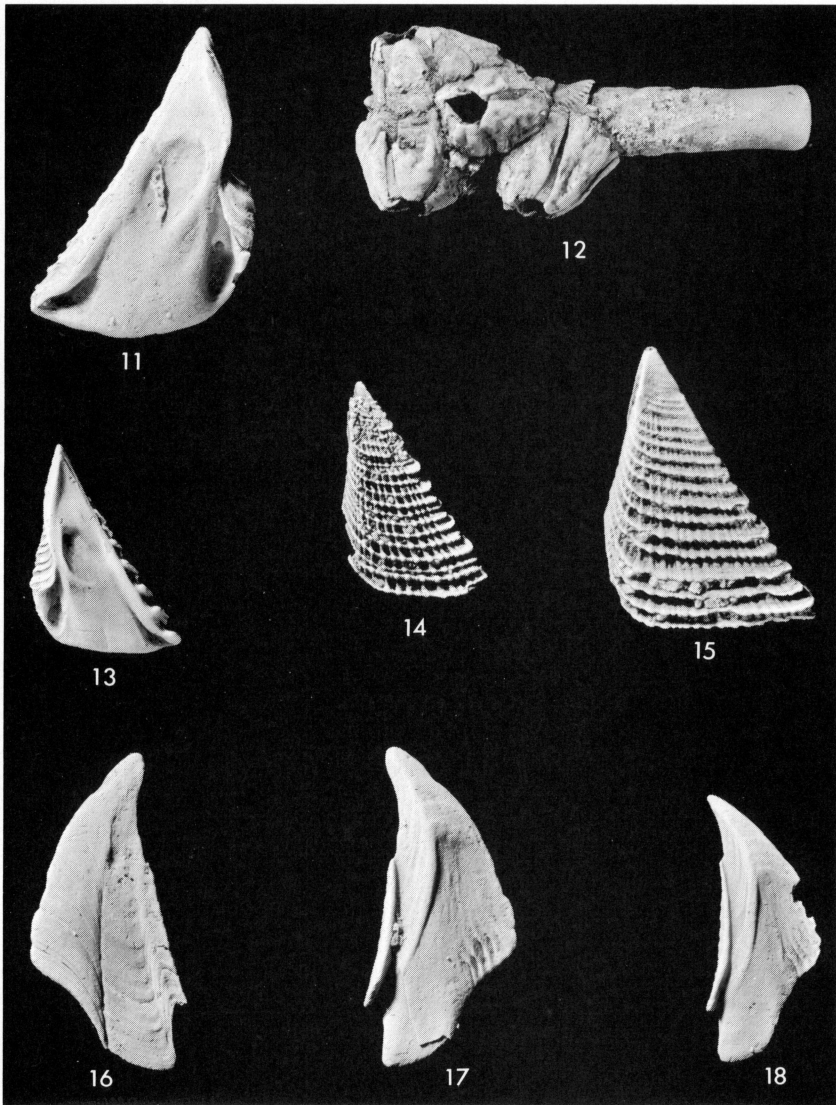
This species is named in honor of Mr. George P. Kanakoff.

***Balanus nubilus* Darwin, 1854**

Figs. 8-10

Balanus nubilus Darwin, 1854a, p. 253, pl. 6, figs. 2a-c; Ross, 1962, p. 24.

Balanus nubilus (*sic*) Darwin. Pilsbry, 1916, p. 131, pl. 30, figs. 1-4, pl. 31, figs. 3, 3a, 4, 5.



Figures 11-18. *Balanus kanakoffi* sp. n., LACM Locality 305; (11) interior of scutum, Paratype LACM 1205, height 8.5 mm; (12) shells on cidaroid spine, Paratype lot LACM 1206, length of group 16 mm; (13) interior of scutum, Paratype CAS 13162, height 6 mm; (14) exterior of scutum, Paratype CAS 13163, height 6 mm; (15) exterior of scutum, Paratype LACM 1207, height 7 mm; (16-17) exterior and interior of tergum, Paratype LACM 1208, height 8.5 mm; (18) interior of tergum, Paratype CAS 13164, height 7 mm.

Occurrence: LACM Loc. 305.

Range: Late Pliocene, California and Baja California; Pleistocene, Oregon to Baja California; Recent, southern Alaska to San Quintin Bay, Baja California.

Remarks: Fragments of two terga and one scutum are referred to this species. *Balanus nubilus* is abundant in the cool water Late Pliocene deposit at Moonstone Beach, California (e.g., UCMP Loc. B-7346; Allison, Durham, and Zullo, 1961), and is found at various Pleistocene localities along the Pacific Coast from Cape Blanco, Oregon (e.g., UCMP Loc. B-7372) south to Baja California (Ross, 1962, p. 27).

Balanus sp., cf. **B. pacificus** Pilsbry, 1916

Figs. 23-25

Occurrence: LACM Locs. 107, 305.

Range: (?) Late Pliocene, San Diego Formation; Pleistocene, central and southern California, Baja California; Recent, San Francisco, California, to northern Peru.

Remarks: Three shells that may be referable to this species were obtained from LACM Loc. 107. In addition, ten scuta from LACM Loc. 305 also appear to represent *B. pacificus*. The internal structure of these scuta is like that of Pleistocene and extant specimens, but the longitudinal striae are not as well developed. This difference may be the result of pre-depositional wear.

Balanus pacificus is a commonly encountered fossil in Late Pleistocene deposits at Tomales Bay (UCMP Loc. B-6354), Newport Beach (UCMP Locs. A-2509, A-3101, A-3102, A-3103), and in southern San Diego County (UCMP Loc. A-9005), California, and at Santa Ynez (UCMP Loc. A-3582) and San Quintin (UCMP Locs. A-8677, A-9586, B-3069) Bays in Baja California. This species has not previously been reported from Pre-Pleistocene rocks, but a possible ancestor occurs in the Late Miocene Santa Margarita Formation of the Nipomo quadrangle, California (UCMP Loc. A-1456).

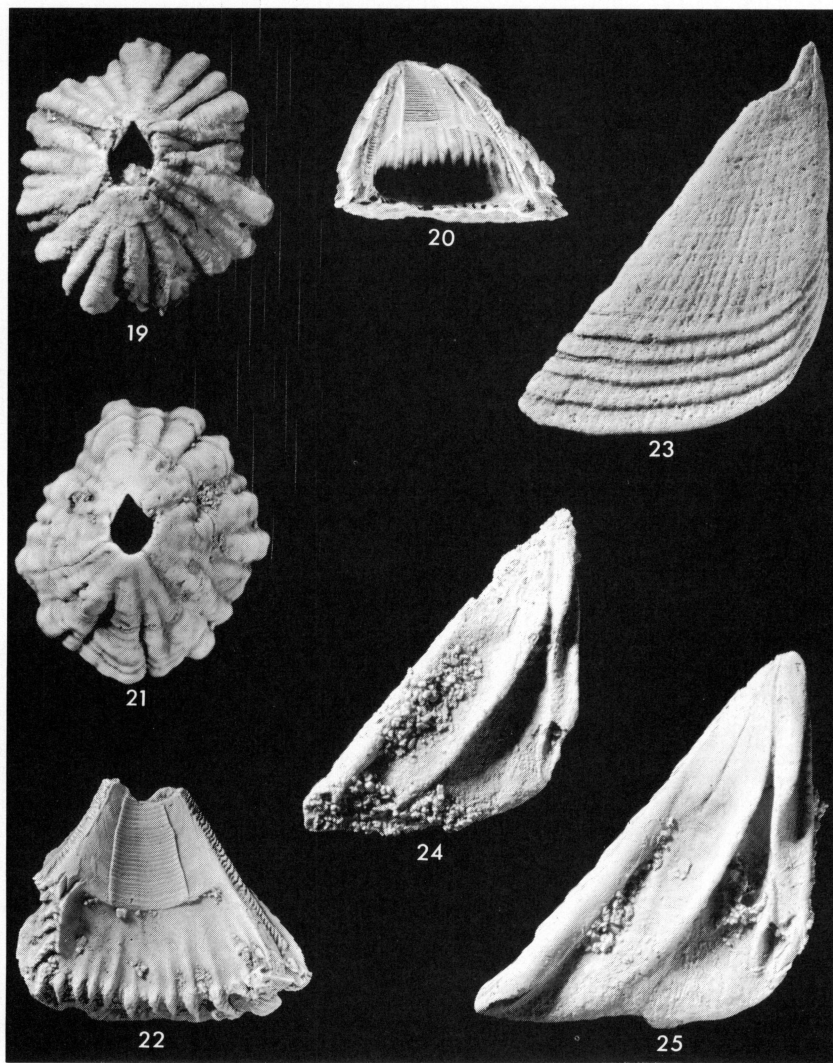
Ross (1964, p. 489) separated this eastern Pacific species from the Tethyan *B. concavus* Bronn complex on the basis of the nearly horizontal rather than oblique summits of the radii and the absence of transverse septa in the parietal tubes.

Subgenus **Megabalanus** Hoek, 1913

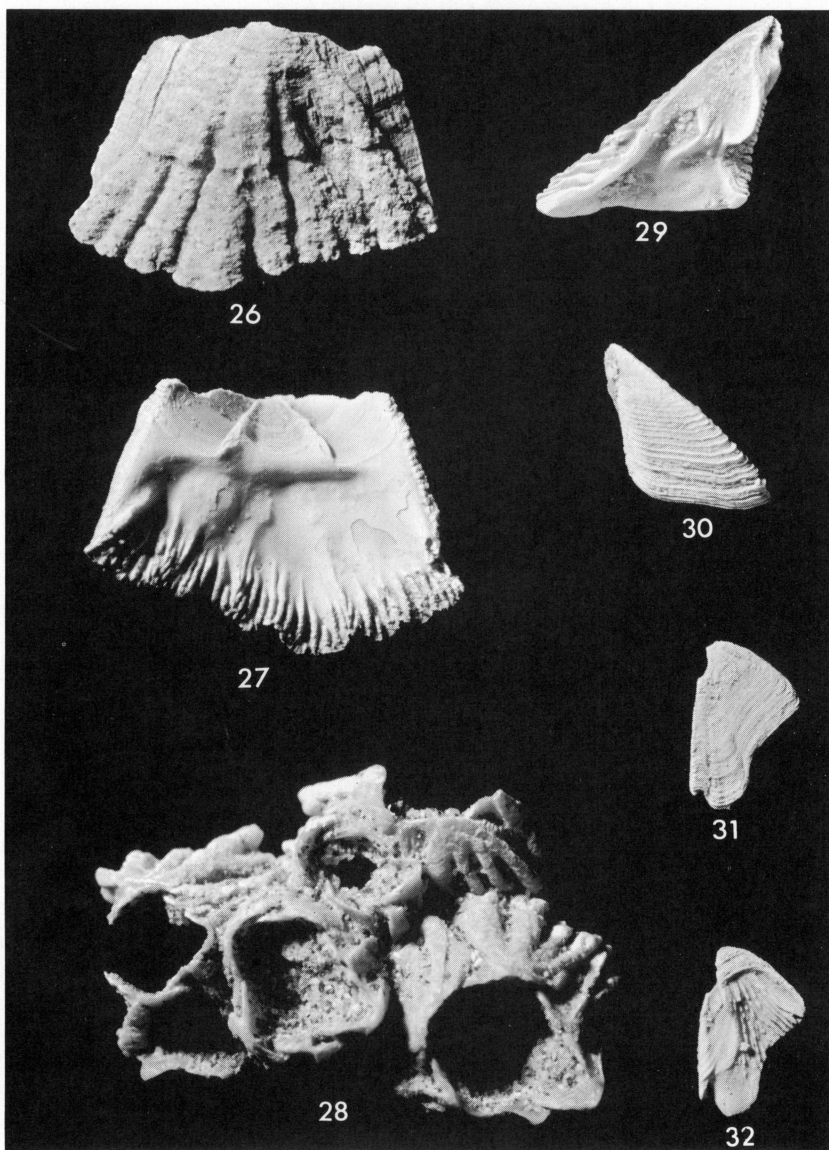
Balanus wilsoni sp. n.

Figs. 33-46

Diagnosis: Cylindric megabalanid with large, subtriangular, untoothed orifice; parietes smooth with narrow, reddish stripes on white background; radii broad with nearly horizontal summits and small radial pores; radial septa



Figures 19-25. 19-22, shells of *Balanus kanakoffi* sp. n., LACM Locality 305; (19) dorsal view of shell, Holotype LACM 1209, carinorostral length 12 mm; (20) interior of shell showing internal ribbing, sutural edges, and tubes in basis, Paratype LACM 1210, basal width 9 mm; (21) dorsal view of shell, Paratype CAS 13165, carinorostral length 12 mm; (22) interior of rostrum showing sutural edges of radii and parietal tubes, Paratype LACM 1211, height 10 mm. 23-25, opercular valves of *Balanus* sp., cf. *B. pacificus* Pilsbry, LACM Locality 305; (23) exterior of scutum. Hypotype LACM 1212, height 10 mm; (24) interior of scutum, Hypotype CAS 206, height 7 mm; (25) interior of scutum. Hypotype LACM 1213, height 10 mm.



Figures 26-32. *Balanus proinus* Woodring; (26-27) exterior and interior of rostrum, Hypotype LACM 1214, LACM Locality 305C, height 6 mm; (28) group of shells, Hypotype LACM 1215, LACM Locality 305C, width of group 15 mm; (29) interior of scutum, Hypotype CAS 13166, LACM Locality 323, height 4 mm; (30-32) exterior of scutum, exterior and interior of tergum, Hypotype LACM 1216, LACM Locality 305C, height of scutum 3 mm; height of terga 3.2 mm.

denticulate on lower sides only; sheath dark red; scutum higher than broad, with narrow, reflexed tergal margin; exterior of scutum sometimes bearing single longitudinal row of square pits; adductor ridge absent; tergum broad, spur furrow closed on scutal side only in young specimens, and completely closed in older individuals; tergal spur narrow, elongate; depressor muscle crests present.

Description: Shell cylindrical; orifice large, subtriangular, untoothed; parietes smooth, with narrow, reddish stripes on white background; parietal tubes large, rectangular, open throughout length; one or two secondary septa usually present on interior of outer lamella between primary parietal septa; radii broad with nearly horizontal summits; sutural edges of radii with secondary septa on lower sides of primaries only; tubes of radii usually small; alae broad with oblique summits; sheath dark red, one-third to one-half height of shell, with dependent lower edge; interior of parietes sharply ribbed below sheath; basis with single row of small, non-septate tubes.

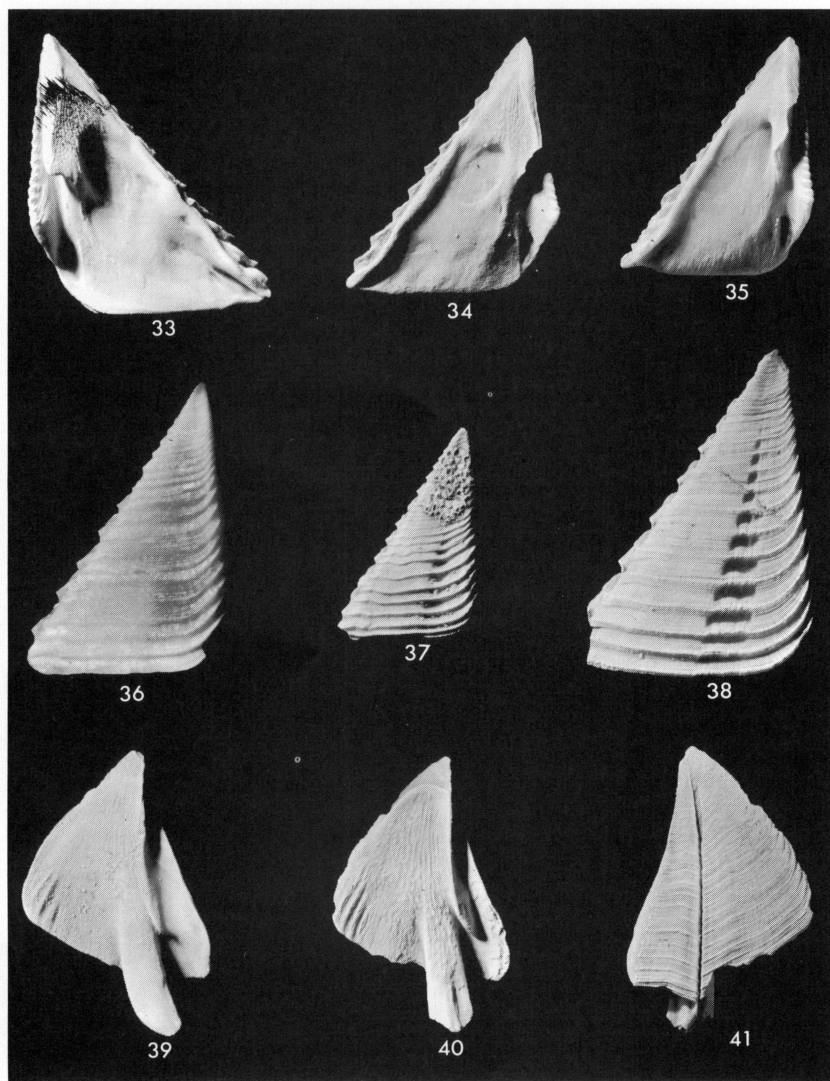
Scutum reddish externally, especially on tergal half, white with pink cast internally; ornamented externally by low, widely spaced major growth ridges, between which are fine, closely spaced minor growth lines; a few scuta with single longitudinal row of large, rectangular pits similar to those of *B. trigonus* Darwin on tergal side of valve center; basitergal corner of scutum truncate parallel to occludent margin; narrow strip of tergal margin sharply reflexed; prominent articular ridge about three-fourths length of straight part of tergal margin, slightly reflexed over deep, broad articular furrow; adductor ridge absent; adductor pit large, oval, deep; apical portion of interior faintly to markedly striate longitudinally; pit for depressor muscle deep, small, elongate.

Tergum white with pink cast, broad, flat, thin, with slightly sinuous basal margin; width of basal margin equal to about two-thirds height of valve; spur narrow, with nearly parallel sides, placed about its own width from basiscutal angle; spur short, length about one and one-half times its own width; base of spur pointed on scutal side; spur furrow closed, except in early stages where carinal side not folded over furrow; articular ridge prominent, erect; articular furrow broad; five or more moderately developed crests for lateral depressor muscles.

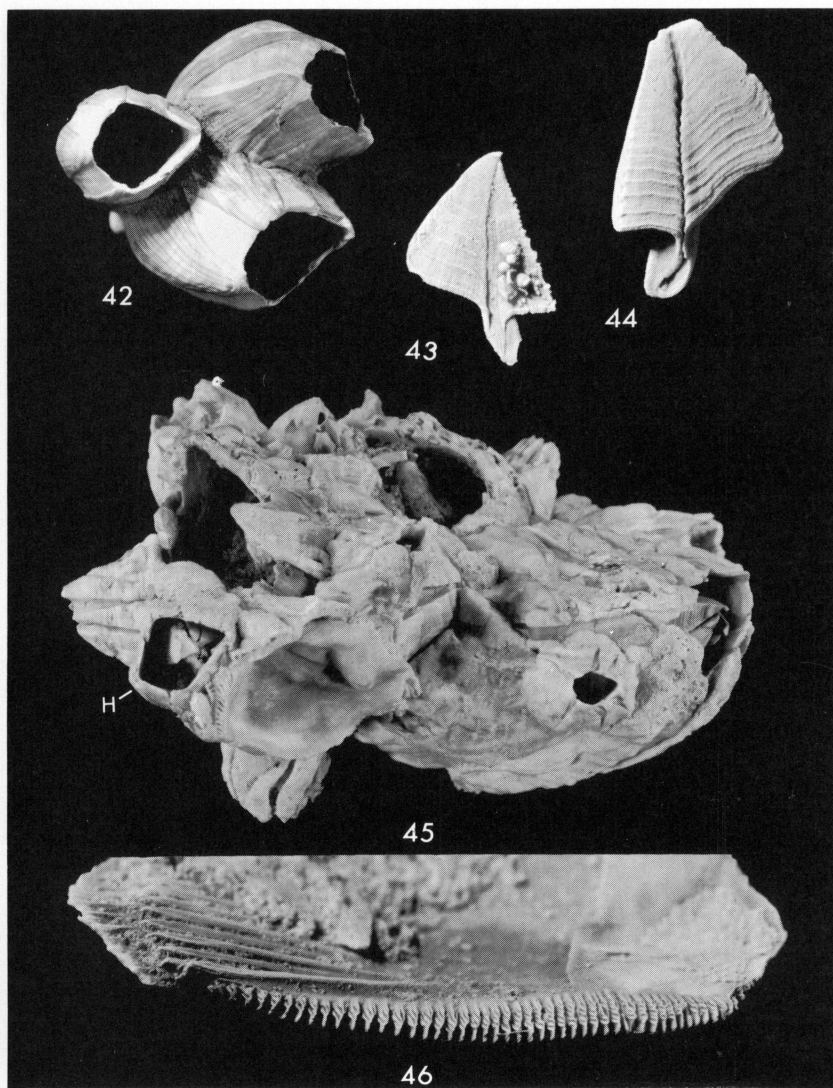
Occurrence and Type Disposition: LACM Locs. 107, 122, 485 (type locality); SDSNH Loc. L-2451; Holotype LACM 1224; Paratypes LACM 1217-1223; Paratypes CAS 13167-13168, 13170; Paratypes SDSNH 04258-04259.

Range: Late Pliocene, San Diego Formation.

Remarks: This barnacle most closely resembles austral species of the subgenus *Megabalanus*, rather than those of the tropics and the Northern Hemisphere (e.g., *Balanus tintinnabulum* complex), in its possession of secondary denticulae on the lower sides only of the primary septa of the radii. Young specimens of *Balanus wilsoni* resemble *B. algicola* Pilsbry from South



Figures 33-41. Opercular valves of *Balanus wilsoni* sp. n., LACM Locality 485; (33) interior of scutum, Paratype LACM 1217, height 10 mm; (34) interior of scutum, Paratype LACM 1218, height 9 mm; (35) interior of scutum, Paratype CAS 13167, height 9 mm; (36) exterior of scutum showing color banding, Paratype LACM 1219, height 10 mm; (37) exterior of scutum with row of pits, Paratype CAS 13168, height 7.5 mm; (38) exterior of scutum with row of pits, Paratype LACM 1220, height 12 mm; (39) interior of tergum, Paratype LACM 1221, height 9 mm; (40-41) interior and exterior of tergum, Paratype CAS 13170, height 14 mm.



Figures 42-46. *Balanus wilsoni* sp. n.; (42) group of shells, SDSNH Paratype 04258, SDSNH Locality L-2451, carinorostral length of orifice of left specimen 12 mm; (43) exterior of tergum of young individual showing partially open spur furrow, Paratype LACM 1222, LACM Locality 122, height 4 mm; (44) exterior of tergum of older individual showing partially open spur furrow in apical half, Paratype LACM 1223, LACM Locality 485, height 10 mm; (45) Holotype LACM 1224 (designated by "H") associated with group of *Balanus gregarius* (Conrad), Hypotype lot LACM 1202, LACM Locality 485, length of group 95 mm; (46) sutural edge of radius of lateral plate (basal edge to left), Paratype SDSNH 04259, SDSNH Locality L-2451, height 17 mm.

Africa in having the spur furrow closed only on the scutal side, but older specimens can be distinguished from this and other austral megabalanids with unbeaked terga by their closed spur furrows.

Aside from the major difference observed in the structure of the sutural edges of the radii, *B. wilsoni* can be distinguished from the extant Californian and Mexican megabalanids *B. tintinnabulum californicus* Pilsbry, *B. tintinnabulum coccopoma* Darwin, and *B. tintinnabulum peninsularis* Pilsbry by its smooth, red striped parietes, the absence of an adductor ridge on the scutum, and the presence of well defined depressor muscle crests on the tergum.

Large specimens of *B. wilsoni* were obtained only at the type locality (and at SDSNH L-2451 which represents the same locality), where they were attached to *B. gregarius*. Young adults attributed to this species were collected at LACM Locs. 107 and 122. These differ from larger individuals in having an uncolored sheath and a tergal spur furrow closed on the scutal side only. The half closed nature of the spur furrow can be seen in apical portions of well preserved terga of large specimens from LACM Loc. 485 (Figs. 43-44).

This species is named in honor of Dr. Edward C. Wilson.

Subgenus **Hesperibalanus** Pilsbry, 1916¹

Balanus proinus Woodring, 1950

Figs. 26-32

Balanus hesperius Pilsbry, var. Woodring, in Woodring, Stewart, and Richards, 1940, pp. 30, 97.

Balanus hesperius proinus Woodring, in Woodring and Bramlette, 1950, p. 92, pl. 14, figs. 11, 15, pl. 16, figs. 1-3, 8-12.

Occurrence: LACM Locs. 305, 305C, 323.

Range: Pliocene, southern California.

Remarks: *Balanus proinus* is represented at the above mentioned localities by complete shells with contained opercular valves and several disarticulated compartmental plates and isolated scuta. Fossil hesperibalanids are common in Cenozoic deposits of the Pacific Coast of North America (Zullo, 1966), and are best distinguished at the specific level on characters of their terga. *Balanus proinus* was originally described as a subspecies of *B. hesperius* Pilsbry, but differs from it and its extant subspecies in the short, broad tergal spur, and is here considered as a distinct species. The scuta of *B. proinus* also differ from those of *B. hesperius* in having a longer basal margin and a less well developed internal callus.

¹Henry and McLaughlin (1967) have synonymized *Hesperibalanus* with *Solidobalanus* Hoek, 1913.

Besides the type locality and the localities described herein, *B. proinus* has been found in the Early Pliocene Pancho Rico Formation of Salinas Valley, California (UCMP Locs. A-4947, A-7570, unpublished data), the Middle Pliocene Foxen mudstone of the Santa Maria District, and the Late Pliocene San Joaquin Formation of the Kettleman Hills, California (Woodring, in Woodring and Bramlette, 1950, p. 92).

Genus *Cetolepas* gen. n.

Diagnosis: Coronulines with short, nearly cylindrical body chamber; parietes bearing radial buttresses terminating in T-shaped flanges forming outer wall; buttresses reduced or absent in older individuals; sheath decidedly, but not strongly, grooved transversely, shorter than inner wall; inner surface of radial plate strongly grooved; sutural edges of radii narrow, linear; short horizontal sutural septa extend inwardly and outwardly from central vertical septum of sutural edge; no specialized alar plate or open space between radii and sheath; sutural edge of ala blunt, coarsely denticulate.

Type Species: *Cetolepas hertleini* sp. n.

Remarks: *Cetolepas* is similar to *Cryptolepas* Dall, but differs in the fainter grooving of the sheath and, most significantly, in the narrow, linear nature of the sutural edge of the radius, which consists of a single, vertical septum from which short, horizontal septa branch alternately on either side. In *Cryptolepas rachianecti* Dall and the fossil *C. murata* Zullo, the grooves of the sheath are deeply incised and the sutural edges of the radii are much broader and consist of a single series of septa that originate on the inner lamella of the radial plate and branch profusely as they pass to the outer half of the sutural edge in a complex pattern of crenulations.

Cetolepas differs from *Cetopirus* Ranzani in the possession of a grooved sheath and in the less complex sutural edge of the radius. In *Cetopirus* the completely branched sutural septa originate on the outer lamella of the radial plate and extend basally.

Cetolepas hertleini sp. n.

Figs. 47-72

Diagnosis: Same as for genus.

Description: Shell in younger stages of growth low conic, composed of nearly cylindrical body chamber from which T-shaped buttresses radiate to form outer wall surrounding large basal cavities; shell conic in progressively eroded older specimens; buttresses in older specimens reduced to low folds, giving shell the appearance of a short *Tubicinella* Lamarck; body chamber formed entirely by sheath; basal opening of body chamber nearly as large as

orifice; inner margins of radial buttresses usually not projecting below sheath in young conic forms; buttresses bifurcate towards base, ornamented externally by conspicuous, regularly spaced, horizontal ridges cut by longitudinal striae into fine beads; adjacent external flanges of buttresses not articulated or closely appressed; in older stages, flanges more distantly spaced, leaving basal cavities open to exterior; surface of large internal cavities longitudinally ribbed; walls of buttresses composed of an outer lamella with single row of small longitudinal tubes and an inner solid lamella; radii broad in conic forms, narrower and more linear in cylindrical specimens; sutural edges of radii linear, having a single vertical septum from which horizontal septa alternately diverge inwardly and outwardly; spaces between outer row of horizontal septa unfilled, forming single row of tubes in radii; inner row of horizontal septa greatly reduced or wanting in older cylindrical examples; no special alar plate and cavity present inward of radii; alae rest directly on inner surface of radii; sutural edges of alae blunt, coarsely denticulate.

Opercular valves unknown.

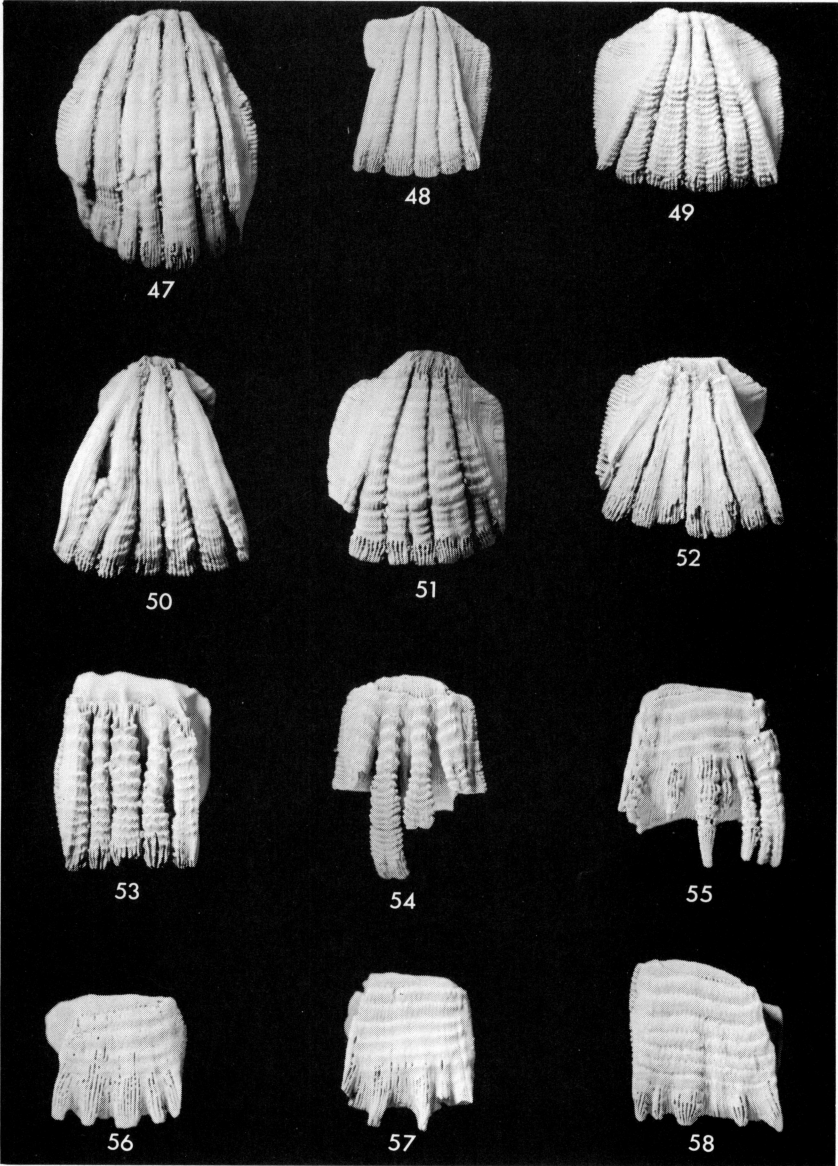
Occurrence and Type Disposition: LACM Locs. 305 (type locality), 305A, 305C, 319, 485; Holotype LACM 1230; Paratypes LACM 1225-1229; Paratypes CAS 13171-13176.

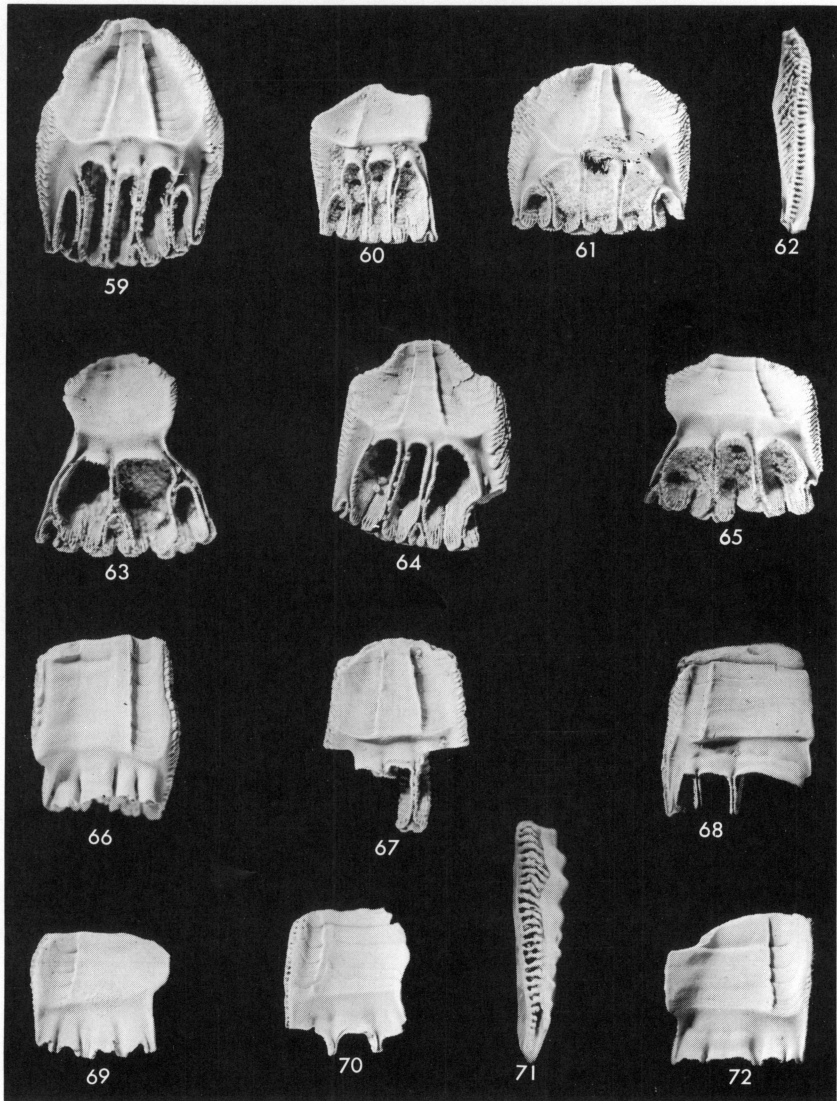
Range: Late Pliocene, San Diego Formation.

Remarks: *Cetolepas hertleini* is readily distinguished from species of *Coronula* Lamarck and *Cryptolepas* by the simple, linear nature of the sutural edges of the radii. Older specimens resemble *Tubicinella* in general shell configuration and in the form of the sutural edge, but differ in the plicate, rather than smooth, basal edge, and the blunt and crenulate, rather than sharp and smooth, edges of the alae.

As previously noted (Zullo, 1961) it would appear that the extant species of *Cryptolepas* evolved from a coronulid ancestor similar to *Coronula* (*Cetopirus*) *complanata* (Mörch) through a form resembling the Late Pleistocene species *Cryptolepas murata*. In several respects, *Cetolepas hertleini* gives the appearance of a form that might have been intermediate between *Cetopirus* and *Cryptolepas murata*. However, the radically different sutural edge of the new species indicates that this is not the case. It seems likely that the sutural edge of *Cetolepas hertleini* is homologous with the outer, unbranched part of

Figures 47-58. Exteriors of compartmental plates of *Cetolepas hertleini* gen. and sp. n., arranged from top left to lower right in increasing age and wear, LACM Locality 305; (47) rostrum, Paratype LACM 1225, height 16 mm; (48) lateral, Paratype CAS 13171, height 10 mm; (49) rostrum, Holotype LACM 1230, height 11 mm; (50) carina, Paratype LACM 1227, height 14 mm; (51) rostrum, Paratype CAS 13172, height 13 mm; (52) lateral, Paratype CAS 13173, height 11 mm; (53) lateral, Paratype LACM 1228, height 12 mm; (54) rostrum, Paratype CAS 13174, height 16 mm; (55) lateral, Paratype LACM 1229, height 11 mm; (56) lateral, Paratype CAS 13175, height 8 mm; (57) lateral, Paratype CAS 13176, height 10 mm; (58) lateral, Paratype LACM 1226, height 10 mm.





Figures 59-72. Interiors of compartmental plates of *Cetolepas hertleini* gen. and sp. n., as shown and arranged in figures 47-58; (59) Paratype LACM 1225; (60) Paratype CAS 13171; (61) Holotype LACM 1230; (62) radial edge of Holotype LACM 1230; (63) Paratype LACM 1227; (64) Paratype CAS 13172; (65) Paratype CAS 13173; (66) Paratype LACM 1228; (67) Paratype CAS 13174; (68) Paratype LACM 1229; (69) Paratype CAS 13175; (70) Paratype CAS 13176; (71) radial edge of Paratype LACM 1226; (72) Paratype LACM 1226.

the sutural edge of *Coronula complanata*, thus suggesting derivation from the *Cetopirus* stock, but independently of the lineage that gave rise to *Cryptolepas*.

The most striking evolutionary clues are those provided by what are here interpreted as the older, eroded stages of growth in *Cetolepas hertleini*. In these stages the shell is reduced to a simple, transversely ringed cylinder with a broadly plicate basal margin. The inner row of horizontal septa are greatly reduced or lacking, leaving only the outer row of septa to form the sutural edge. The spaces between septa are unfilled, and the septa tend to branch towards the outer lamella.

Thus, the morphology of these older stages is that of a *Tubicinella*, differing only in the basal plications and the crenulations of the alar sutural edges. If the earlier stages of growth and especially the development of the radial buttresses were arrested, it would appear a simple matter to derive the shell of *Tubicinella* from a form similar to *Cetolepas hertleini*.

The derivation of *Tubicinella* from *Cetolepas* rather than from *Cryptolepas* is supported by a comparison with the growth stages seen in *C. rachi-anecti*. Pilsbry (1916, p. 280) recognized two growth stages: 1) a young stage with a thick disk, rounded periphery, and simple buttresses; and 2) an older stage in which the buttresses are longer and freely branched. If these are indeed growth stages of a single species, then their ages relative to each other should be reversed. In the freely branched stage the radial buttresses converge at the apex, are nearly parallel when viewed from the base, and the shell exhibits little or no wear dorsally. In the cylindrical stage the short, simple buttresses are nearly parallel both dorsally and ventrally, and the dorsal surface of the shell is clearly eroded. Thus, as in *Cetolepas hertleini*, the more complex growth form with convergent buttresses represents the younger stages in the development of the shell, which, as it grows and becomes progressively worn away dorsally, assumes a cylindrical form in which the buttresses cease to converge. Except for the reduction of the buttresses, these older stages retain the characteristics of the younger growth form, and exhibit no tendency to assume the features characteristic of *Tubicinella*.

The generic name is derived from a combination of *Cetopirus* and *Cryptolepas*. The species name honors Dr. Leo G. Hertlein.

Genus **Coronula** Lamarck, 1802

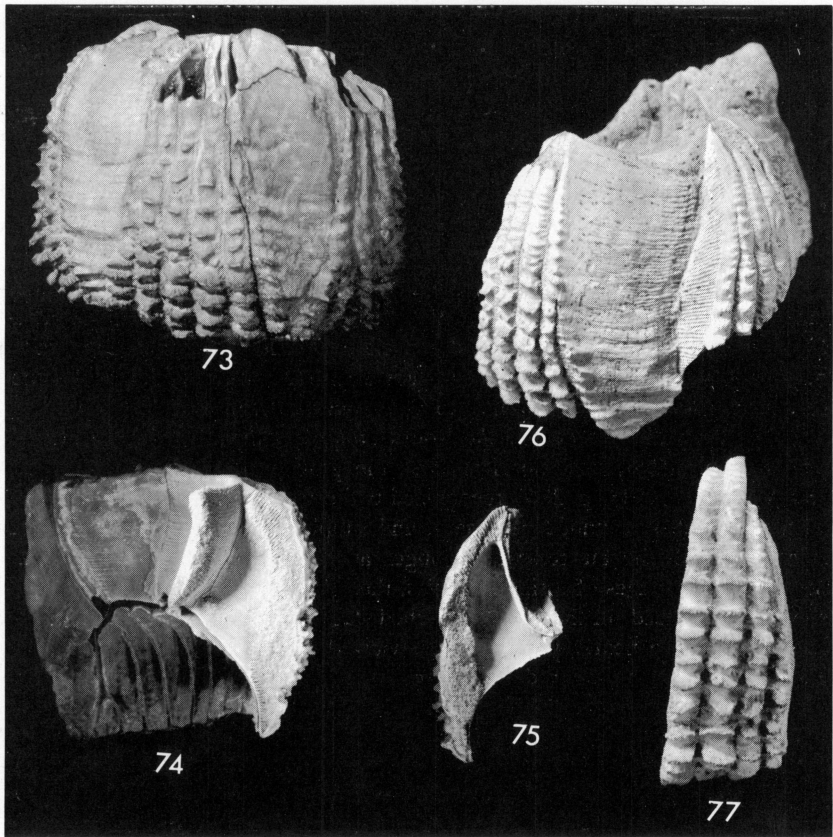
Coronula barbara Darwin, 1854 (?)

Figs. 73-77

Coronula barbara Darwin, 1854a, p. 421, pl. 15, fig. 6; 1854b, p. 38, pl. 2, figs. 8a-e; Alessandri, 1895, p. 72, pl. 3, figs. 8a-b; 1906, p. 317, pl. 18, fig. 12.

Occurrence: LACM Loc. 305.

Range: Pliocene and Early Pleistocene, Europe; (?) Late Pliocene, southern California.



Figures 73-77. *Coronula barbara* Darwin (?); (73-75) exterior, alar edge, and radial edge, Hypotype LACM 1231, LACM Locality 305, height (73-74) 36 mm, (75) 30 mm; (76-77) exterior and sculpture, Hypotype USNM 651308, U. S. Geological Survey locality M-2090, width (76) 36 mm, height (77) 35 mm.

Remarks: The single large specimen agrees with Darwin's (1854a, b) description of *C. barbara* in having prominent transverse ridges on the exterior of the shell and the interior surfaces of the transverse flanges, and in the zig-zag pattern of the teeth that serve to interlock adjacent flanges of the outer shell wall. The space between the radius and the special alar plate is not as completely filled in the San Diego specimen as it is in the examples figured by Darwin (1854a, b) and Alessandri (1906), and more closely approximates the condition seen in *C. diadema* (Linnaeus). For this reason the identification of the San Diego specimen with *C. barbara* is questioned. Another specimen that is specifically identical to the San Diego *Coronula* was collected by Dr. J. Vedder of the U.S. Geological Survey, Menlo Park, California, from the Late

Pliocene upper part of the Fernando Formation of the Tustin quadrangle, Orange County, California (U.S. Geological Survey Loc. M-2090, 1650 ft. SE and 900 ft. SW of N corner Irvine Block 57).

KEYS TO THE BALANOMORPH CIRRIPIEDIA
OF THE SAN DIEGO FORMATION

Scuta

1. Exterior longitudinally striate 2.
Exterior lacking longitudinal striae 4.
2. Adductor ridge clearly present 3.
Adductor ridge absent *Balanus kanakoffi*
3. Adductor ridge bifurcate *Balanus gregarius*
Adductor ridge single *Balanus pacificus*
4. Adductor ridge present 5.
Adductor ridge absent *Balanus wilsoni*
5. Ridged callus between articular and adductor ridges *Balanus proinus*
No such callus; vertical rib present
in depressor muscle pit *Balanus nubilus*

Terga

1. Spur furrow open 2.
Spur furrow at least partially closed 4.
2. Base of spur truncate 3.
Base of spur broadly rounded *Balanus proinus*
3. Juncture of spur with basal margin
gently arched on both sides *Balanus nubilus*
Juncture angular on scutal side,
gently arched on carinal side *Balanus kanakoffi*
4. Exterior growth lines crossed by longitudinal striae at
least on scutal side *Balanus gregarius*
No longitudinal striae externally 5.
5. Base of articular ridge confluent with scutal margin *Balanus pacificus*
Base of articular ridge widely
separated from scutal margin *Balanus wilsoni*

Shells

1. Compartmental plates solid throughout *Balanus proinus*
Compartmental plates, when viewed from base, with rows
of pores or large enclosed cavities 2.
2. Radii, as well as parietes, porose 3.
Radii without pores 4.
3. Shell smooth externally, with color stripes *Balanus wilsoni*
Shell with conspicuous horizontal and/or vertical ridges
forming distinct external sculpture *Cetolepas herileini*

4. Parietal "septa" as seen from base in form of T-shaped buttresses enclosing large basal cavities; base of shell wall as thick as diameter of body cavity *Coronula* spp.
 Parietal septa not T-shaped; shell wall much thinner than diameter of body cavity 5.
5. Parietal tubes with transverse septa; basis usually elongate and filled at least in part with vesicular material *Balanus gregarius*
 Parietal tubes without transverse septa; basis flat and not vesiculose 6.
6. No radii visible externally between carina and carinolaterals *Balanus kanakoffi*
 Radii clearly present between carina and carinolaterals 7.
7. Shell externally roughened and plicate; without color pattern *Balanus nubilus*
 Shell smooth externally; usually showing color stripes *Balanus pacificus*

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