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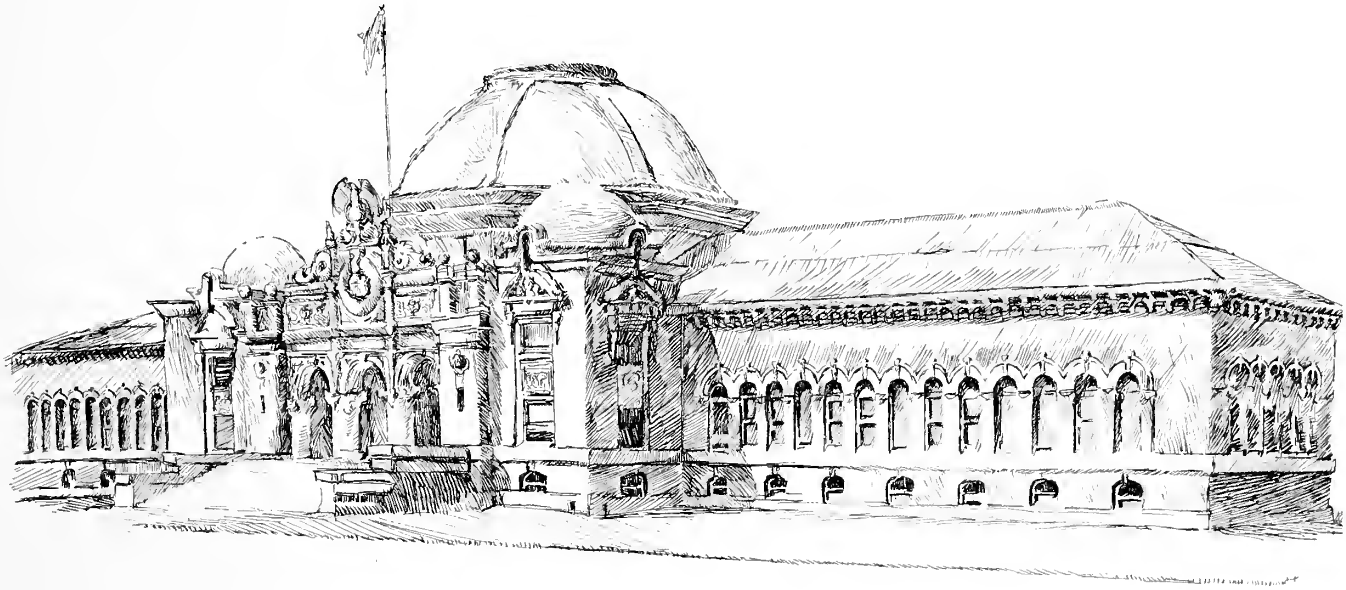

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Front Cover: The 1913 façade of the Natural History Museum of Los Angeles County.
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A KEY TO NEOTROPICAL REGION FROG-EGG–FEEDING SPECIES OF *MEGASELIA* (DIPTERA: PHORIDAE), WITH A NEW SPECIES FROM PANAMA[1]

BRIAN V. BROWN[2] AND ROBERT V. HORAN III[3]

ABSTRACT. A new species of phorid fly, *Megaselia randi* sp. nov., is described from Panama. Adults of both sexes were reared from eggs of the frog *Agalychnis spurrelli* Boulenger. A key to the three species of phorid flies so far reared from neotropical frog eggs is given.

INTRODUCTION

The genus *Megaselia* Rondani is one of the largest genera in the Diptera, and perhaps one of the largest genera of living organisms (Bickel, 2009). The 1,500 species currently described in this genus are a small fraction of the true diversity, which may be ten times larger than this number. Single sites can have tremendous species richness, with the current record going to a site in Sweden where 330 species were identified (Bonet, 2006). No estimates are available for tropical sites, for which diversity is presumably much higher (as it is for many phorid genera).

Species of *Megaselia* have a wide variety of lifestyles (Disney, 1994), but are commonly thought of as generalized scavengers, probably because of the ubiquitous, polyphagous, often synanthropic species *Megaselia scalaris* (Loew) (Disney, 2008). It is difficult to imagine 300 or more species of generalized scavengers sharing the same lifestyle at one site, however, and as expected, research is continually uncovering examples of extremely specialized larval feeding in this genus (Ceryngier et al., 2006; Disney and Weinmann, 1998; Disney et al., 2001; Gonzalez et al., 2002).

In addition to opportunistic depredation by *M. scalaris* (Villa and Townsend, 1983), larvae of at least one other *Megaselia* species are known to attack frog eggs in the New World tropics (Downie et al., 1995; Neckel-Oliveira and Wachlevski, 2004). Herein we describe another species of *Megaselia* with this lifestyle.

METHODS AND MATERIALS

The study site, Barro Colorado Island (BCI), Panama, is a 1,500-ha island located in the center of the Panama Canal. The vegetation is characterized as a tropical moist forest with a canopy height of 35–40 m. Average rainfall is 2,600 mm a year, with a distinct dry season from December to April (Leigh, 1999). Kingfisher Pond, the breeding location of the frog *Agalychnis spurrelli* Boulenger (Hylidae), is located on the northwestern section of BCI and is a seasonally filled pond approximately 175 square meters in size. The pond typically fills during the early rainy season, in July, and dries by February.

Larvae were collected directly from infested frog eggs, and adults reared within test tubes under ambient outdoor conditions.

Specimens are deposited in the Natural History Museum of Los Angeles, CA, USA (LACM), Museo de Invertebrados Graham B. Fairchild, Universidad de Panama, Estafeta Universitaria, Panama (MIUP), and the Smithsonian Institution, Washington, DC, USA (USNM).

Megaselia randi new species

(Figs. 1–6)

DESCRIPTION. Body length 1.5–1.7 mm. Frons brown, matte, frontal setae long (Fig. 1). Ventral interfrontal setae displaced laterally to eye margin. Ventral supra-antennal setae about one-half length and thickness of dorsal supra-antennal setae. Flagellomere 1 round, brown. Palpus yellow, with well-developed setae. Scutum and scutellum brown; anterior scutellar setae small, similar in size to scutal setulae. Pleuron brown, except venter of anepisternum, all of katepisternum and meron yellow. Anepisternum without setae. Legs yellowish, except anterior face of hind femur light yellowish-brown with brown spot apically. Hind femur with long ventral setae on basal one-half. Hind tibia with differentiated row of posterodorsal setae only. Mean wing length 1.54 mm, range 1.43–1.78 mm (Fig. 2); mean costal length 0.57 wing length, range 0.56–0.58. Mean costal sector ratio 3.15:2.91:1, range 2.67–4.00: 2.44–3.50:1. Wing vein R_{2+3} present. Halter brown.

Male abdomen. Tergites brown. Ventral membrane gray, with scattered setae. Epandrium brown, hypoproct and cercus yellowish brown. Left lobe of hypandrium with long, truncate process (Fig. 3).

Female abdomen. Dufour's mechanism broadly rounded, large (Fig. 4). All tergites present and well developed (Fig. 5), brown in color. Ventral membrane gray, with scattered setae. Tergite 7 quadrate, sternite 7 triangular (Fig. 6). Tergite and sternite 8 both pair of separate sclerites.

HOLOTYPE. ♂, PANAMA: Barro Colorado Island, Kingfisher Pond, 2.x.2009, R. Horan, reared from *Agalychnis spurrelli* eggs [LACM ENT 237515] (LACM).

PARATYPES. 5♂, 11♀, same data as holotype (LACM, MIUP, USNM).

RECOGNITION. This species keys easily to the genus *Megaselia* in the latest key to world phorid genera (Disney, 1994). In traditional classifications of this genus, *M. randi* would be placed in subgenus *Megaselia*, because of the lack of setae on the anepisternum, and in "group VII" because of its relatively long costa and short anterior scutellar setae. Such groups have recently been abandoned, however, with the realization that they are not monophyletic assemblages.

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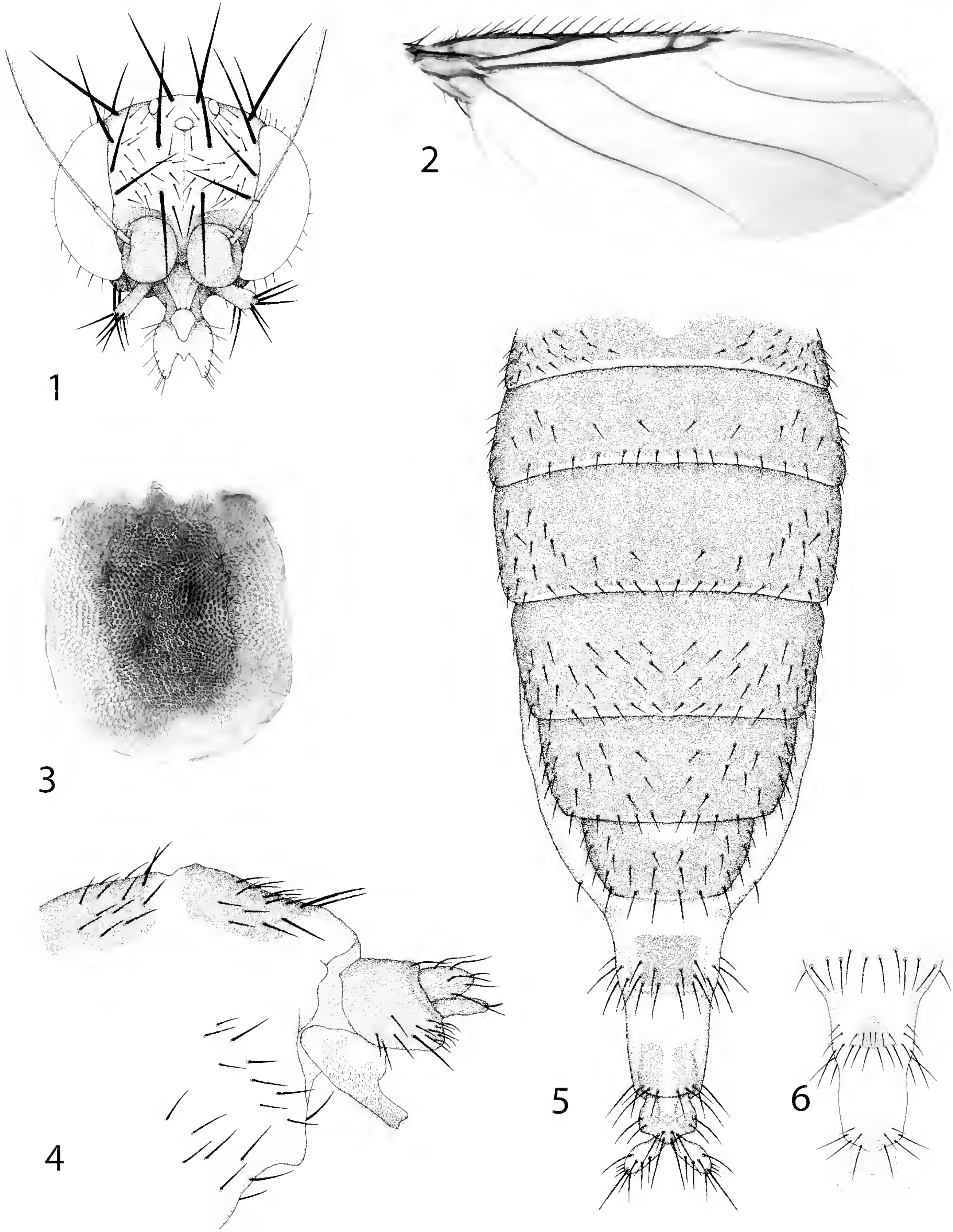
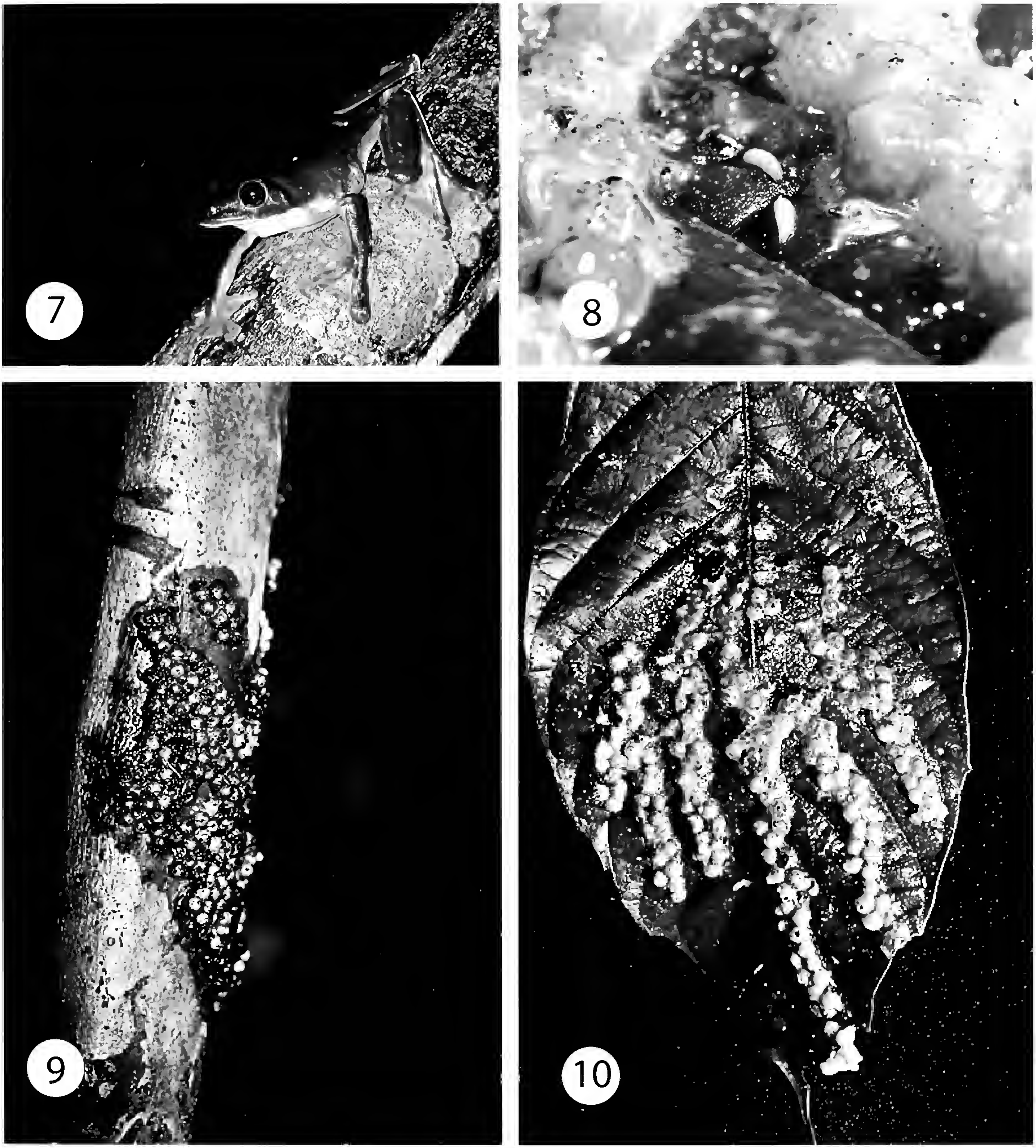


Figures 1–6 1. head; 2. wing; 3. Dufour's mechanism; 4. male abdomen: lateral; 5–6. female abdomen: 5, dorsal; 6, ventral apex.



Figures 7–10 7. adult female *Agalychnis spurrelli*; 8. phorid larvae on frog eggs; 9. healthy egg mass; 10. infected egg mass.

One of the difficulties presented by this genus is the scattered nature of its associated literature. In the latest keys to neotropical *Megaselia* (Borgmeier, 1962, 1969, 1971), *M. randi* does not key to any known species. In Borgmeier (1962), it keys to couplet 45 of the Group VII key on page 309, but does not fit either option. The first lead in couplet 45 is (translated from German) "ventral interfrontal setae almost immediately under ventral fronto-orbital setae; costa 0.47 wing length… *M. zeno* n. sp. " and fits *M. randi* in the first character, but not in the second (the costal length is much longer in *M. randi*). Furthermore, the halter is yellow in *M. zeno*, but brown in *M. randi*, and *M. zeno* is found in southern Brazil. Keying is similarly unsuccessful in Borgmeier's other papers (1969, 1971). All of the 22 species described since Borgmeier's last work (Boesi et al. 2006; Disney, 1982, 1989, 1995; Disney and Berghoff, 2007; Disney and Rettenmeyer, 2007; Disney and Sakai, 2001; Disney and Sinclair, 2008; Disney and Weinmann, 1998; Downie et al., 1995; Gonzalez et al., 2002; Kung and Brown, 2004; Weinmann and Disney, 1997) also differ from ours.

The adults of the three known phorid flies reared from eggs of neotropical frogs can be identified using the following key:

1 Halter knob yellow; all abdominal tergites dark brown with yellow markings; male with extremely robust, feathered (with small microtrichia) seta at tip of proctiger clearly longer and thicker than setae on cercus; female with tergite 6 short, extremely broad, extending laterally on segment . . . . *Megaselia scalaris* (Loew)

– Halter knob brown; at least some tergites wholly brown; seta at tip of male proctiger subequal in size to those on cercus and not feathered; female with tergite 6 of normal size, smaller and narrower than tergite 5 2

2 Anepisternum bare; anterior scutellar setae much smaller than posterior pair; all female tergites large, only gradually reduced in size posteriorly; tergite 4 larger than tergite 5 . . . . *Megaselia randi* sp. nov.

– Anepisternum with small setae; anterior scutellar setae subequal to posterior pair; female tergite 4 greatly reduced, rounded, about one-half size of tergite 5 or less . . . . *Megaselia nidanurae* Disney

NATURAL HISTORY OBSERVATIONS. First observations of egg clutches of *Agalychnis spurrelli*, the gliding leaf frog (Fig. 7), were made on August 11, 2009. Frogs sporadically laid clutches with no sign of fly infestation (Fig. 9) until mid-September, when maggot-infested clutches were observed (Figs. 8, 10). By October 2, 2009, the majority of clutches appeared to be infested with maggots. Larvae were collected on this date and reared in moist-cotton–filled test tubes capped with aluminum foil and held at ambient temperature in an outdoor field lab. Maggots appeared to become dormant soon after being placed within the tubes. Adult flies emerged on October 18, when most were discovered already dead in the tubes and preserved in ethanol immediately. All clutches infested with larvae were considered completely failed. It is not known whether the eggs were infertile, damaged by another organism and scavenged by the flies, or directly preyed upon by the flies.

DERIVATION OF SPECIFIC EPITHET. We name this species in honor of herpetologist Stan Rand, who was a key influence on R.V.H.'s work.

ACKNOWLEDGMENTS

Figures 1–6 were skillfully produced by Brian Koehler. Figures 7–10 were photographed by Robert Horan. David Donoso provided critical assistance in rearing larvae and other early stages of this discovery. Brian Brown was supported by National Science Foundation grant DEB-1025922 to Brian Brown and Paul Smith. Robert Horan was partially supported by the Latin American and Caribbean Studies Institute of the University of Georgia and the Smithsonian Tropical Research Institute during the field portion of this research, as well as by the United States Department of Energy Contract DE-FC-09-96SR18546 with The University of Georgia Research Foundation.

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ADDITIONS TO LATE CRETACEOUS SHALLOW-MARINE LIMOPSID BIVALVES AND NEOGASTROPODS FROM CALIFORNIA[1]

RICHARD L. SQUIRES[2]

ABSTRACT. A search of collections at four museums in California revealed new mollusks that improve the poorly known geologic record of limopsid bivalves and neogastropods from shallow-marine Upper Cretaceous strata in California. A single specimen of the bivalve *Limopsis* sp. (Cenomanian undifferentiated) from central California is significant because it is the earliest record of this genus from the northeast Pacific and the only known Cenomanian record. The morphology and distribution of *Limopsis silveradoensis* Packard, 1922, which was previously the only known Cretaceous *Limopsis* in the study area, are better established because newly detected specimens have much better preservation than previously known ones. The geologic range of this species is extended downward from late Turonian to include the early Turonian, and its geographic distribution is extended northward from Southern California to northern California. It is the only known Turonian record of this genus. Locally abundant specimens of *Limopsis demerei* new species (late Campanian to possibly early Maastrichtian) from Southern California represent the first post-Turonian *Limopsis* recognized from the northeast Pacific.

Two single specimens of large-sized neogastropods of latest Campanian to possibly early Maastrichtian age are reported from San Diego, in Southern California. Their familial and generic identifications are tentative because the specimens are not well preserved; nevertheless, the specimens are significant because the Late Cretaceous record of neogastropods is meager. One specimen is possibly the volutid *Misricymbiola*? sp., which is otherwise only known from similar age strata in Egypt and Tunisia. The San Diego specimen is 15.6 cm in height (incomplete) and is the largest known gastropod from Upper Cretaceous strata of the northeast Pacific. The other specimen is possibly the turbinellid *Turbinella*? sp.

INTRODUCTION

This study concerns the description and geologic implications of some shallow-marine bivalves and gastropods whose geologic records in the northeast Pacific region are poorly known. The geologic record of the limopsid bivalve *Limopsis* Sassi, 1827, in this area was heretofore known from only a single species, the Turonian *Limopsis silveradoensis* Packard, 1922. The Cenomanian *Limopsis* sp. and the latest Campanian to possibly early Maastrichtian *Limopsis demerei* new species are now added to this record. Two single specimens of neogastropods of latest Campanian to possibly early Maastrichtian age are described from Southern California. Although incompletely preserved, each represents an important addition to the scarce record of Cretaceous neogastropods. One specimen is possibly the volutid gastropod *Misricymbiola*? sp., and the other specimen is possibly the turbinellid gastropod *Turbinella*? sp.

The areas where the species were collected are shown on Figure 1, and their designations are used throughout the paper (e.g., Area 2). Locality details are in the Localities section. The localities west of the San Andreas Fault have been tectonically transported from a more southerly region (see Saul and Squires, 2008). Temporal ranges of the studied species are plotted on Figure 2. Their combined Cretaceous range in the study area spans the Cenomanian to possibly early Maastrichtian, an interval of approximately 30 million years. The paleoclimate that existed during this interval in the study area was generally warm temperate (Saul and Squires, 2008; Squires and Saul, 2009).

MATERIALS AND METHODS

This study is based on 232 specimens found in Cretaceous holdings of four major museums in California. Preservation is generally good. The fragile bivalve specimens were cleaned by use of very sharp needles. The gastropod specimens were cleaned by means of a high-speed drill and diamond-coated drilling wheels. Morphologic terms for the bivalves are from Newell (1969), and those for the gastropods are from Cox (1969).

The studied specimens identified as "sp." probably represent new species, but they are not named here because they are based on single specimens that represent either a juvenile or an incomplete adult.

Current summaries of the geological details of the formations and members containing the studied specimens can be found in the following papers (listed in ascending chronostratigraphic order): Panoche Formation, Big Tar Canyon area, Reef Ridge (Squires and Saul, 2004); Budden Canyon Formation, lower Gas Point Member (Squires and Saul, 2004); Ladd Formation, upper Baker Canyon Member (Squires and Saul, 2001) and lower Holz Shale Member (Saul, 1982); Point Loma Formation (Loch, 1989; Coombs and Deméré, 1996; Squires and Saul, 2001); and Cabrillo Formation (Squires and Saul, 2009).

ABBREVIATIONS: Abbreviations used for locality and/or catalog and numbers are CASG (California Academy of Sciences, Geology Section, San Francisco), LACMIP (Natural History Museum of Los Angeles County, Invertebrate Paleontology Section), SDSNH (San Diego Society of Natural History), and UCMP (University of California Museum of Paleontology, Berkeley, California).

LOCALITIES

LACMIP: 4898. 117°23′W, 33°08′26″N. Dark gray mudstone in east-facing roadcut on El Camino Real; opposite and south of drive to Madonna Hill Guest Home (5392 El Camino Real); outside of the Carlsbad city limits (in June, 1973). Locality is 1.4 km (0.85 mi.) north of the intersection of Palomar Airport Road and El Camino Real. San Luis Rey Quadrangle (7.5-minute, 1968), northern San Diego County, Southern California. Point Loma Formation. Age: Late Campanian to possibly early Maastrichtian. Collector: G.L. Kennedy, June 10, 1973. **7792.** 117°20′W, 33°08′N. Temporary cut bank (now covered) in mudstone near some "claypits" south of Letterbox Canyon, at the Carlsbad Research Center on north side of Faraday Avenue, east of the intersection with Rutherford Road, approximately 1088 m (3570 ft.) north, 2966 m (9730 ft.) west of southeast corner of San Luis Rey Quadrangle (7.5-minute, 1968), northern San Diego County, Southern California. Locality is approximately

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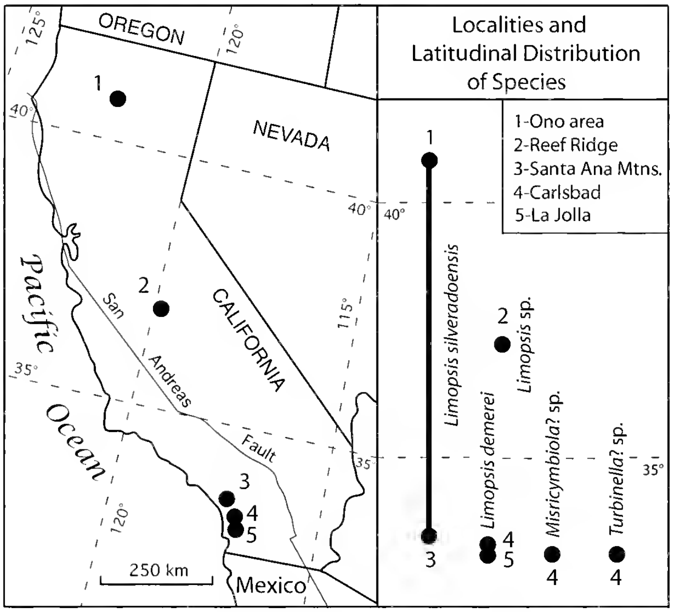


Figure 1 Localities map and latitudinal distribution of the studied species.

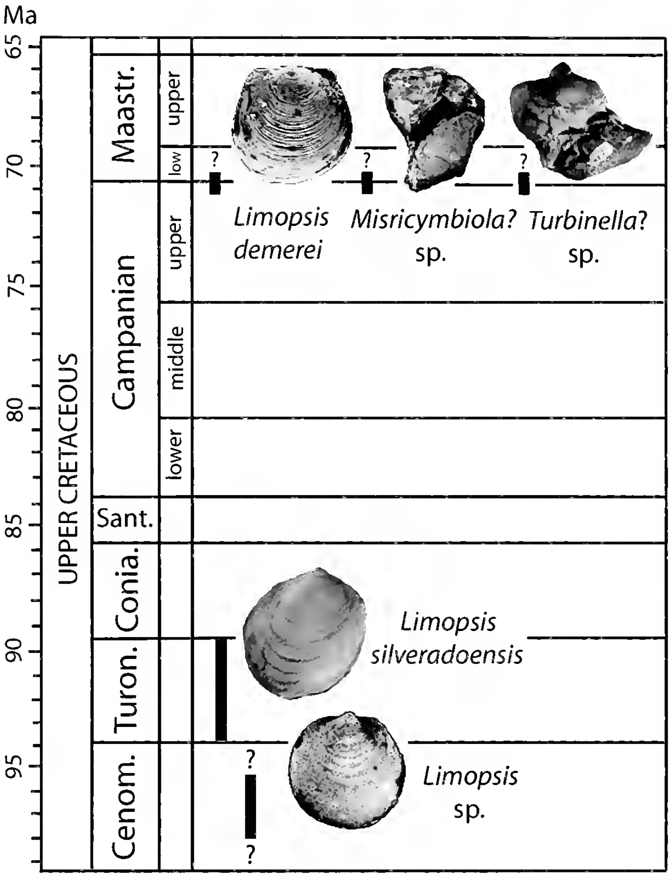


Figure 2 Geologic ranges of the studied species. Ages of stage boundaries are from Gradstein et al. (2004).

1.6 km (1 mi.) east of the city limits of Carlsbad. Point Loma Formation. Age: Late Campanian to possibly early Maastrichtian. Collector: J. D. Loch, 1984. **8198.** 117°37'25"W, 33°44'15"N. Very fine-grained sandstone, NW 1/4 of SW 1/4 of section 16, T 5 S, R 7 W, Santiago Peak Quadrangle (7.5-minute, 1954), Santa Ana Mountains, Orange County, Southern California. Ladd Formation, upper Baker Canyon Member. Age: Late Turonian. Collector: W.P. Popenoe, March 14, 1934. [= California Institute of Technology loc. 1069]. **23817.** 122°32'45"W, 40°24'45"N. Graywacke in mudstone section, third major west-heading tributary of the North Fork of Cottonwood Creek south of the mouth of Huling Creek, 762 m (2500 ft.) east and 549 m (1800 ft.) south of the SE corner of section 29, T 30 N, R 6 W, Ono Quadrangle (15-minute, 1952), Shasta County, northern California. Budden Canyon Formation, Gas Point Member. Age: Early Turonian. Collector: P.U. Rodda, August 1956. [= CASG loc. 70509]. **23930.** 122°33'25"W, 40°25'30"N. Red-brown limestone nodule in gray mudstone in low east bank of canyon, 213 m (700 ft.) west and 747 m (2450 ft.) south of NE corner of section 29, T 30 N, R 6 W, Ono Quadrangle (15-minute, 1952), Bald Hills, Shasta County, northern California. Budden Canyon Formation, Gas Point Member. Age: Early Turonian. Collector: P. Rodda, August 1956. [= CASG loc. 70508]. **25526.** 120°09'10"W, 35°54'45"N. On ridge with conglomerate beds west of Roof Spring and just east of the Big Tar Canyon Road, 887 m (2910 ft.) north and 518 m (1700 ft.) west of SE corner of section 20, T 23 S, R 17 E, Reef Ridge area, Garza Peak Quadrangle (7.5-minute, 1953), Kings County, central California. Panoche Formation. Age: Cenomanian (undifferentiated) clasts in a Campanian conglomerate. Collector: E.V. Tamesis, early 1960s.

SDSNH: Both listed below are in mudstone exposed during grading but now covered by development at Carlsbad Research Center, in vicinity of Letterbox Canyon, Carlsbad area, San Luis Rey Quadrangle (7.5-minute, 1968), northern San Diego County, Southern California. Point Loma Formation. Age: Late Campanian or possible early Maastrichtian. **3456.** 117°25'45"W, 33°08'30"N. Near north end of College Boulevard. Collector: Museum Field Party, 1987. **3458.** 117°26'50"W, 33°08'08"N. Elevation 69 m (225 ft.), cut into and below a large abandoned clay pit shown on old topographic maps, is slightly east of intersection of Faraday Avenue with College Boulevard. Collecter: B.O. Riney, February 4, 1987.

UCMP: 2143. 117°38'30"W, 33°44'38"N. Black mudstone from elevation 366 m (1200 ft.) on east side of Silverado Canyon, below the narrows 228 m (750 ft.) north on section line between sections 7 and 8, T 5 S, R 7 W, El Toro Quadrangle (7.5-minute, 1949), Santa Ana Mountains, Orange County, Southern California. Ladd Formation, Holz Shale Member. Age: Late Turonian. Collector: E.L. Packard, late 1910s.

SYSTEMATICS

Class Bivalvia Linnaeus, 1758

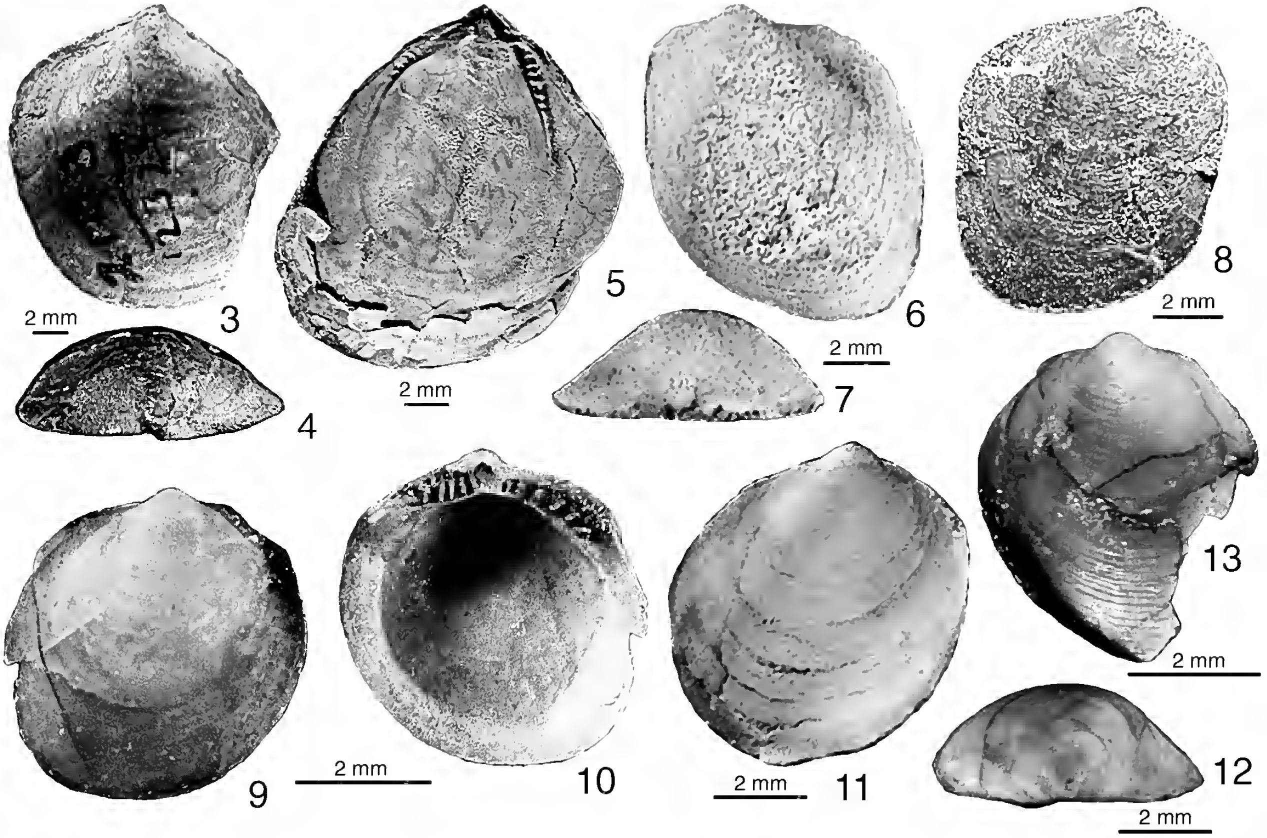
Order Arcida Gray, 1854

Superfamily Limopsoidea Dall, 1895

REMARKS. Oliver and Holmes (2006) reported that limposids and philobryids alone make up the Limoposoidea.

Family Limopsidae Dall, 1895

REMARKS. Malchus and Warén (2005) reported that Limopsidae evolved from parallelodontids and that limopsids gave rise to philobryids, but not to glycymeridids.



Figures 3–13 *Limopsis silveradoensis* Packard, 1922. 3–4. Holotype UCMP 12324, UCMP loc. 2143, left valve: 3. exterior, 4. dorsal view; 5. paratype UCMP 12323, UCMP loc. 2143, mostly an internal mold of left valve; 6–7. hypotype LACMIP 13712, LACMIP loc. 8198, left valve: 6. exterior, 7. dorsal view; 8. hypotype LACMIP 13713, LACMIP loc. 8198, right valve; 9–10. hypotype CASG 70937, LACMIP loc. 23930, right valve: 9. exterior, 10. interior; 11–12. hypotype CASG 70936, LACMIP loc. 23817, right valve: 11. exterior, 12. dorsal view; 13. hypotype CASG 70938, LACMIP loc. 23930, left valve.

Genus *Limopsis* Sassi, 1827

TYPE SPECIES. *Arca aurita* Brocchi, 1814, by original designation, Recent, Mediterranean Sea.

REMARKS. The genus name is derived from the Latin *Lima*, a file, and the Greek, *opsis*, aspect; the gender is feminine (Coan et al., 2000). Tevesz (1977) reported about 17 available generic or sugbeneric names for *Limopsis*, based on species that resemble *Limopsis aurita* (Brocchi). He reported, furthermore, that this proliferation of names stemmed from a lack of information about the range of morphologic variation in *Limopsis* and from workers not bothering to compare their prospective genus with *L. aurita*. *Limopsis* has been split into several groups on the basis of sculpture, especially whether the ventral margin is crenulate or not, but, according to Coan et al. (2000), these characters are mutable and numerous intergrades occur.

Limopsis silveradoensis Packard, 1922
(Figs. 3–13)

Limopsis silveradoensis Packard, 1922:419, pl. 27, figs. 2, 4.

SUPPLEMENTAL DESCRIPTION. Shell size medium small (up to height 20.1 mm and length 17.5 mm, same specimen). Shell ovate, forwardly oblique, anterior-dorsal margin commonly concave. Equilateral. Valves moderately convex. Shell smooth but juveniles can have weak, flat commarginal ribs; adults can have commarginal undulations, especially on medial part of disk. Umbones prominent and dorsally projecting, slightly anterior of center to centrally located. Ligament alivincular, short, located in central triangular resilifer. Dorsal margin of valves long and straight or short and sloped. Hinge plate arched, especially on adults. Taxodont dentition in two unequal curving series, with posterior series longest and extending more ventrally with growth. Approximately five teeth in anterior series and six to seven teeth in posterior series. Pallial line entire. Inner margin of valves smooth.

DIMENSIONS. Table 1.

HOLOTYPE. UCMP 12324 (left valve).

TYPE LOCALITY. UCMP loc. 2143.

PARATYPE. UCMP 12323, UCMP loc. 2143.

GEOLOGIC AGE. Turonian.

STRATIGRAPHIC DISTRIBUTION. Lower Turonian. Budden Canyon Formation, lower Gas Point Member, Tehama County, Bald Hills, northern Ono area, northern California (new stratigraphic occurrence) (Area 1). **Upper Turonian.** Ladd Formation, upper Baker Canyon and lower Holz members, Santa Ana Mountains, Orange County, Southern California (Area 3).

REMARKS. The examined material consisted of 33 specimens: 26 from the Gas Point Member, and seven from the Baker Canyon and Holz Shale members. The specimens of *L. silveradoensis* in the Gas Point Member are from the member's lower part and represent juveniles. The Gas Point Member juvenile specimen (height 4.3 mm) illustrated in Figure 10 is the first to show the actual teeth of *L. silveradoensis* and the first to show the right-valve dentition. The paratype (Fig. 5),

Table 1 Measurements (mm) of specimens figured herein.

Taxa	Height	Length or diameter*	Convexity (single valve)
Bivalves			
Limopsis silveradoensis			
UCMP holotype 12324	17.2	14.7	4.9
UCMP paratype 12323	20.0	17.0	3.5
LACMIP hypotype 13712	7.1	6.3	1.4
LACMIP hypotype 13713	8.9	7.3	1.1
GASG hypotype 70937	4.3	4.7	1.5
CASG hypotype 70936	7.2	6.2	2.5
CASG hypotype 7093	5.2	4.2	1.8
Limopsis demeri			
LACMIP holotype 13714	7.9	8.0	1.8
LACMIP paratype 13715	6.2	6.9	1.3
LACMIP paratype 13716	7.8	8.0	1.7
LACMIP paratype 13717	7.0	6.9	1.5
LACMIP paratype 13718	6.1	6.3	1.3
Limopsis sp.			
LACMIP hypotype 13719	4.5	4.6	1.6
Gastropods			
Misricymbiola? sp.			
SDSNH hypotype 32678	156.0	133.0	
Turbinella? sp			
SDSNH hypotype 86561	72.4 (incomplete)	89.8	

* Length refers to bivalves; diameter refers to gastropods.

which is from the Ladd Formation, is the largest known specimen (height 20.1 mm). It is mostly an internal mold, including its hinge.

The valves of *L. silveradoensis* exhibit morphologic variability. Juveniles (less than height 9 mm) have a longer and straighter dorsal-shell margin than do the adults, which have noticeably shorter and sloped dorsal-shell margins. This variability might be a function of paleoecology, given that *Limopsis* is an endobyssate bivalve (Tevesz, 1977:4). The juveniles might have needed a straighter dorsal margin for shell stability in the substrate than did the adults. The location of the umbones is variable but is not a function of growth stage. For example, a juvenile (Fig. 9) has a central umbo, as does an adult (Fig. 3). Other specimens, juvenile and adult, have an anteriorwardly located umbo (e.g., Figs. 6, 8, and 11). All the examined specimens show valve obliqueness, except for the paratype (Fig. 3). The specimen shown in Figure 13 has an incomplete posterior ventral area, thus its obliqueness cannot be adequately discerned.

Limopsis silveradoensis is commonly found associated with *Glycymerita pacifica* (Anderson, 1902). Sundberg (1980) reported that *L. silveradoensis* was a shallow-infaunal, nonsiphonate suspension feeder in the shallow-marine "*Parallelodon–Eriphyla–Limopsis* Association" within the Holz Shale Member, Orange County, Southern California.

Limopsis demerei new species
(Figs. 14–23)

Limopsis n. sp. Sundberg, 1979:table 2; Sundberg and Riney, 1984:table 1.

DIAGNOSIS. Shell size small, subquadrate, lowly convex, numerous and closely spaced commarginal ribs, hinge teeth in two nearly equal series with maximum of 15 anterior and 16 posterior teeth, central interior of valves with radial striae.

DESCRIPTION. Shell size small (up to height 7.9 mm, diameter 8.1 mm, same specimen). Shell subquadrate, slightly forward oblique. Equivalved and equilateral. Valves lowly convex. Shell with numerous and closely spaced commarginal ribs. Umbones commonly low, central or slightly anterior of center. Ligament alivincular, short, located in central triangular resilifer. Cardinal area long, smooth. Hinge plate arched. Taxodont dentition in two, nearly equal-length curving series. Number of hinge teeth increases with growth stage; maximum of 15 teeth in anterior series and 16 teeth in posterior series. Heteromyarian, with anterior adductor scar approximately one-half size of posterior adductor scar. Pallial line entire. Central interior area of valves with radial striae. Inner margin of valves smooth.

COMPARISON. The new species has the same subquadrate shape as *Limopsis maggae* Heinberg (1979:105–106, fig. 1) from Maastrichtian chalk beds in Denmark, but the new species has sculpture, whereas *L. maggae* is smooth. The new species can have the same ornament as *Limopsis ravni* Heinberg (1976:64–66, figs. 11–12) from Maastrichtian chalk beds in Denmark, but the new species has less prominent and much less projected beaks, a much less inflated umbonal region, a much longer dorsal anterior margin, and approximately twice as many teeth in both the anterior and posterior series.

The new species also has the same subquadrate shape as *Limopsis kogata* (Ichikawa and Maeda, 1958:90, pl. 5, figs. 4–7, 10) from Campanian to Maastrichtian beds in southern Japan, but the new species has more, narrower, and more closely spaced commarginal ribs.

The new species differs from *L. silveradoensis* by having smaller maximum size, subquadrate shape, less-oblique and much less-inflated valves, sculpture of prominent commarginal ribs (unless abraded, e.g., Fig. 20), dorsal-shell margin not short, muscle scars prominent, central valve–interior striae prominent, and many more hinge teeth. In addition, the new species differs by having umbones that are smaller, much less inflated (almost flat on some specimens), commonly much less projecting, and commonly central. If located anteriorward, the umbones are less so than those found on *L. silveradoensis*. A specimen of *L. demerei* (Fig. 18) approximately the same size as *L. silveradoensis* (Fig. 6, interior filled with matrix) also shows the exterior differences listed above.

DIMENSIONS. Table 1.

HOLOTYPE. LACMIP 13714 (right valve).

TYPE LOCALITY. LACMIP loc. 4898.

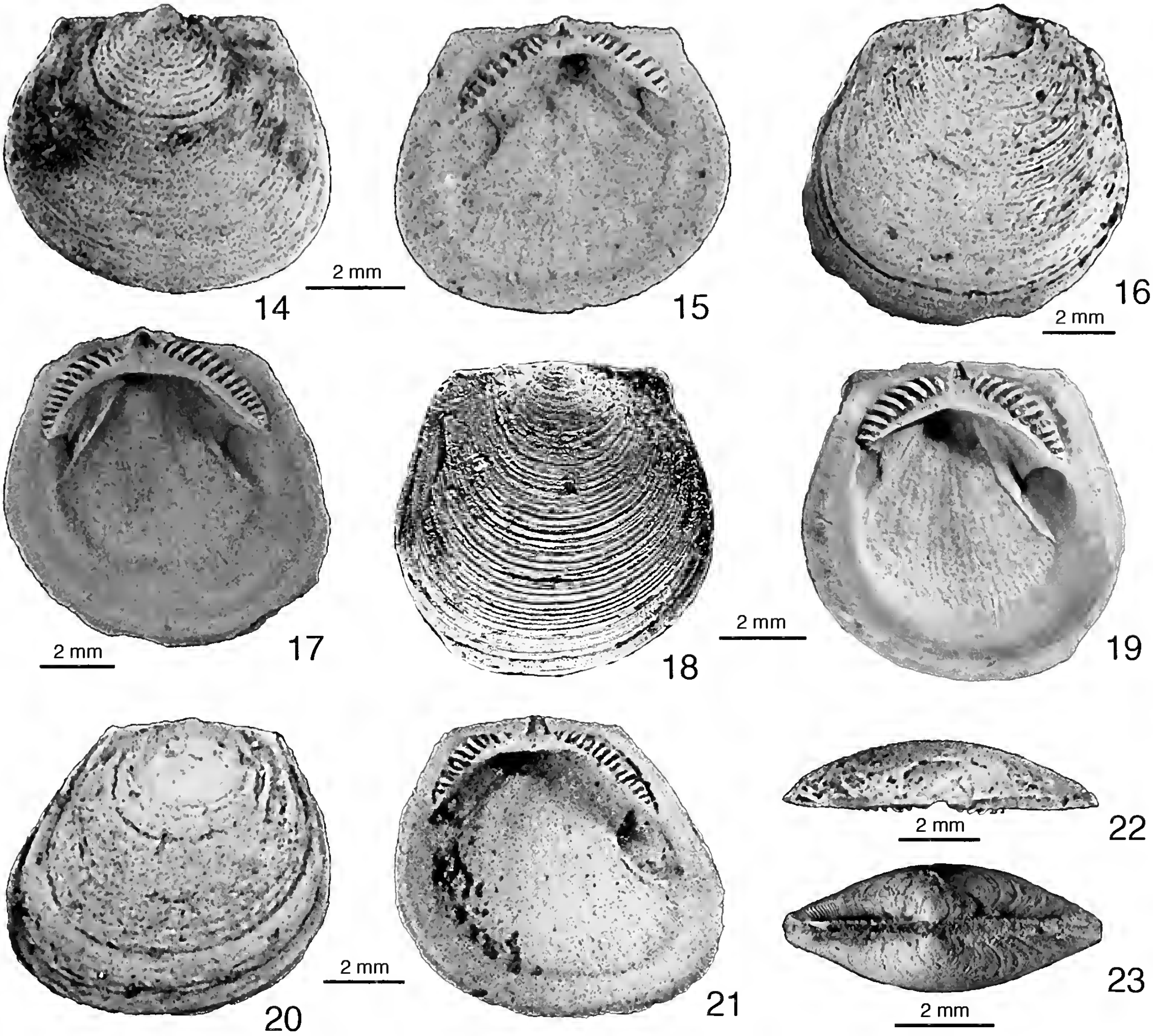
PARATYPES. LACMIP 13715 to 13718, all from LACMIP loc. 4898.

GEOLOGIC AGE. Late Campanian to possibly early Maastrichtian.

STRATIGRAPHIC DISTRIBUTION. Point Loma Formation, southeast of Carlsbad, northern San Diego County, Southern California (Area 4); reworked Point Loma Formation fossils in Cabrillo Formation, Bird Rock, south of La Jolla, San Diego County, Southern California (Area 5).

REMARKS. The new species is based on 195 specimens: 182 from mudstone at LACMIP loc. 4898 (Madonna Hill Guest Home) and 13 from mudstone at LACMIP loc. 7792 (Carlsbad Research Center). Locality 7792 is approximately 1 km southeast of locality 4898. Nearly all the specimens show excellent preservation. Of the 195 specimens, eight are closed-valved and four show gastropod boreholes. On some specimens (e.g., Figs. 14, 20), the sculpture is abraded, thereby producing a smooth appearance.

The geology at LACMIP loc. 7792 (Carlsbad Research Center) was discussed by Loch and Bottjer (1986), who also recognized an aporrhaid–*Limopsis* paleocommunity there. This paleocommunity, later named the *Teneposita–Limopsis* paleocommunity by Loch (1989), does not represent a diminutive fauna, in spite of the



Figures 14–23 *Limopsis demerei* n. sp., LACMIP loc. 4898. **14–15.** Paratype LACMIP 13715, left valve: **14.** exterior, **15.** interior; **16, 17, 22.** paratype LACMIP 13716, right valve: **16.** exterior, **17.** interior, **22.** dorsal view; **18–19.** paratype LACMIP 13717, right valve: **18.** exterior, **19.** interior; **20–21.** holotype LACMIP 13714, right valve: **20.** exterior, **21.** interior; **23.** paratype LACMIP 13718, closed-valved, dorsal view (dorsal valve on top).

assertions by Loch and Bottjer (1986) and Loch (1989). The species are actually of normal size in comparison to their size elsewhere.

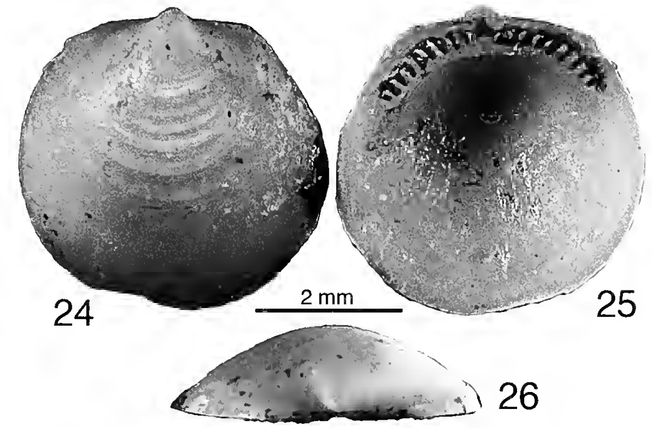
ETYMOLOGY. Named for Thomas Deméré, in recognition of his many contributions to the study of fossils found in the San Diego area.

Limopsis sp.
(Figs. 24–26)

REMARKS. The new species is based on a well-preserved, single left valve (hypotype LACMIP 13719) of a presumed juvenile collected from reworked clasts of Cenomanian age from LACMIP loc. 25526 in central California (Area 2). The valve is small (height 4.5 mm; Table 1) and differs from a same-sized specimen (Fig. 9) of *Limopsis silveradoensis* by having an orbicular rather than an oblique shape, no apparent obliqueness, commarginal undulations, nine (rather than five) anterior teeth, and nine (rather than six) posterior teeth. Although *L.* sp. has a shape similar to *L. demerei*, the former differs by having more rounded ends of the dorsal-shell margin, commarginal undulations rather than prominent and closely spaced commarginal ribs, and a more inflated umbo.

Class Gastropoda Cuvier, 1797
Clade Neogastropoda Wenz, 1938
?Family Volutidae Rafinesque, 1815
?Subfamily Caricellinae Dall, 1907

REMARKS. Although workers (e.g., Wenz, 1943) traditionally relegated Caricellinae to the volutid subfamily Scaphellinae Gray, 1857, Bandel (2003) reinstituted Caricellinae as a separate taxon based on newly found and well-preserved fossil material. There is no consensus as to which genera should be included in this subfamily. In this present paper, genera that comprise it are *Caricella* Conrad, 1835, and *Misricymbiola* Bandel, 2003.



Figures 24–26 *Limopsis* sp., hypotype LACMIP 13719, LACMIP loc. 25526, left valve. **24.** exterior, **25.** interior, **26.** dorsal view.

?Genus *Misricymbiola* Bandel, 2003

TYPE SPECIES. *Caricella chalmasi* Quaas, 1902, by original designation; Late Cretaceous (Maastrichtian), Egypt.

REMARKS. *Misricymbiola* is characterized by a pear-shaped shell with a constricted base, large rounded protoconch, low conical spire, angular periphery, flattened sides of whorls with or without with short axial ribs, three oblique columellar whorls on early whorls, single columellar swelling on last whorl, and a long siphonal canal (Bandel, 2003).

Misricymbiola differs from *Caricella* by having a larger size, subquadrate shell (rather than fusiform), possible presence of strong nodes on shoulder, wider aperture, one less columellar fold on its early whorls, and a single columellar swelling on last whorl. The protoconch of *Misricymbiola* differs from that of *Caricella* by having no spiral cords or fine axial ribs that together form a cancellate pattern where the protoconch ends and the teleoconch begins. Also the protoconch of *Miscymbiola* has no tendency to have a pointed apex.

Misricymbiola? sp.
(Figs. 27–31)

REMARKS. This species is based on a single, very large incomplete specimen (height 156 mm; Table 1); despite missing its spire and probably some of its anterior canal, the specimen is the largest known gastropod from Upper Cretaceous strata of the northeast Pacific. The apparent absence of ornament on the shell might be the result of poor preservation. The abapertural exterior surface is riddled with boreholes, most likely made by the boring sponge *Cliona*. This specimen cannot be unequivocally assigned to *Misricymbiola* because it is missing its protoconch, and because it cannot be determined if the specimen has three columellar folds on its early whorls. On the mature last whorl, it has one fold on its columella, and the fold is moderately strong and located deep inside on the middle part of the columella (Fig. 28). The specimen is pseudo-umbilicate (chink) and has a raised columellar shield. The posterior canal region near outer lip has a large subsutural welt that causes the growth line to arch backward over the welt. Elsewhere, its growth line is nearly orthocline.

Misricymbiola? sp. resembles specimens of *Misricymbiola chalmasi* (Quaas, 1902) illustrated by Bandel (2003, figs. 15–19, 21–24, 31–36) from Maastrichtian beds in the Western Desert of Egypt, but the California species differs by having a subsutural welt near the outer lip, shorter siphonal canal, and an absence of the following: a raised columellar shield, a pseudo-umbilicus, and nodes on the shoulder of the last whorl. *Misricymbiola*? sp. also resembles *Misricymbiola conocoi* Bandel (2003, p. 88–89, figs. 20, 25–28, 37, 38) from Maastrichtian beds in the Western Desert in Egypt, but the California species differs by having a subsutural welt near the outer lip, and an absence of the following: distinct carina along the shoulder of the last whorl, parietal callus, spiral keel near base of last whorl, raised columellar shield, and pseudo-umbilicus.

Misricymbiola? sp. is very similar to a specimen identified as *Aulica stromboides* (Munier-Chalmas, 1881) by Collignon (1971:157–158, pl. C, fig. 3), who reported it from Tunisia and near the Campanian–Maastrichtian boundary in age. His specimen is not an *Aulica* Gray, 1847 and is quite unlike *Aulica stromboides* (Munier-Chalmas, 1881:80–81, pl. 5, figs. 10–11). The columellar area of Collignon's specimen is not exposed and needs cleaning. It is very likely a *Misricymbiola* and has the overall shape, pseudo-umbilicus, and raised columellar shield just like the new species. The California specimen differs by having a larger size and a tabulate ramp.

?Family Turbinellidae Swainson, 1835
[= Vasidae H. Adams and A. Adams, 1853 = Xancidae Pilsbry, 1921]

REMARKS. Although the classification of this family has undergone revision in recent years, according to Harasewych (2011), it currently comprises three subfamilies: Turbinellinae Swainson, 1835; Vasinae H. Adams and A. Adams, 1853; and Columbariinae Tomlin, 1928. Vasines and turbinellines are shallow-marine dwellers, whereas the columbariines are bathyal to abyssal (Harasewych, 2011).

?Subfamily Turbinellinae Swainson, 1835

REMARKS. There is no consensus as to which genera should be included in this subfamily. In this present paper, genera that it comprises are *Turbinella* Lamarck, 1799, and *Syrinx* Röding, 1798. Harasewych and Petit (1989) placed *Syrinx*, which they reported as being the known largest-shelled gastropod (nearly 1 m in height), in Turbinellinae because the radula of *Syrinx auranus* (Linnaeus, 1758) is nearly identical to that of *Turbinella pyrum*.

?Genus *Turbinella* Lamarck, 1799

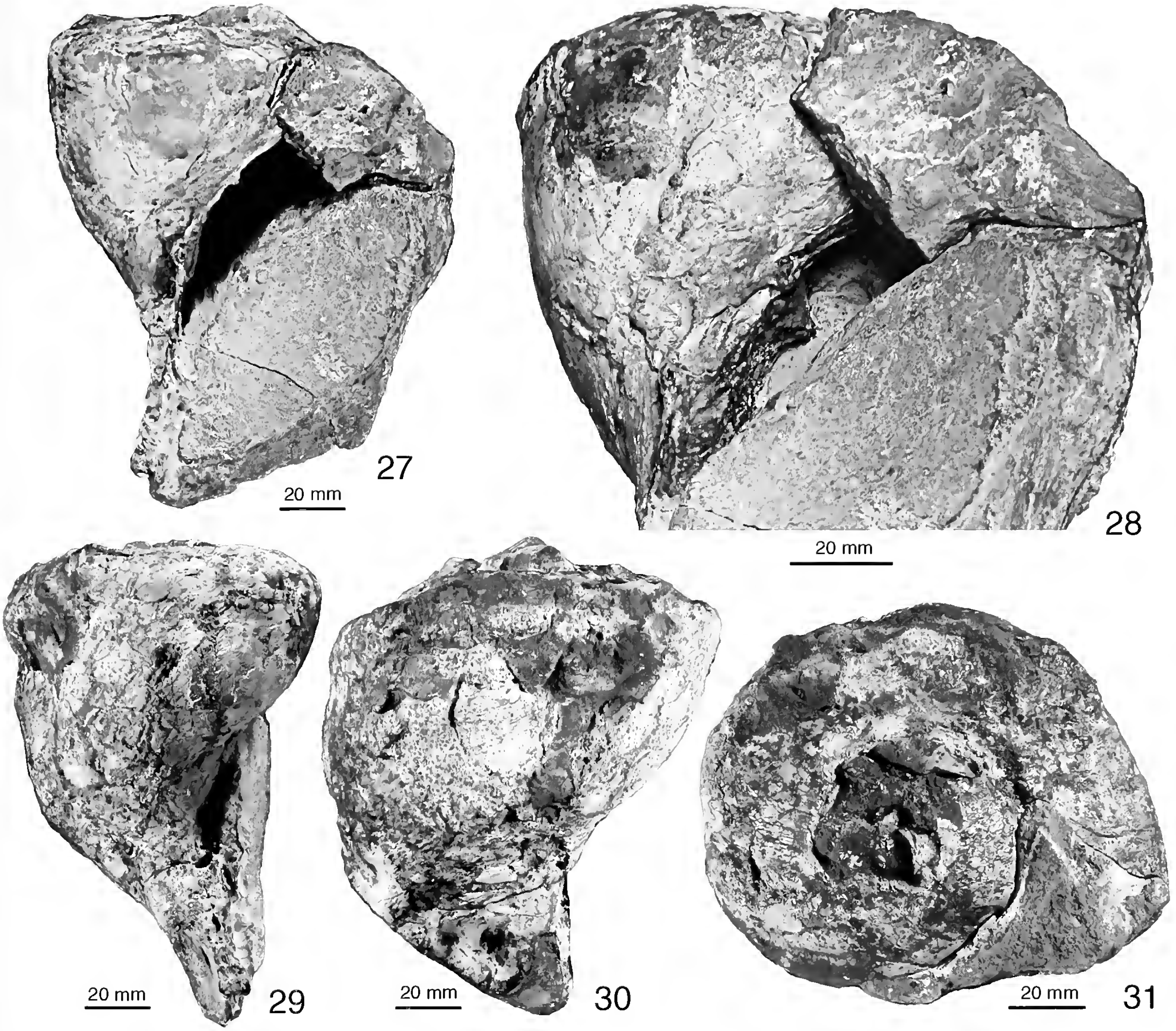
TYPE SPECIES. *Voluta pyrum* Linnaeus, 1767, by original designation; Recent, southern India region.

REMARKS. According to Bandel (1975), *Turbinella* has a multi-whorled, high protoconch whose first whorls are usually destroyed and whose end is demarcated by a septum, and this protoconch distinguishes this genus from similar-looking gastropods (e.g., the volutid *Misricymbiola*). Other distinguishing characteristics of *Turbinella* are a possible pyriform shell, ornament of spiral ribs and weak nodes becoming obsolete on the last whorl, low siphonal fasciole adjacent to a narrow umbilical slit, aperture oval, outer lip internally smooth, three to five columellar folds, and a long siphonal canal long that has an anterior notch (Davies, 1935).

Turbinella differs from *Syrinx* by having a smaller size, possible pyriform shell, and several columellar folds (i.e., none on *Syrinx*).

Turbinella? sp.
(Figs. 32–34)

REMARKS. This species is based on a single moderately large specimen (height 72.4 mm [incomplete]; Table 1) that is



Figures 27–31 *Misricymbiola*? sp., hypotype SDSNH 32678, SDSNH loc. 3458. **27.** apertural view; **28.** oblique apertural view showing deep inside columellar lip; **29.** right-lateral view; **30.** abapertural view; **31.** dorsal view.

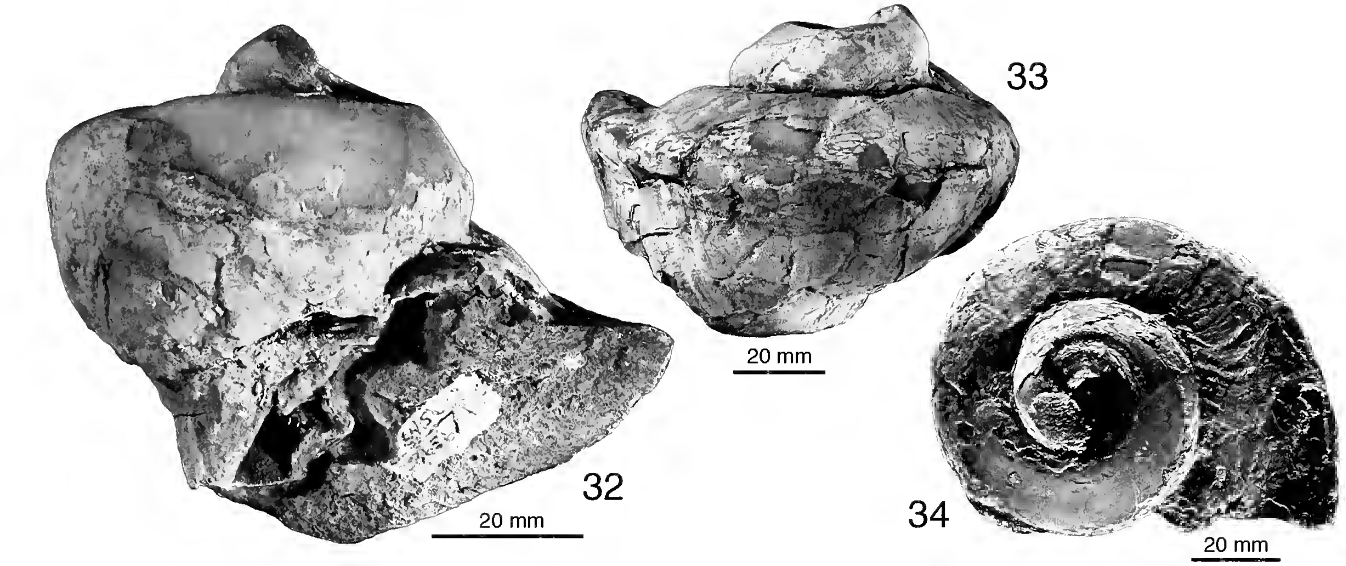
somewhat crushed and is missing the early half of its spire and its siphonal canal. Crushing probably accounts for the ramp being more steeply sloping and the shoulder being more angular on the abapertural side of the specimen versus the apertural side. The crushing also apparently created a wide depression on the ramp near the outer lip. The shell is pseudoumbilicate and the columella bears at least two strong folds, with the posterior one stronger. The anterior end of the columella is missing, thus it cannot be determined if the specimen had additional folds. The growth line is preserved only on the ramp of the last quarter-turn of the last whorl, near the outer lip. In the medial part of that area, the growth line is arched adaperturally, but near the suture, the growth line is bent in the opposite direction.

The rapidly descending last whorl of *Turbinella*? sp. is like that of the extant *Turbinella angulata* (Lightfoot, 1786). *Turbinella*? sp. cannot be unequivocally assigned to *Turbinella* because the specimen is incomplete, especially in regard to its missing protoconch.

Turbinella? sp. differs from the Point Loma Formation *Misricymbiola*? sp. by having a much smaller size, at least two columellar folds, no subsutural welt, a growth line on the ramp that bends in the opposite direction, and a narrow, triangular aperture. In addition, the last whorl of *T.*? sp. rapidly descends.

AGE AND BIOGEOGRAPHIC IMPLICATIONS OF THE NEW MATERIAL

The earliest *Limopsis* was reported as Middle Jurassic (Bathonian) in age by Newell (1969) and Hallam (1977), but they did not cite which species this age is based on. Tevesz (1977:39) reported that the earliest *Limopsis* is the Middle Jurassic (Bathonian) *Limopsis minimus* (Sowerby, 1824:114, pl. 472, fig. 5) of England and southern Europe, but Oliver (1981:71)



Figures 32–34 *Turbinella*? sp., hypotype SDSNH 86561, SDSNH loc. 3456. 32. apertural view; 33. abapertural view; 34. dorsal view.

disputed this claim and asserted that the first truly recognizable *Limopsis* is the Early Cretaceous (Albian) *Limopsis albiensis* (Woods, 1899:71–72, pl. 15, figs. 1a–d, 2–4) from England. Marlière (1939) put *L. albiensis* in synonymy with *Limopsis coemansi* Briart and Cornet, 1868 from upper Albian strata of France. Casey (1961) refined the lower limit of the geologic range of *L. albiensis* to be latest Aptian. He reported *Limopsis dolomitica* Casey (1961:576, pl. 79, fig. 4) of middle late Aptian age from England but, unfortunately, the rare specimens do not show the hinge.

Oliver (1981) reported that the entire Cretaceous fossil record of *Limopsis* is scant. Based on an inspection of the literature, the present author found the same results. *Limopsis* sp. from northern California is apparently the only known Cenomanian record of this genus. *Limopsis silveradoensis*, which is apparently the only Turonian record of this genus, was the most widespread Cretaceous *Limopsis* in the northeast Pacific. The author found no Coniacian or Santonian reports of *Limopsis* anywhere. Gabb (1864) reported a so-called *Limopsis transversa* Gabb (1864:200, pl. 26, fig. 186) from Texas Flat, Placer County, northern California. Squires and Saul (2009) reported that this locality is the same as the "Granite Bay" or "Rock Corral" locality and that the strata there are early Campanian in age. This "Granite Bay" species, however, is not a *Limopsis* because its shape is rectangular and its resilifer is not centrally located.

Oliver (1981:71) reported that *Limopsis* underwent a radiation during the Maastrichtian, when species became more quadrate than earlier ones. *Limopsis demerei* shows this change in shape. It also is less oblique than earlier species, has a straighter dorsal margin, less projecting beak, more hinge teeth, and has commarginal ribbing. *Limopsis demerei* shows that this "Maastrichtian" radiation began as early as late Campanian.

Volutidae ranges from Cenomanian to Recent, with the earliest member being *Carota* Stephenson, 1952 from Texas (Stephenson, 1952; Taylor et al., 1980). Although the earliest record of caricellines is very poorly known, a tentative geologic range of this group is Maastrichtian (Bandel, 2003) to Eocene (Palmer and Brann, 1966). If future collecting does establish that the latest Campanian to possibly early Maastrichtian *Misricymbiola*? sp. from Southern California does belong to this genus, then it would be the earliest known caricelline and the first record of this genus outside of the tropical western Tethys Sea region in western Egypt (Bandel, 2003) and possibly Tunisia (Collignon, 1971). The record of *Misricymbiola*? in Southern California is slightly earlier than the Egyptian occurrence and approximately the same age as the presumed Tunisian occurrence of this genus. Known species of *Misricymbiola*, however, have large protoconchs that indicate direct development (Bandel, 2003), and this type of larval stage (i.e., no planktonic stage) would have made it difficult for genus to achieve widespread distribution during only the latest Campanian to possibly early Maastrichtian. Future collecting might show that it was present earlier elsewhere.

Taylor et al. (1980:text, fig. 7) reported that Turbinellidae [= Vasidae] originated during the middle Albian but did not provide any documentable evidence. The earliest known Turbinellidae is the vasine *Fimbrivasum robustum* Squires and Saul, 2001 of latest Santonian age from Vancouver Island, British Columbia, Canada. The earliest known columbariine is *Columbarium heberti* (Briart and Cornet, 1880) of Maastrichtian age from the Netherlands (Darragh, 1969:64). Prior to the detection of *Turbinella*? sp., the geologic record of turbinelline genera was reported to be Oligocene to Recent for *Turbinella* (Cossmann, 1901; Davies, 1935) and Pliocene to Recent for *Syrinx* (see Wenz, 1943). The latest Campanian to possibly earliest Maastrichtian *Turbinella*? sp. potentially represents the earliest known turbinelline. Weller (1907) and Richards and Ramsdell (1962) reported a few species of so-called *Turbinella* mainly from Maastrichtian and, to a lesser degree, from Campanian rocks in New Jersey, but these species are based on internal molds that are also mostly very incomplete. Much better specimens are needed to establish the presence of turbinellids in Cretaceous beds of New Jersey. *Turbinella*? sp. potentially helps establish that turbinellines, like vasines and columbariines, evolved during the Late Cretaceous.

Taylor et al. (1980) and Sohl (1987) hypothesized that the Neogastropoda originated in temperate seas. At least for Turbinellidae, the northeast Pacific record supports their hypothesis. Using the approximate latitudinal limits depicted for the northeast Pacific during the Late Cretaceous (Saul and

Squires, 2008:fig. 3), *Fimbrivasum robustum*, the earliest known vasine would have lived in somewhat northerly warm-temperate waters. *Turbinella*? sp., as well as *Misricymbiola*? sp., would have lived in more southerly waters nearer the boundary of warm-temperate and tropical waters. The molluscan species found at the type localities of both new species lived elsewhere on the northeast Pacific in warm-temperate environments. Additional evidence for warm-temperate seas is the presence of rudist bivalves found elsewhere in intertidal sandstones of the Point Loma Formation in the Carlsbad area. Although the rudists and the studied neogastropods did not inhabit a common ecotope, the rudists are indicators of at least marginal tropicality because of their wider reported low-latitude occurrence (e.g., Sohl, 1987).

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Polyplacophora (Mollusca) from the San Diego Formation: A Remarkable Assemblage of Fossil Chitons from the Pliocene of Southern California[1]

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and Christine Z. Fernandez[5]

ABSTRACT. A rich chiton assemblage consisting of more than 15,000 valves (shell plates) was collected by George P. Kanakoff (1897–1973) from Pliocene exposures of the San Diego Formation just north of the U.S./Mexican border. The assemblage includes 16 extant species, three extinct species (*Callistochiton sphaerae* n. sp., *Lepidozona kanakoffi* n. sp., and *Amicula solivaga* n. sp.), and three indeterminate species. The collection is dominated by the genus *Callistochiton* and also includes the genera *Leptochiton*, *Oldroydia*, *Lepidozona*, *Stenoplax*, *Amicula*, *Mopalia*, *Placiphorella*, *Tonicella*, *Dendrochiton*, and *Nuttallina*.

This assemblage expands the known stratigraphic and paleogeographic ranges of many chiton genera and species and provides information about an apparent late Cenozoic diversification of chitons along the Pacific Coast of North America. Chitons appear to have diversified in the northeastern Pacific from the middle Miocene to Pleistocene, driven in part by regional increases in productivity and environmental heterogeneity during that time.

The chitons are interpreted to have been deposited at inner-neritic depths (~25 m) in the mouth of a bay or in a continental shelf environment, and the annual temperature range and seasonality are inferred to have been similar to those that occur off the nearby San Diego coast today. However, the fossil assemblages also include a mixture of taxa that today range only to the north or to the south.

The large sample sizes of chiton valves allow rigorous analysis of the ratio of valve types, revealing a divergence from the expected pattern. This divergence is even greater on average than what occurs in assemblages of chiton valves in Holocene sediments, revealing that taphonomic factors bias valve ratios long after valves are disarticulated.

New foraminiferan and molluscan data indicate a middle or late Pliocene age of deposition for these beds, between 3.3 to 2.5 million years ago (Ma), and possibly about 3.0 Ma.

INTRODUCTION

George P. Kanakoff and assistants in the 1950s and 1960s collected more than 15,000 chiton valves from outcrops of the San Diego Formation near the international border between California and Mexico (Figure 1, Appendix 1). At the time, Kanakoff was the curator of invertebrate paleontology at the Natural History Museum of Los Angeles County Invertebrate Paleontology Department (LACMIP), a position he held from 1948 to 1966 (Marincovich, 1974). Kanakoff led groups of volunteers, many of whom were high school students, to collect and subsequently sort vast amounts of fossil material from the Border localities (E.C. Wilson and P.I. LaFollette, personal communication to M.J.V., 2006). Kanakoff instructed his students to "save everything" during field and laboratory work (Marincovich, 1974:64), and so these collections probably provide an accurate representation of the fossil assemblages at the localities collected and are not as highly skewed towards well-preserved or complete valves as is normal for chiton fossil collections. As a result of his thorough methodology and because of the incredible richness of this fauna, Kanakoff and colleagues managed to recover the largest and most diverse assemblage of fossil chitons known in the world.

Most of the fossil chitons from LACMIP historic locality 305 were originally examined by Spencer R. Thorpe, Jr., then at the California Academy of Sciences (E.C. Wilson, personal communication to M.J.V., 2006). Thorpe provided some identifications and advised Leo G. Hertlein on geographic ranges of modern chitons for the summary of the chiton fauna that was to appear in their intended paper on the gastropods and chitons of the San Diego Formation, although the description of the chiton fauna in their draft is only two pages long.

Few chitons have been described, or even listed, from fossil localities in California, and most of these are from Pleistocene deposits. Chitons have been described from Cenozoic sedimentary rocks in California by Pilsbry (1892), Chace (1916a, b), Chace and Chace (1919), Berry (1922, 1926), Kennedy (1978), Roth (1979), Squires and Goedert (1995), and Dell'Angelo et al. (2011). Chitons, as minor faunal elements, have also been mentioned by Orcutt (1889), Ashley (1895), Oldroyd (1914), Moody (1916), Clark (1918), Valentine (1961), Valentine and Meade (1961), Chace (1966), Marincovich (1976), Kennedy et al. (1981, 1992 [1993]), Davis (1998), Powell (1998), and Powell et al. (2002). Perhaps as testament to their typical rarity in California fossil assemblages, chitons were entirely omitted from the *Check list of California Tertiary Marine Mollusca* (Keen and Bentson, 1944), as well as from compilations by Grant and Gale (1931) and Weaver (1942 [1943]). The collection described herein therefore provides significant additional information on the diversification of late Cenozoic chitons along the Pacific Coast of North America. The rich San Diego Formation chiton fauna from the Pliocene stands in striking cotrast to the paucity of reported chitons from the older and warmer Miocene deposits

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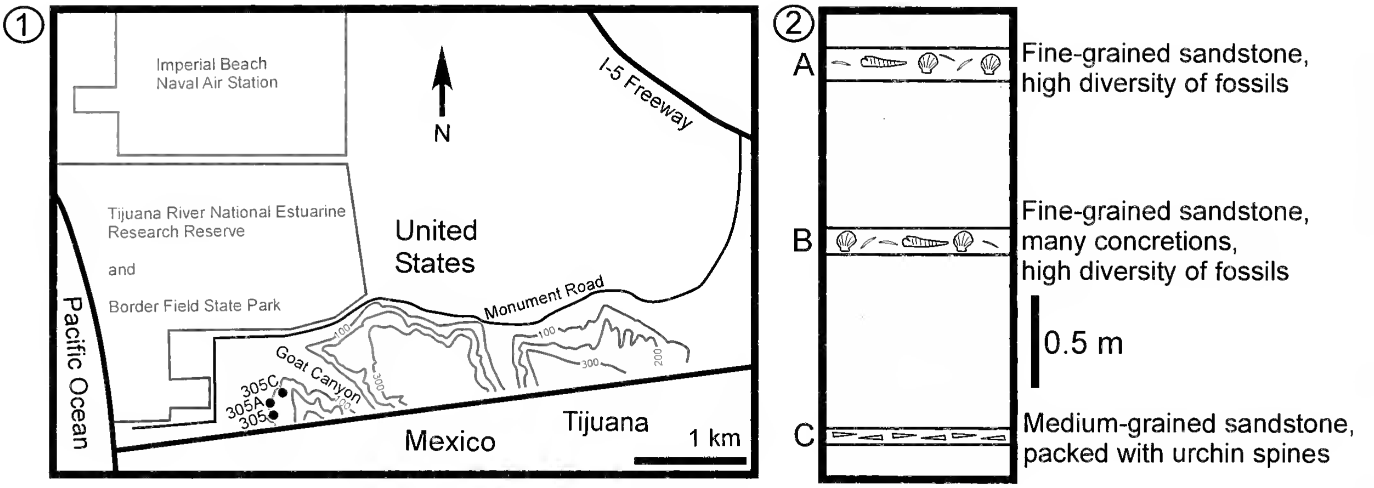

Figure 1 Locality and stratigraphy. 1, map showing location of the three main historic localities described here; 2, stratigraphy of the exposed portion of the San Diego Formation at the Border locality near or at LACMIP locality 305 (A=SDNHM locality 6241; B=SDNHM locality 6242; C=SDNHM locality 6243).

along the Pacific Coast of North America, even though the latter have extensive molluscan fossils and these are generally well studied. Dell'Angelo et al. (2011) have recently described multiple new chiton species, represented by 140 total valves, from even older Paleogene deposits from Washington State. These appear to have little in common with the Pliocene fauna described here, instead having affinities to more southern or Old World chiton faunas, but their discovery could indicate that Miocene chitons will eventually be found if they are searched for specifically.

Herein we describe the chiton fauna from the San Diego Formation and discuss the following: (1) how this assemblage provides evidence for a major, recent chiton diversification event on the Pacific Coast; (2) migration of chitons during the Cenozoic; (3) new evidence on the age of the localities of the San Diego Formation from which these fossils were collected; (4) aspects of the paleoenvironment of these fossils; and (5) the taphonomy of chiton valves. These analyses were based primarily on fossil specimens from LACMIP as well as modern specimens from the Natural History Museum of Los Angeles County, Malacology Department (LACM).

STRATIGRAPHY OF THE SAN DIEGO FORMATION

The San Diego Formation consists of up to 84 m of terrestrial and continental-shelf marine sediments exposed over a nearly 60-km-long arc extending from Pacific Beach, San Diego, to northern Baja California (Rowland, 1972; Deméré, 1982, 1983). The informal lower member is characterized by up to 75 m of massive, fine-grained, friable, marine sandstone with occasional thin conglomerate layers, and the informal upper member consists of up to 9 m of nonmarine, massive, fine-grained, friable sandstone with occasional thin conglomerate layers (Deméré, 1983). In addition, Wagner et al. (2001) described the presence of nonmarine beds below the lower member described by Deméré (1983) exposed in the eastern part of the San Diego depositional basin.

The fossils of the San Diego Formation were first listed by Dall (1874, 1898), who assigned the name "San Diego beds" to fossiliferous rocks extracted in the process of digging a well in Cabrillo Canyon near San Diego, California (now Balboa Park). Arnold (1903) later referred to the sediments as the "San Diego Formation" and described the fauna from a different stratigraphic section at Pacific Beach, San Diego. Hertlein and Grant (1944) argued that the old San Diego well in Balboa Park should be considered the type locality. However, the well has since been filled and the Pacific Beach section is the best remaining exposure of the San Diego Formation. Arnold (1903:57–58) recognized two biostratigraphic divisions of the San Diego Formation at the Pacific Beach section: a "lower horizon" characterized by the bivalves *Flabellipecten stearnsii* (Dall, 1874) [=*Euvola stearnsii*] and *Patinopecten healeyi* (Arnold, 1906), and the gastropod *Opalia anomala* Stearns, 1875 and its synonym *Opalia varicostata* Stearns, 1875; and an "upper horizon" characterized by the bivalve *Pecten bellus* (Conrad, 1856b) replacing *E. stearnsii*, rare *Patinopecten healeyi*, the gastropod *Crepidula princeps* Conrad, 1855, and the echinoid *Dendraster ashleyi* (Arnold in Arnold and Anderson, 1907). Deméré (1982) followed Arnold's (1903) lead in recognizing a lower biostratigraphic unit at Pacific Beach characterized by *Euvola* (as *Flabellipecten*) *stearnsii*, *Patinopecten healeyi*, and *O. varicostata*, and an upper unit with *Pecten bellus*, *D. ashleyi*, and the gastropod *Nucella lamellosa* (Gmelin, 1791).

The specimens described here are from localities of the San Diego Formation near the international border between the United States and Mexico. The following discussions of stratigraphic correlation, age, taphonomy, and paleoenvironment focus specifically on three primary localities from which Kanakoff collected chitons, LACMIP localities 305, 16817 (ex 305A), and 16862 (ex 305C) ("Border beds" or "Border localities" herein).

CORRELATION OF THE BORDER BEDS OF THE SAN DIEGO FORMATION

The LACMIP Border locality collections reveal abundant specimens of *Opalia varicostata*, *Euvola stearnsii*, and *Patinopecten healeyi*, characteristic of the lower unit of the San Diego Formation at the Pacific Beach section *sensu* Deméré (1982), but also abundant *Pecten bellus*, characteristic of Deméré's upper unit. Paleoenvironmental data also provide equivocal evidence for correlation. Ingle (1967, 1980) observed foraminifers from Pacific Beach and inferred a warm-water, outer-shelf assemblage

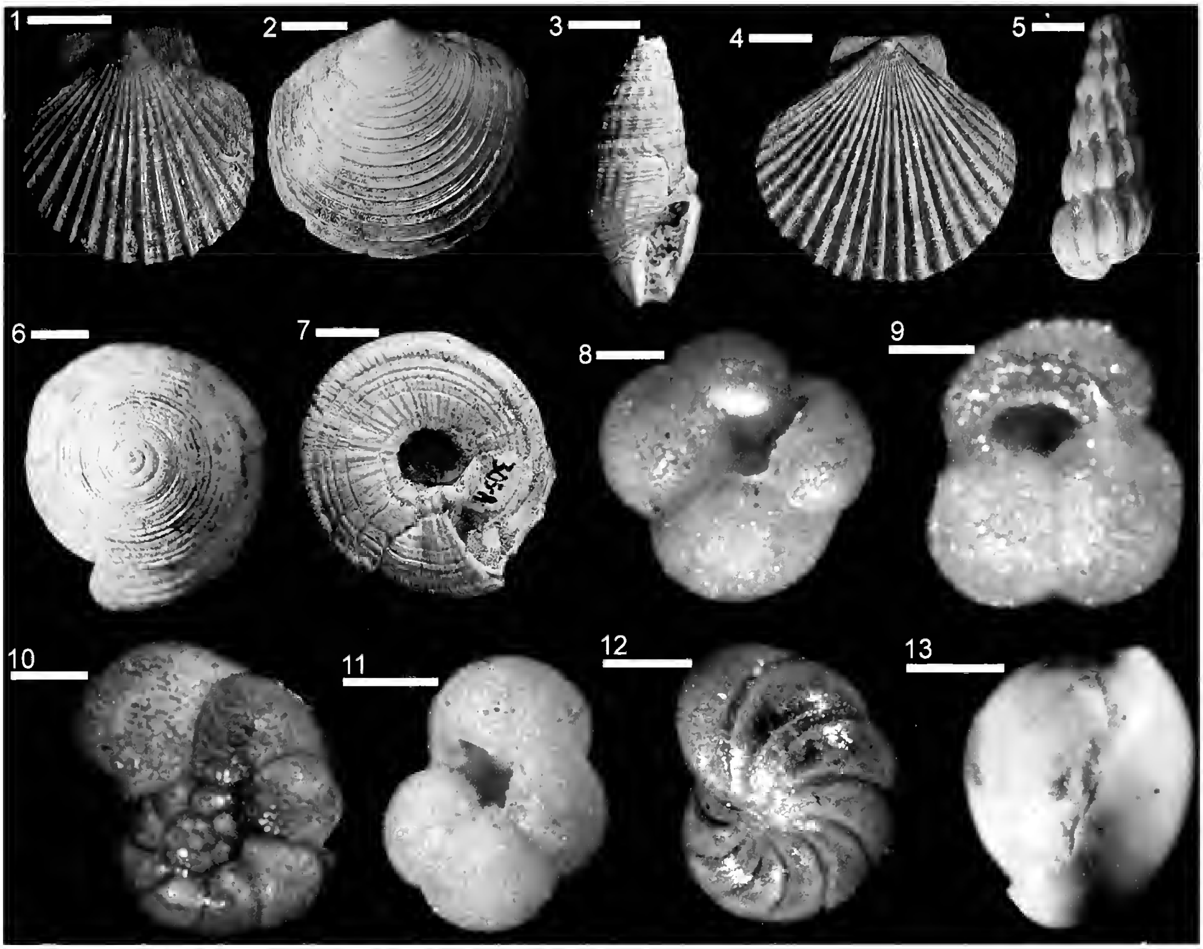

Figure 2 Fossils of biostratigraphic and paleoenvironmental significance from LACMIP locality 305. 1, *Patinopecten healeyi* (Arnold, 1906) (scale bar=1 cm); 2, *Lucinoma annulatum* (Reeve, 1850) (scale bar=1 cm); 3, *Strictispira* (*Crassispira*) *zizyphus* (Berry, 1940) (scale bar=0.5 cm); 4, *Euvola stearnsii* (Dall, 1874) (scale bar=1 cm); 5, *Opalia varicostata* Stearns, 1875 (scale bar=0.5 cm); 6–7, *Architectonica nobilis* Röding, 1798 (scale bar=1 cm); 8, *Neogloboquadrina asanoi* (Maiya, Saito, and Sato, 1976) (scale bar=250 μm); 9, *Globigerinoides ruber* (d'Orbigny, 1839) (scale bar=250 μm); 10, *Globorotalia tumida* (Brady, 1877) (scale bar=100 μm); 11, *Globigerina bulloides* (d'Orbigny, 1826) (scale bar=250 μm); 12, *Hanzawaia nitidula* (Bandy, 1953) (scale bar=250 μm); 13, *Quinqueloculina lamarckiana* d'Orbigny, 1839 (scale bar=250 μm).

in the lower part of the section and a cool-water, shallower assemblage in the upper part of his section. Wicander (1970) examined planktonic Foraminifera from Pacific Beach and other localities of the San Diego Formation, and inferred cooler water throughout the formation. Later, Mandel (1973) examined planktonic foraminifers from exposures near the border (including localities he listed as LACMIP 305A and C) and recognized a decidedly warm-water, outer-shelf assemblage. Deméré (1982) regarded Mandel's (1973) warm-water fauna to be correlative with the warm-water facies of the lower unit at Pacific Beach. Most of the fossils from the Border localities occur off of San Diego today, with a few extralimital southern and northern species (species whose ranges are entirely south or north of the fossil locality). Nearly all of the species in these assemblages today occur in the Californian biogeographic province (also "warm-temperate" *sensu* Valentine, 1966, or "San Diegan" *sensu* Briggs, 1974). The Border localities show a mixture of warm and cold, moderately deep-water fauna (see "Discussion"), which matches neither the warm, shallow-water characteristic of the lower part of the section at Pacific Beach, nor the cooler, deep-water characteristic of the upper part in the same section (Deméré, 1982, 1983). However, the fauna from the Border localities is overall more similar to that in the lower part of the Pacific Beach section, and so we conclude that the Border beds probably correlate with the lower part or with a hypothetical transitional zone between the lower and upper parts.

A detailed record of the stratigraphy of the fossiliferous section from which Kanakoff collected is unknown. Kanakoff listed the height (in feet) above the dirt road at each of his fossil localities (Appendix 1), which indicates each sample was collected from within a narrow stratigraphic range. LACMIP localities 305, 16862 (305A), and 16817 (305C) occur within 1 km of each other and all contain very similar faunas, indicating they came from the same, or closely spaced, stratigraphic horizons.

Most of the chitons studied are from LACMIP localities 305 and 16817 (305C). With assistance from Scott Rugh (San Diego Natural History Museum [SDNHM]), we (C.Z.F. and M.J.V.) were able to locate exposures near or at Kanakoff's original collecting localities. The locality we discovered near LACMIP locality 305 had the most easily accessible fossiliferous exposures, with three shell beds within a 2-m section (Figure 1, SDNHM localities 6241–6243) exposed along a road-cut. The

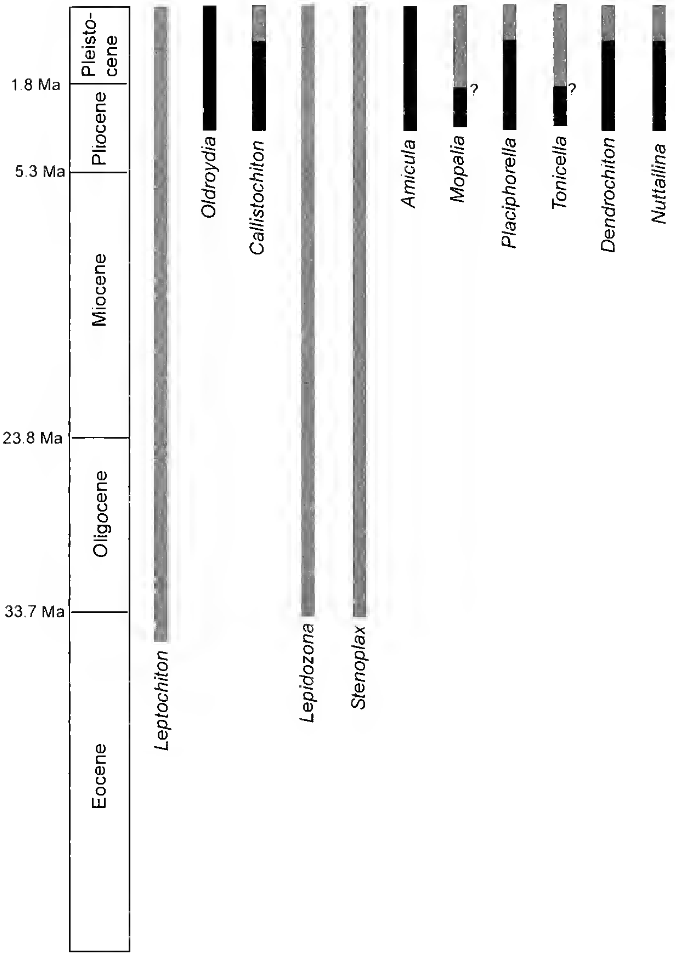

Figure 3 Known stratigraphic ranges of chitons on the Pacific Coast of North America. Gray bars show previously reported range; black bars show range extension based on specimens described herein. The first appearance datum of Eocene/Oligocene for *Lepidozona* is based on one valve, and that for *Stenoplax* is based on just a few valves (Dell'Angelo et al., 2011); otherwise the San Diego Formation assemblage provides the oldest records of these genera on the Pacific Coast of North America.

shell beds were separated by units of structureless fine-grained sand that lacked obvious fossils. The lowest fossil bed averaged about 5 cm in thickness and consisted of shell hash dominated by sea urchin spines in a medium-grained sand matrix. The middle bed averaged about 20 cm in thickness and contained a more diverse fossil assemblage dominated by mollusks. This shell bed had a matrix of fine-grained sand but with common massive concretions that in places encompassed the entire fossil bed. The uppermost shell bed averaged about 20 cm in thickness and contained abundant fossils dominated by mollusks in a fine-grained sand matrix. The upper two shell beds contain abundant fossils in diverse orientations, a good incidence of complete shells, and many examples of articulated bivalves.

AGE OF THE BORDER BEDS

The precise age range of the San Diego Formation at the Border localities remains unclear. Estimates of the age of the San Diego Formation have ranged, in general, between early Pliocene and earliest Pleistocene. Whereas some have considered it exclusively Pliocene (Hertlein and Grant, 1944, 1972; Corey, 1954; Milow and Ennis, 1961; Oakeshott, 1964; Ingle, 1967; Rowland, 1969; Wicander, 1970), others have argued that it extends into the earliest Pleistocene (Arnold, 1903; Allison, 1964; Deméré, 1983; Wagner et al., 2001). Deméré (1982, 1983) tentatively suggested that known planktonic foraminiferans from the formation indicated an age range from no older than from 3.0 million years ago (Ma) to at least as young as 1.5 Ma, although he did not state which species allowed such inferences. Barnes (1976:332–334) assigned fossil vertebrates, mainly marine mammals, from the formation to the Blancan North American Land Mammal Age (4.8–1.8 Ma). Recently, combined land mammal biostratigraphic and magnetostratigraphic dating has been applied to nonmarine facies within the lower part of the San Diego Formation in Chula Vista where an age of 3.6 to 3.5 Ma was assigned (Wagner et al., 2001). Planktonic foraminifera and calcareous nannoplankton from the San Diego Formation on the south side of Mount Soledad (LACMIP locality 17228) indicate a probable early Pliocene age of between 3.8 and 4.2 Ma (Boettcher, 2001; Kling, 2001) and correlated with Calcareous Nannoplankton Zone CN11b. The combined data currently available thus indicate an age range from as old as 4.2 Ma to possibly as young as 1.5 Ma for the San Diego Formation.

Schatzinger (1972) concluded that beds at localities he considered LACMIP 305 and 16862 (305A) were deposited during the Pliocene, citing the occurrence of many fossils inferred to have gone extinct during that epoch. Mandel (1973) used ranges of foraminifers to conclude that the sediments at what he considered to be LACMIP 16862 (305A) and 16817 (305C) were deposited during the latest Pliocene, but possibly ranging into the earliest Pleistocene. Extinct mollusks from the Border localities include the bivalves *Anadara trilineata* (Conrad, 1856b), *Arca sisquocensis* Reinhart, 1937, *Barbatia illota* (Sowerby, 1833), *Basterotia hertleini* Durham, 1950, *Chlamys hastata ellsi* Hertlein and Grant, 1972, *C. jordani* (Arnold, 1903), *Euvola stearnsii*, *Limaria orcutti* (Hertlein and Grant, 1972), *Lyropecten cerrosensis* (Gabb, 1866), *Myrakeena veatchii* (Gabb, 1866), *Patinopecten healeyi*, *Pecten bellus*, *Protothaca tenerrima alta* (Waterfall, 1929), *Rhamphidonta frankiana* (Hertlein and Grant, 1972), *Securella kanakoffi* (Hertlein and Grant, 1972), *Swiftopecten parmeleei* (Dall, 1898), *Thracia trapezoides* Conrad, 1849, and the gastropods *Calliostoma coalingense catoteron* Woodring and Bramlette, 1950, *Calyptraea filosa* Gabb, 1866, *C. inornata* (Gabb, 1866), *Cancellaria fergusoni* Carson, 1926, *Crepidula princeps*, *Nassarius* sp. cf. *N. grammatus* (Dall, 1917), *Opalia varicostata*, and *Tegula hemphilli* Oldroyd, 1921. *Rhamphidonta frankiana* and *Limaria orcutti* are restricted to the San Diego Formation and so are of little use in refining the age of this part of the San Diego Formation. In addition, detailed stratigraphic ranges of most mollusks are poorly known in California because of the lack of appropriate dating techniques and thus have not been correlated with a numerical time scale. Nevertheless, the molluscan assemblage indicates a middle to late Pliocene, and not Pleistocene, age for the Border localities. Observations in support of this claim include the occurrence in the Border beds of the following: (1) common *Patinopecten healeyi* and *Opalia varicostata* (Figures 2.1, 2.5), two index fossils for the Pliocene (Shimer and Shrock, 1944; Groves and Squires, 1988; Groves, 1991); (2) *Turcica brevis* Stewart in Woodring, Stewart, and Richards 1940 [1941], a fossil restricted to the Pliocene (Powell et al., 2004); (3) *Pecten bellus* and *Crassispira zizyphus*, which may indicate middle/late Pliocene to early Pleistocene age (Powell and Stevens, 2000); and (4) the terminal Pliocene fossils *Lyropecten cerrosensis* and *Terebra martini* English, 1914 (Groves, 1991). More recently, Powell

Table 1 Summary of taxonomy of chitons from the San Diego Formation.

- Class Polyplacophora Gray, 1821
  - Order Lepidopleurida Thiele, 1910
    - Suborder Lepidopleurina Thiele, 1910
      - Family Leptochitonidae Dall, 1889
        - *Leptochiton* Gray, 1847b
          - *Leptochiton rugatus* (Pilsbry, 1892)
          - *Leptochiton nexus* Carpenter, 1864
        - *Oldroydia* Dall, 1894a
          - *Oldroydia percrassa* (Dall, 1894a)
  - Order Chitonida Thiele, 1910
    - Suborder Chitonina Thiele, 1910
      - Family Ischnochitonidae Dall, 1889
        - *Callistochiton* Dall, 1879
          - *Callistochiton palmulatus* Dall, 1879
          - *Callistochiton sphaerae* n. sp.
        - *Lepidozona* Pilsbry, 1892
          - *Lepidozona mertensii* (von Middendorff, 1847)
          - *Lepidozona pectinulata* (Carpenter *in* Pilsbry, 1893)
          - *Lepidozona* sp. cf. *L. rothi* Ferreira, 1983
          - *Lepidozona* sp. cf. *L. radians* (Carpenter *in* Pilsbry, 1892)
          - ***Lepidozona kanakoffi*** **n. sp.**
        - *Stenoplax* Dall, 1879
          - *Stenoplax circumsenta* Berry, 1956
          - *Stenoplax fallax* (Carpenter *in* Pilsbry, 1892)
          - *Stenoplax* sp. cf. *S. heathiana* Berry, 1946
    - Suborder Acanthochitonina Bergenhayn, 1930
      - Family Mopaliidae Dall, 1889
        - *Amicula* Gray, 1847a
          - ***Amicula solivaga*** **n. sp.**
        - *Dendrochiton* Berry, 1911
          - *Dendrochiton* sp. indeterminate
        - *Mopalia* Gray, 1847a
          - *Mopalia sinuata* Carpenter, 1864
          - *Mopalia* sp. cf. *M. swanii* Carpenter, 1864
          - *Mopalia* sp. indeterminate
        - *Placiphorella* Dall, 1879
          - *Placiphorella velata* Dall, 1879
          - *Placiphorella* sp. cf. *P. mirabilis* Clark, 1994
        - *Tonicella* Carpenter, 1873
          - *Tonicella* sp. cf. *T. venusta* Clark, 1999
      - Family Lepidochitonidae Iredale, 1914
        - *Nuttallina* Dall, 1871
          - *Nuttallina* sp. indeterminate

et al. (2008a, b, 2009) used the presence of the extralimital southern gastropod *Architectonica* (Figures 2.6–2.7) and other warm-water mollusks to correlate several sites in Southern California, including the Border localities, with the mid-Pliocene warm event that occurred between about 3.3 and 3.0 Ma (Dowsett and Robinson, 2009). If *Architectonica* is a valid indicator of this warm event (but see "Discussion"), it would indicate a possible age of 3.3 to 3.0 Ma for these deposits.

The collections from LACMIP locality 16817 (305C) contain the planktonic foraminifer *Neogloboquadrina asanoi* (Maiya, Saito, and Sato, 1976; Figure 2.8), identified by J.P. Kennett (personal communication to M.J.V., 2007), and lack any foraminifers exclusively younger than middle Pliocene, indicating deposition during the California margin planktonic foraminiferal zone 6 of Kennett et al. (2000) and a likely age between 3.25 and 2.5 Ma (see fig. 2 in Kucera and Kennett, 2000). Kennett's age determination matches up well with that estimated by Powell et al. (2008a, b, 2009) for the San Diego Formation Border localities; the overlap of the two age ranges is 3.25 to 3.0 Ma.

SYSTEMATICS

This massive chiton assemblage consisting of more than 15,000 valves from about 22 species, including three new species, is the largest and most diverse fossil chiton assemblage known. The chitons comprise three suborders, four families, and 11 genera. The assemblage extends the known fossil record for nine chiton genera along the Pacific Coast (Figure 3). A summary of the taxonomy of these chitons is provided in Table 1.

The taxonomy of chitons in the temperate northeastern Pacific is far from settled, and key distinguishing characters among similar chiton species are often not preserved in fossils. For example, species of *Mopalia* are often characterized by the nature of girdle setae (Eernisse et al., 2007). This makes taxonomic assignments of fossil chiton valves difficult, and in some cases here we favor an open nomenclature, including indications of uncertainty such as "cf." or "indeterminate." Many valve fragments in this assemblage could not be reliably assigned to genus, and we have left them unnamed. Nevertheless, the exquisite preservation of the tegmental sculpture in thousands of valves and the abundance of each type of valve (head, intermediate, tail) in many species has allowed detailed taxonomic analyses in those cases. Measurements here were made on digital photographs using ImageJ software (Rasband 1997–2009). Chiton shell terminology is depicted in Figure 4; readers are referred to Schwabe (2010) for a more detailed description of chiton terminology.

Unfigured specimens of the three new species from their type localities should be considered to be paratypes. By necessity here instead we refer to them as part of "unfigured topotype lots." However, these specimens did inform us in our descriptions of the new species and we have no reason to doubt their classification as such.

Hertlein and Grant's original unpublished manuscript contained a list of 15 chiton species from LACMIP locality 305 that were identified by Spencer Thorpe. This list differs from ours in a number of ways, but the overall classification is similar. We could find no indication of which sets of specimens at LACMIP were examined and/or identified by either Thorpe or Hertlein, and so we have reidentified all of the specimens ourselves.

Institutional abbreviations used herein include the following: ANSP, Academy of Natural Sciences of Philadelphia; LACM, Natural History Museum of Los Angeles County, Malacology Department; LACMIP, Natural History Museum of Los Angeles County, Invertebrate Paleontology Department; PRM, Peter Redpath Museum, McGill University, Montreal, Canada; SBMNH, Santa Barbara Museum of Natural History, and USNM, United States National Museum of Natural History.

Class Polyplacophora Gray, 1821
Order Lepidopleurida Thiele, 1910
Genus *Leptochiton* Gray, 1847b

DISTRIBUTION. This genus occurs worldwide (see Kaas and Van Belle, 1985a). Five described species of *Leptochiton* are known from the eastern Pacific (Ferreira, 1979a), although this is likely an underestimate. For example, specimens collected from greater than 15-m depth in Southern California previously identified as the wide-ranging *Leptochiton rugatus* (Pilsbry, 1892) belong to a second, undescribed deeper-water species, based primarily on DNA evidence (D.J. Eernisse and R. Kelly, unpublished data; see also Stebbins and Eernisse, 2009).

Fossils classified as *Leptochiton* have been found worldwide, and may date back to the Mesozoic (Van Belle, 1981). However, Sirenko (2006) recorded a range of only Eocene to Recent for *Leptochiton*, and according to his list the Eocene occurrence is

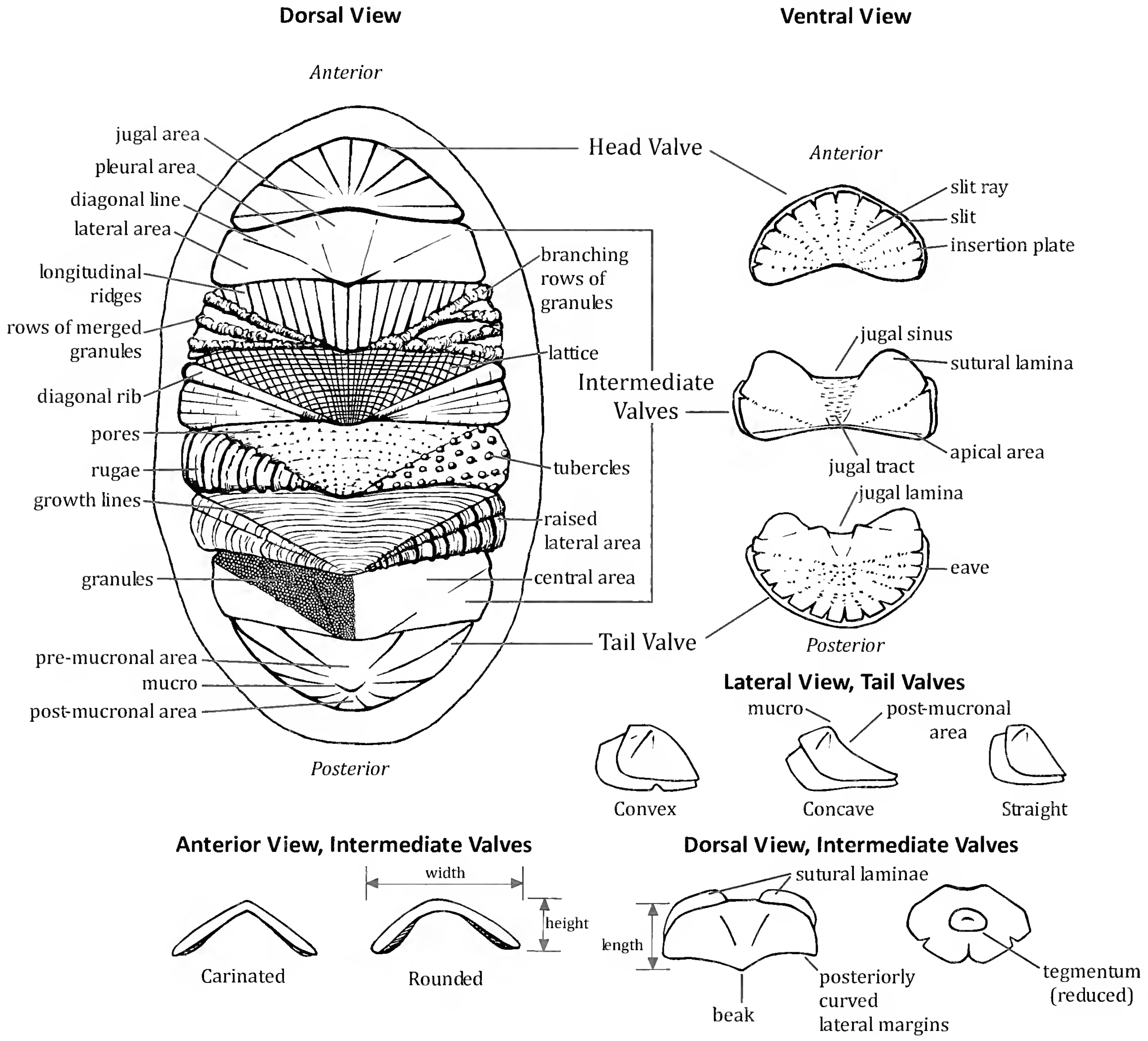

Figure 4 Terminology for chiton valves. Note there is some overlap and gradation in tegmental sculpture terminology. For example, "lattice" by definition contains "longitudinal ridges." Also, the small, closely spaced bumps labeled "granules" grade into the larger, more widely spaced bumps labeled "tubercles." See Schwabe (2010) for more details on chiton terminology.

the oldest record of an extant chiton species. Sigwart et al. (2007) subsequently described *Leptochiton faksensis* from the Paleocene of Denmark. In any case, there is a sparse fossil record of this genus in the temperate eastern Pacific, although the modern species *Leptochiton alveolus* (Lovén, 1846) is reported from the latest Eocene and earliest Oligocene of Washington (Squires and Goedert, 1995), one valve assigned to *Leptochiton* sp. was described from the latest Eocene or earliest Oligocene of Washington (Dell'Angelo et al., 2011), and one valve of *Leptochiton nexus* Carpenter, 1864, was reported from a Pleistocene marine terrace at Upper Newport Bay, California (Kanakoff and Emerson, 1959).

Leptochiton rugatus (Pilsbry, 1892) species complex
Figure 5 (1–17)

Leptochiton internexus rugatus: Dall, 1879:319 (*nomen nudum*).
Lepidopleurus rugatus Pilsbry, 1892:11, pl. 3, figs. 67–70.
Leptochiton rugatus Thiele, 1909:12–13, pl. 1, figs. 41–50; Ferreira 1979a:146, figs. 1–2, 7, 33–34 (contains more complete synonymies).
Lepidopleurus internexus Dall, 1879:319 (*nomen nudum*).
Leptochiton internexus: Smith 1947a:4; 1947b:17.
Leptochiton cancellatus: Dall, 1879:315 (not *Chiton cancellatus* Sowerby, 1839).

? *Lepidopleurus alascensis* Thiele, 1909:11, pl. 1, figs. 51–60; Taki and Taki, 1929:162.
? *Leptochiton alascensis*: Smith, 1947a:3.
Not *Lepidopleurus assimilis* Thiele, 1909: Kaas and Van Belle, 1994:15, 17 (contra synonymy by Ferreira 1979a).

DISTRIBUTION. LACMIP locality 305 (3 head valves, LACMIP 13730–13732, 3 intermediate valves, LACMIP 13733–13734, 13736, and 2 tail valves, LACMIP 13737–13738).

TYPE SPECIMENS. Three syntypes (ANSP 35586); two complete specimens and one with disarticulated valves (Ferreira, 1979a).

TYPE LOCALITY. Designated as Monterey, California, to Bahía Todos Santos, Baja California, Mexico, but label on syntypes indicates these specimens were collected near San Tomas River, Baja California (Ferreira, 1979a).

REMARKS. These fossil valves share with modern representatives of *Leptochiton rugatus* the same small size, low length:width ratio, rounded anterior profile (argued by Ferreira [1979a:147] to be "a constant diagnostic feature" of this species), tegmental sculpture of faint longitudinal rows of granules on head/tail valves and lateral areas of intermediate valves, and rounded lateral margins on intermediate valves. They also show slightly raised lateral areas and occasional "coarse concentric wrinkles" (Pilsbry, 1892:11) that characterize this species.

Some head and tail valves here assigned to this species are larger than what has been reported for this species by Ferreira (1979a), who stated the largest specimen he observed was 15.8 mm in length excluding girdle. For example, one head valve (Figures 5.5–5.6) is 2.5 mm long, corresponding to an animal that would have been about 20 mm in length. However, the similar tegmental sculpture of irregular "wrinkles" overlying faint longitudinal ridges and similar overall shape (including rounded anterior profile in all valves and shape of sutural laminae in the tail valve) indicates that these specimens are best classified in this species.

These recovered tail valves are more elongate and have more prominent rugae than in the similar *Leptochiton nexus*. One tail valve (Figures 5.16–5.17) has only faint rugae, and is slightly wider than those of most modern *L. rugatus* specimens, but it is within the typical size range for this species. The valve is similar enough to the figured tail valve in the original description (Pilsbry, 1892:pl. 3, fig. 70) that we identify it as this species. The specimens differ from *L. nexus* in having a more rounded anterior profile of intermediate valves (Figure 5.10). These fossils differ from *L. alveolus* (Lovén, 1846) in having a lower aspect ratio (greater width) of intermediate valves and in lacking the prominent granules of *L. alveolus*; they differ from *L. albemarlensis* Smith and Ferreira, 1977, in lacking the prominent quincunx arrangement of tegmental granules; and from *L. incongruous* (Dall, 1908) in lacking its prominent longitudinal ridges on the valve surface.

Leptochiton rugatus has been considered by some to be widespread throughout the North Pacific (Ferreira, 1979a; Kaas and Van Belle, 1985a), whereas others have considered the northwestern Pacific specimens to belong to *L. assimilis* (Saito, 1994, 2000; Sirenko and Agapova, 1997). Specimens from the Aleutians are considered distinct from either *L. rugatus* or *L. assimilis* (R.N. Clark, personal communication to D.J.E., 2009). Both mitochondrial and nuclear DNA sequences (D.J. Eernisse and R. Kelly, unpublished data) have indicated all of these are distinct species and have revealed several more undescribed species. One of these is so far only known from greater depths than *L. rugatus* in Southern California. Although Ferreira (1979a) reports *L. rugatus* to occur at depths ranging from the intertidal zone to 458 m, this might correspond to a summary for the entire species complex. In central California, most individuals of *L. rugatus* occur most commonly at about 8-to-12-m depths, but can also be found in the intertidal zone, and some occur within kelp holdfasts (Eernisse et al., 2007). Because the syntypes (ANS 35586) of *L. rugatus* were collected from the intertidal zone of northern Baja California, it is likely that the specimens often found in the intertidal zone between Baja California and central California are also *L. rugatus*, whereas the putative deeper-water species must be a different species.

This is the first fossil report of *L. rugatus* or a member of the *L. "rugatus"* species complex. If evidence indicates that the members of this species complex lack diagnostic valve differences, then it might never be possible to distinguish between such apparently cryptic species.

Leptochiton nexus Carpenter, 1864
Figure 5 (18–34)

Leptochiton nexus Carpenter, 1864:612, 650; Ferreira, 1979a:149, figs. 3–6, 8, 35–36 (contains more complete synonymies).
Lepidopleurus nexus: Pilsbry, 1892:11.
Chiton (Leptochiton) nexus: Dall *in* Orcutt, 1885:544.
Lepidopleurus (*Xiphiozona*) *heathi* Berry, 1919a:5.
Lepidopleurus heathi: Dall, 1921:187.
Leptochiton (Xiphiozona) heathi: Berry, 1919b:6–8, pl. 1, figs 1–2, pl. 2.
Leptochiton heathi: Smith, 1947a:4.
Lepidopleurus ambustus Berry, 1907:47 (*nomen nudum*).
Lepidopleurus (Leptochiton) ambustus: Dall, 1919:499.
Lepidopleurus ambustus: Dall, 1921: 187.
Lepidopleurus (Pilsbryella) ambustus: Leloup, 1940:4, figs. 1–7.
Lepidopleurus (*Leptochiton*) *lycurgus* Dall, 1919:500.
Lepidopleurus lycurgus: Dall, 1921:187.
Leptochiton lycurgus: Smith, 1947a:4.

DISTRIBUTION. LACMIP localities 305 (3 head, 29 intermediate, and 64 tail valves; 4 figured intermediate valves, LACMIP 13739–13742, and 4 figured tail valves, LACMIP 13743–13746; all remaining valves in unfigured lot LACMIP 14294), 16817 (305C; 1 tail valve, LACMIP 14295) and 16862 (305A; 1 tail valve, LACMIP 14296).

TYPE SPECIMEN. Holotype, USNM 16270.

TYPE LOCALITY. Santa Catalina Island, California.

REMARKS. The specimens from the San Diego Formation are very similar to modern representatives of *Leptochiton nexus* in terms of valve sculpture and shape in anterior profile. In particular, the valves are characterized by a uniform ornamentation of fine granules, with poorly defined lateral areas, and with a gothic arch in anterior view (Pilsbry, 1892) compared with a rounded arch in the similar *L. rugatus*. Some modern specimens assigned to this species and some fossils in this sample have faint rugae in the lateral areas that are reminiscent of those on *L. rugatus*, but the sculpture on the latter is much more prominent.

These specimens differ from *Leptochiton asellus* (Gmelin, 1791) in having less distinct granules on the tegmental surface and in being much smaller (maximum length 18 mm; Kaas and Van Belle, 1985a). These fossils differ from *L. rugatus* in having a subcarinated anterior profile of intermediate valves (Figure 5.20). They also differ from *L. alveolus* (Lovén, 1846) and *L. albemarlensis* Smith and Ferreira, 1977 in lacking the prominent granules of these species; and from *L. incongruous* (Dall, 1908) in lacking its prominent longitudinal ridges on the valve surface.

Some valves in the fossil sample are from individuals much larger than modern specimens of *L. nexus*. These valves are

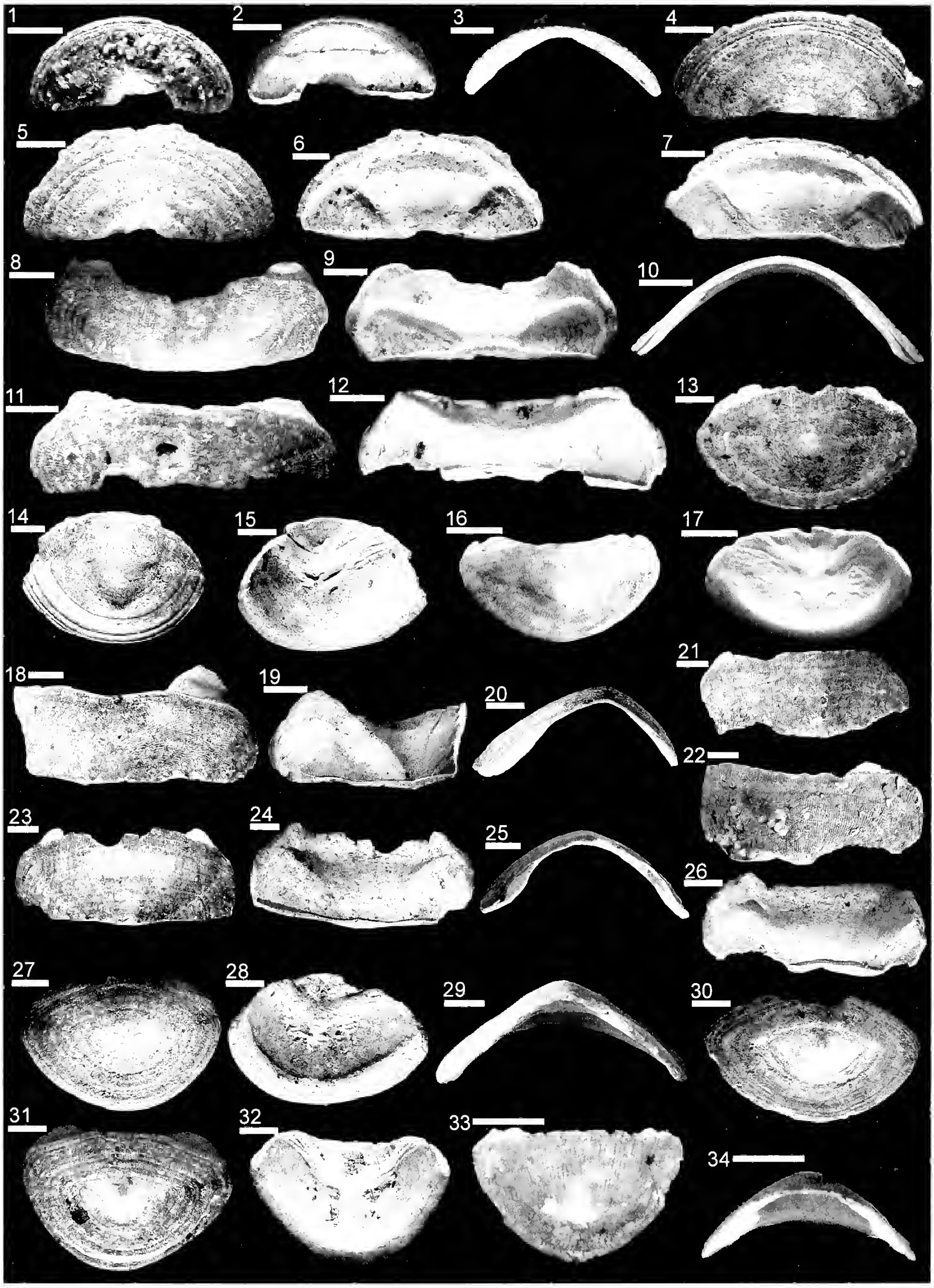

Figure 5 *Leptochiton* spp. 1–34, from LACMIP locality 305. **1–17**, *Leptochiton rugatus* Pilsbry, 1892: head (1–7), intermediate (8–13), and tail (14–17) valves. 1–3, LACMIP 13730; 4, 7, LACMIP 13731; 5–6, LACMIP 13732; 8–10, LACMIP 13733; 11–12, LACMIP 13734; 13, LACMIP 13736; 14–15, LACMIP 13737; 16–17, LACMIP 13738; **18–34**, *Leptochiton nexus* Carpenter, 1864: intermediate (18–26) and tail (27–34) valves. 18–20, LACMIP

~5 mm long, indicating an animal length of ~45 mm long (based on measurements of modern specimens); in comparison, Ferreira (1979a) claimed *L. nexus* usually ranges up to 20 mm in length, with one specimen he observed to be 25 mm in length. However, there is not a good reason to exclude the smaller valves in the fossil sample from *L. nexus*, and the larger valves may indicate variation in that population unknown in modern populations.

Modern members of *L. nexus* range from the intertidal zone to 139–141-m depths, with a median depth of 50 m (Ferreira, 1979a). They typically live on the sides and tops of rocks well covered or surrounded by sand (Eernisse et al., 2007). Seven specimens were reported from six stations at depths of 18 to 82 m sampled as part of local benthic monitoring programs off of Palos Verdes, Santa Monica Bay, and the northern Channel Islands (Stebbins and Eernisse, 2009). These fossils extend the range of this species to the Pliocene.

Genus *Oldroydia* Dall, 1894a

REMARKS. *Oldroydia* is a monotypic genus with a distinct valve morphology. However, its single species *Oldroydia percrassa* (Dall, 1894a) is closely aligned with members of the genus *Deshayesiella* Dall, 1879, including the recently revived *Deshayesiella spicata* (Berry, 1919b), which was argued by Sirenko and Clark (2008) to differ mainly in having a less distinct jugal area and longer pleural areas than *O. percrassa.* The San Diego Formation fossil valves differ from those of other lepidopleurids in having the *Oldroydia* characteristics of a thick tegmentum, prominent jugal ridge that extends anterior to the other regions of tegmentum, coarse tegmental sculpture, and subtriangular sutural laminae.

Oldroydia percrassa (Dall, 1894a)
Figure 6

Lepidopleurus percrassus: Dall, 1894a:90 (original description).

Lepidopleurus (Oldroydia) percrassus: Berry, 1907:47.

Oldroydia percrassa: Thiele, 1910: 71, 105, pl. 7, figs. 1–8; Ferreira, 1979a:160, fig. 20 (contains more complete synonymies).

Not *Deshayesiella spicata* (Berry, 1919b): Sirenko and Clark, 2008:2 (contra synonymy by Ferreira 1979a).

DISTRIBUTION. LACMIP localities 305 (26 head, 132 intermediate, and 52 tail valves; 3 figured head valves, LACMIP 13747–13749, 2 figured intermediate valves, LACMIP 13750–13751, 2 figured tail valves, 13735, 13755; all remaining valves in unfigured lot LACMIP 14297), 16817 (305C; 2 head, 9 intermediate, and 5 tail valves; 2 figured intermediate valves, LACMIP 13752–13753, and 1 figured tail valve, LACMIP 13754; all other valves in unfigured lot LACMIP 14298), and 16868 (305A; 1 head and 1 tail valve, in unfigured lot LACMIP 14299).

TYPE SPECIMENS. Holotype and two paratypes (USNM 107274).

TYPE LOCALITY. 137-m depth, near Catalina Island, California (33°45′N, 118°11′W).

REMARKS. Valves of *O. percrassa* are thick and with prominent callus underneath (Dall, 1894a); intermediate and tail valves with a raised, relatively smooth jugal area that extends farther anteriorly than the rest of the tegmentum; latero-pleural areas coarsely sculptured with rows of irregular granules that are often merged into wavy ridges; and prominent sutural laminae. The Border locality fossils show all these features and otherwise do not differ from valves of modern representatives of this species.

Oldroydia percrassa ranges from Monterey Bay, California, to the Sea of Cortez, Mexico, and is found at depths from the intertidal zone to 730 m, with a median depth of 40 m (Ferreira, 1979a). This species typically occurs under rocks (Eernisse et al., 2007). This species is one of the more common chiton species recovered from rock dredges off San Pedro, California (D.J.E., personal observation), but it was not found in any of the benthic (>30-m water depth) samples from the Southern California Bight surveys (Stebbins and Eernisse, 2009) or in benthic (50–250 m) samples from the Santa Maria Basin and western Santa Barbara Channel (Eernisse, 1998).

This is the first published record of an *O. percrassa* fossil, although Itoigawa et al. (1976) reported "*Oldroydia*? sp." from the Pleistocene of Japan. Subsequently, Sirenko and Clark (2008) demonstrated that *Deshayesiella* currently occurs in place of the similar form *Oldroydia* in the northwestern Pacific, and thus the specimen Itoigawa et al. (1976) noted may belong to *Deshayesiella* instead.

Order Chitonida Thiele, 1910
Suborder Chitonina Thiele, 1910
Family Ischnochitonidae Dall, 1889
Genus *Callistochiton* Dall, 1879

DISTRIBUTION. This genus is widespread, occurring in cool to warm waters worldwide (Kaas and Van Belle, 1994).

Several specimens, primarily of *Callistochiton palmulatus* Dall, 1879, and to a lesser extent *C. decoratus* Pilsbry, 1893, *C. crassicostatus* Pilsbry, 1893, and others, are known from Pleistocene marine terrace deposits on the Southern California coast (e.g., Chace, 1916a, 1966; Chace and Chace, 1919; Berry, 1926; Kanakoff and Emerson, 1959; Valentine, 1961; Valentine and Meade, 1961; Marincovich, 1976). Davis (1998) reported it as rare (<10 specimens) in the Upper Pliocene Pico Formation of downtown Los Angeles, California. Globally, *Callistochiton* has been reported from as early as the Miocene in Japan (Itoigawa et al., 1981) and Tanzania, East Africa (Davis, 1954).

REMARKS. Coan (1985; followed by Turgeon et al., 1998) suggested recognition of Josiah Keep's (1887) little-known descriptions of several *Callistochiton* species that occur in California. Keep based his descriptions on the unpublished manuscript by P. Carpenter that was also used extensively by W. Dall, H. Pilsbry, and other contemporary conchologists after Carpenter's untimely death. Stebbins and Eernisse (2009) clarified that following Coan's suggestion would both affect the authority for *C. decoratus*, potentially giving priority to Keep (1887) instead of Pilsbry, 1893 (from Carpenter manuscript), and could potentially make *C. crassicostatus* Pilsbry, 1893 a junior synonym of *C. fimbriatus* Keep, 1887. A third Carpenter manuscript name had already been validated earlier, as *Callistochiton palmulatus* Dall, 1879 (from Carpenter manuscript), so Keep's 1887 description of it would not have priority. Despite the possible priority that Keep's descriptions of *C. decoratus* and *C. fimbriatus* might have over the more commonly recognized

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13739. 21; LACMIP 13740; 22, 26, LACMIP 13741; 23–25, LACMIP 13742; 27–29, LACMIP 13743; 30, LACMIP 13744; 31–32, LACMIP 13745; 33–34, LACMIP 13746. Scale bars = 1 mm.

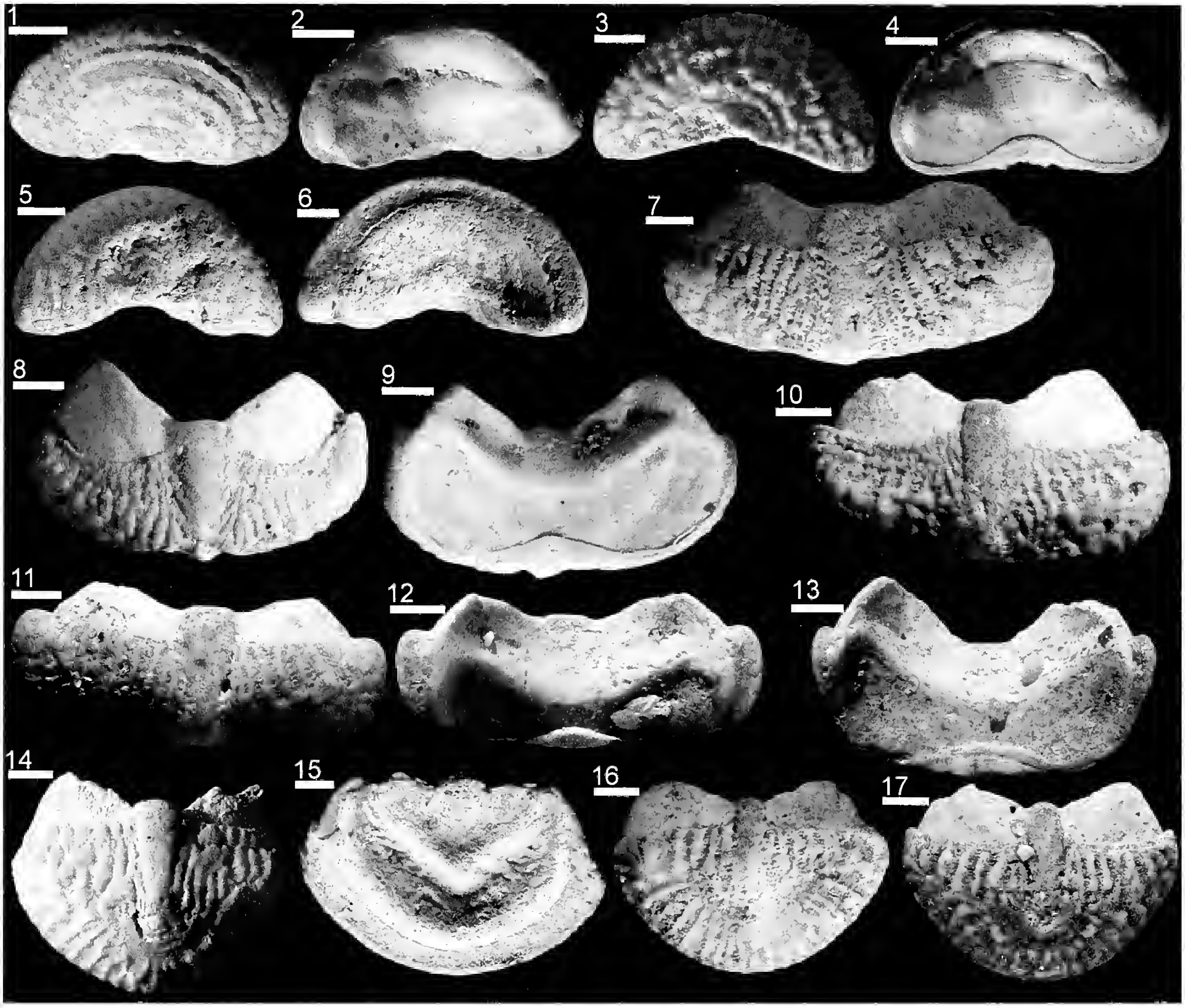


Figure 6 *Oldroydia percrassa* (Dall, 1894a): head (1–6), intermediate (7–13), and tail (14–17) valves. 1–9, 16–17, from LACMIP locality 305; 10–15, from LACMIP locality 16817 (305C). 1–2, LACMIP 13747; 3–4, LACMIP 13748; 5–6, LACMIP 13749; 7, LACMIP 13750; 8–9, LACMIP 13751; 10, 13, LACMIP 13752; 11–12, LACMIP 13753; 14–15, LACMIP 13754; 16, LACMIP 13755; 17, LACMIP 13735. Scale bars=1 mm.

names or authorities, Stebbins and Eernisse (2009) concluded that Keep's 1887 names remain *nomina dubia* because the corresponding type material for these two species could not be located and because Keep's descriptions, by themselves, are entirely inadequate to distinguish any of the three co-occurring species. It is still possible that someone could select neotypes for Keep's *C. decoratus* and *C. fimbriatus* but, until then, we agree with Stebbins and Eernisse (2009) that the conventional names and authorities are best used.

Callistochiton palmulatus Dall, 1879
Figure 7

Callistochiton palmulatus Dall, 1879:297, pl. 2, fig. 20; Ferreira, 1979b:445, fig. 1 (contains more complete synonymies); Kaas and Van Belle, 1994:168 (contains more complete synonymies).

Callistochiton palmulatus mirabilis Pilsbry, 1893:263, pl. 58, figs. 7–11.

Callistochiton acinatus Dall, 1919:510.

Callistochiton celetus Dall, 1919:510.

Callistochiton connellyi Willett, 1937:25, pl. 2, fig. 13.

DISTRIBUTION. LACMIP localities 305 (about 2,500 head valves, 196 intermediate valves, and about 6,100 tail valves; 1 figured head valve, LACMIP 13757 and 3 figured tail valves, 13764–13766; all other specimens in unfigured lot LACMIP 14300), 16817 (305C; 125 head, 15 intermediate, and 449 tail valves; 3 figured head valves, LACMIP 13756, 13758–13759, 3 figured intermediate valves, 13760–13762, and 1 figured tail valve, 13763; all other specimens in unfigured lot LACMIP 14301), and 305A (23 head, 31 intermediate, and 65 tail valves, all in unfigured lot LACMIP 14302).

TYPE SPECIMENS. The holotype is apparently lost, and the original description covers only the radula (Ferreira, 1979b). Ferreira (1979b) designated a neotype, PRM 48. Syntypes of the subspecies *Callistochiton palmulatus mirabilis* Pilsbry, 1893 (ANSP 118682) are from San Diego, California.

TYPE LOCALITY. Santa Barbara, California.

MATERIAL EXAMINED. Topotypes of *Callistochiton palmulatus* from modern collections at the SBMNH.

REMARKS. The San Diego Formation fossils share with modern representatives of this species strong sculpture of the following: prominent rows of large granules in the head valve,

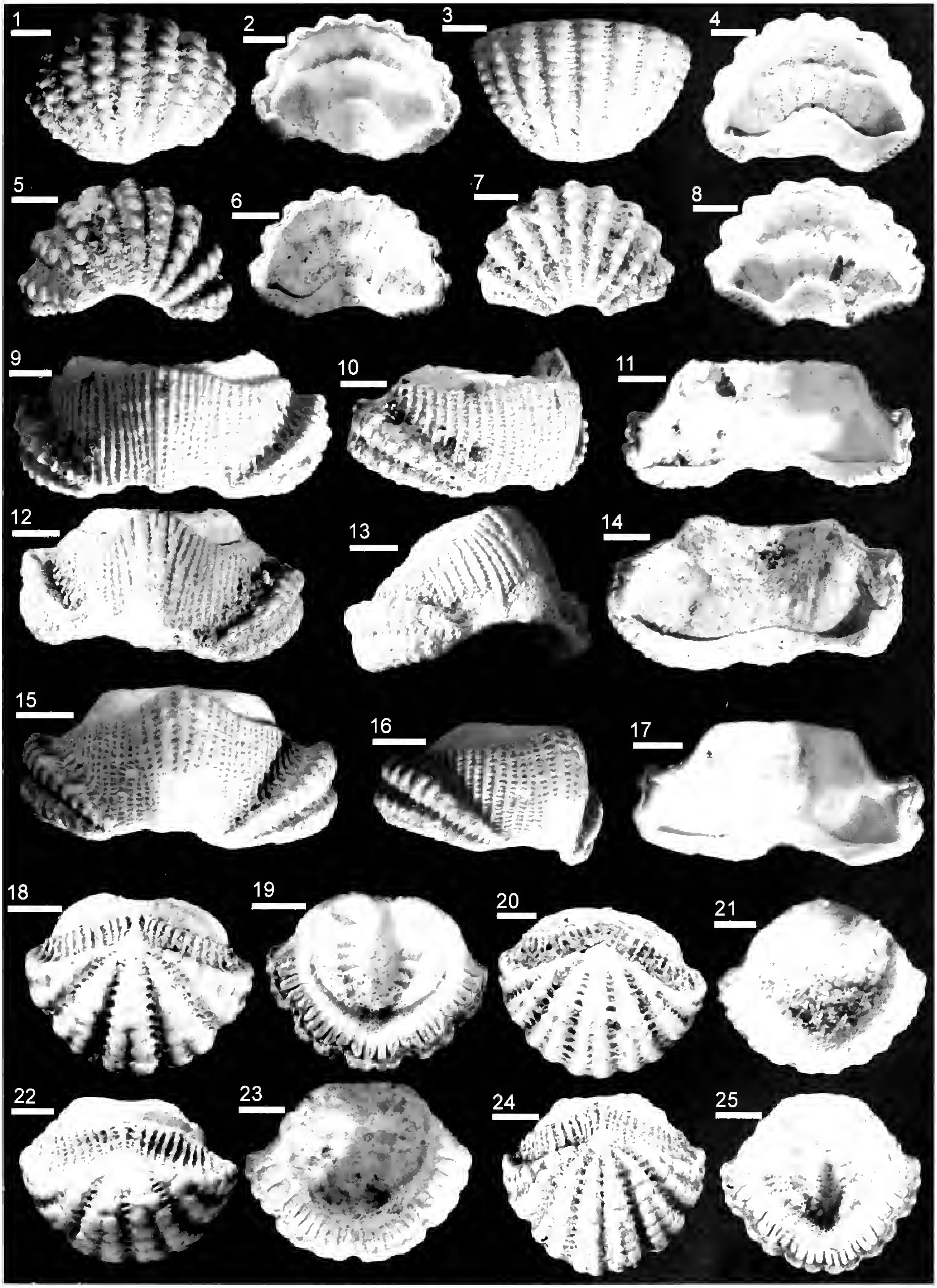
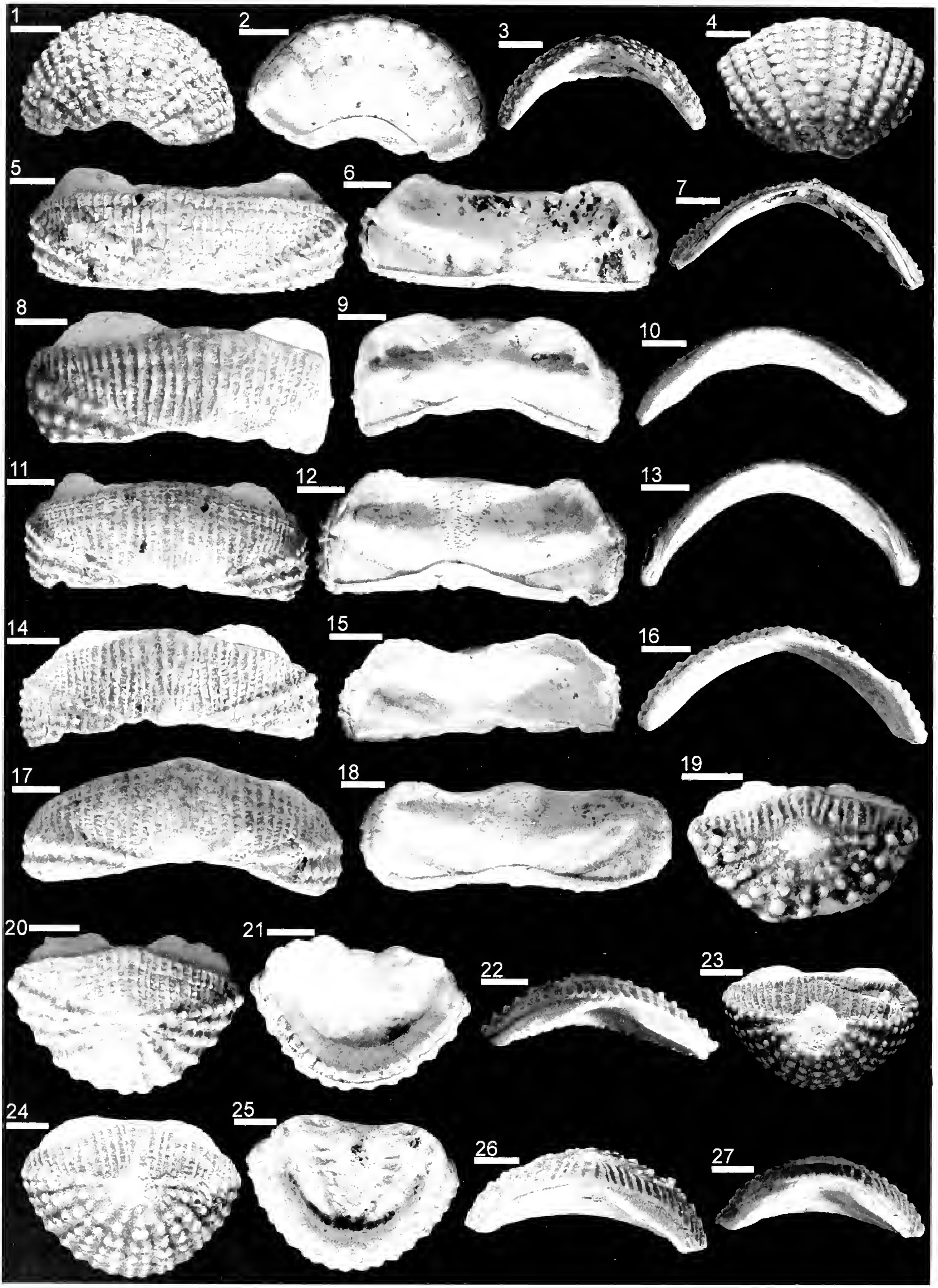


Figure 7 *Callistochiton palmulatus* Dall, 1879: head (1–8), intermediate (9–17), and tail (18–25) valves. 3–4, 20–25, from LACMIP locality 305; 1–2, 5–19, from LACMIP locality 16817 (305C). 1–2, LACMIP 13756; 3–4, LACMIP 13757; 5–6, LACMIP 13758; 7–8, LACMIP 13759; 9–11, LACMIP 13760; 12–14, LACMIP 13761; 15–17, LACMIP 13762; 18–19, LACMIP 13763; 20–21, LACMIP 13764; 22–23, LACMIP 13765; 24–25, LACMIP 13766. Scale bars=1 mm.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lateral areas of intermediate valves, and postmucronal area of tail valves; and longitudinal ridges with weak cross-hatching in the central area of intermediate valves and premucronal area of tail valves. Moreover, the lateral areas of intermediate valves and postmucronal area of the tail valve are significantly raised (this is one of the main diagnostic characters of the San Diego subspecies *C. palmulatus mirabilis* Pilsbry, 1893). However, Leloup (1953) and Ferreira (1979b) pointed out the morphological and ecological gradation between *C. p. mirabilis* and *C. palmulatus sensu stricto*, so we refrain from using the subspecific name *mirabilis*. An extensive study of the allometry of this species (D.J. Eernisse and A. Draeger, unpublished) supports this taxonomic opinion.

The raised, heavily sculptured lateral areas of these fossil intermediate valves are seen in both *Callistochiton palmulatus* and *C. crassicostatus*. However, the San Diego Formation fossils differ from *C. crassicostatus* in having more longitudinal riblets in the central area of intermediate valves (~15 vs. 12) and more ribs on tail valves, and a tail valve with a much shorter premucronal area. Although there appears to be much variation in valve morphology in *C. decoratus*, these fossils differ from *C. decoratus* in having lateral areas raised higher and more prominent longitudinal ridges (vs. more of a lattice in *C. decoratus*) and more distinctly by a much taller, more spherical tail valve. These fossils differ from *C. asthenes* (Berry, 1919b) in having more distinct, less smooth tegmental sculpture, and by having a taller, subspherical tail valve; they differ from *C. leei* Ferreira, 1979b, in having much more arched valves; from *C. colimensis* (Smith, 1961) in having more arching of valves, especially the tail valve; and from *C. elenensis* (Sowerby, 1832) in having more highly arched, thicker valves, and in lacking a jugal articulamentum plate.

Callistochiton palmulatus is continuously distributed between Mendocino County, California, and Punta San Pablo (27°12′N), Baja California, Mexico, and ranges from the intertidal zone to 73–82 m (Ferreira, 1979b). This species is particularly common in the shallow subtidal zone under rocks or in mussel borings in rocks on a sandy or silty substrate (Eernisse et al., 2007). It is also the most common chiton collected from rock dredges off San Pedro at depths up to 85 m, and it is often found inside empty mudstone burrows vacated by boring bivalves (Stebbins and Eernisse, 2009).

Callistochiton sphaerae n. sp.

Figure 8

DISTRIBUTION. LACMIP localities 305 (35 head, 92 intermediate, and 86 tail valves; 2 figured head valves, LACMIP 13767–13768, 5 figured intermediate valves, LACMIP 13769–13773, and 3 figured tail valves, LACMIP 13774–13776; all other specimens in the topotype lot, LACMIP 14303), 16817 (305C; 3 head, 9 intermediate and 11 tail valves; 1 figured tail valve, LACMIP 13854; all other specimens in unfigured lot, LACMIP 14304), and 16862 (305A; 2 head and 6 tail valves, all in unfigured lot, LACMIP 14305).

TYPE SPECIMENS. Holotype (LACMIP 13769; Figures 8.5–8.7) and 8 figured paratypes (LACMIP 13767–13768, and 13770–13776; Figures 8.1–8.4, 8.8–8.27); 33 head, 87 intermediate, and 83 tail valves in topotype lot, LACMIP 14303.

TYPE LOCALITY. LACMIP locality 305.

DIAGNOSIS. Valves of moderate size, between 0.5 and 1 cm in width; tegmental sculpture a lattice dominated by longitudinal ridges in central area of intermediate valves, and branching rows of large, distinct granules in the somewhat raised lateral areas.

DESCRIPTION. Head valves half-moon–shaped in dorsal profile; 12 slits; about 22 branching rows of large, distinct granules; apical area prominent; slit rays distinct; anterior profile rounded (not carinate). Intermediate valves with relatively low aspect ratio; lateral areas with branching rows of distinct granules; central areas with lattice dominated by longitudinal ridges; about 30–35 longitudinal ridges in one intermediate valve; sutural laminae long and broad, but with a distinct jugal sinus; apical area prominent; pores in jugal sinus distinct; muscle scars tend to be prominent; anterior region of ventral surface of intermediate valves thin; valve rounded in anterior profile. Tail valves low; 13–14 slits; mucro near midpoint but slightly closer to anterior margin; sutural laminae rounded and broad, but with distinct jugal sinus; ventral surface shows thickening at the posterior margin, thin anterior to that; muscle scars tend to be prominent; anterior view broadly rounded.

ETYMOLOGY. From Latin *sphaerae* meaning spheres or balls, so named because this species differs from California species of *Callistochiton* in having rows of more distinct, less merged, subspherical granules on the lateral areas of the valves.

REMARKS. This species is known from more than 130 specimens, but it is not as common as *C. palmulatus*, which is known from thousands of specimens in this assemblage. *Callistochiton sphaerae* n. sp. is distinct from all other California species of *Callistochiton* in having much more distinct granules in the rows of the lateral areas. Moreover, it differs from most eastern Pacific forms in having low elevation of the tail valve even when large. *Callistochiton sphaerae* n. sp. differs from *C. crassicostatus* and *C. palmulatus* in having much less raised lateral areas. Although *C. decoratus* and *C. elenensis*, species otherwise similar to *C. sphaerae*, can have a similar low elevation of the tail valve at small sizes, *C. sphaerae* differs from those species in having more isolated and smaller granules and a significantly shorter premucronal area in the tail valve. *Callistochiton sphaerae* n. sp. also differs from *C. elenensis* in lacking a distinct jugal plate, and in having more distinct granules. *Callistochiton expressus* and *C. gabbi* are considered junior synonyms of *C. elenensis*. *Callistochiton sphaerae* differs from *C. asthenes* in being much larger and having stronger tegmental sculpture; from *C. leei* Ferreira, 1979b, in having a more strongly sculptured tegmental surface; from *C. colimensis* in having more distinct granules that are somewhat less raised, and in having a relatively longer premucronal area on tail valves; and from the more southern species *C. pulchellus* (Gray, 1828), which ranges from Ecuador to Patagonia, and *C. periconis* Dall, 1908, a species from the Panamic biogeographic province, in

←

Figure 8 *Callistochiton sphaerae* n. sp.: head (1–4), intermediate (5–18), and tail (19–27) valves. 1–18, 20–27, from LACMIP locality 305; 19, from LACMIP locality 16817 (305C). 1–2, LACMIP 13767, paratype; 3–4, LACMIP 13768, paratype; 5–7, LACMIP 13769, holotype; 8–10, LACMIP 13770, paratype; 11–13, LACMIP 13771, paratype; 14–16, LACMIP 13772, paratype; 17–18, LACMIP 13773, paratype; 19, LACMIP 13854; 20–22, LACMIP 13774, paratype; 23, 24–26, LACMIP 13776, paratype, 27, LACMIP 13775, paratype. Scale bars = 1 mm.

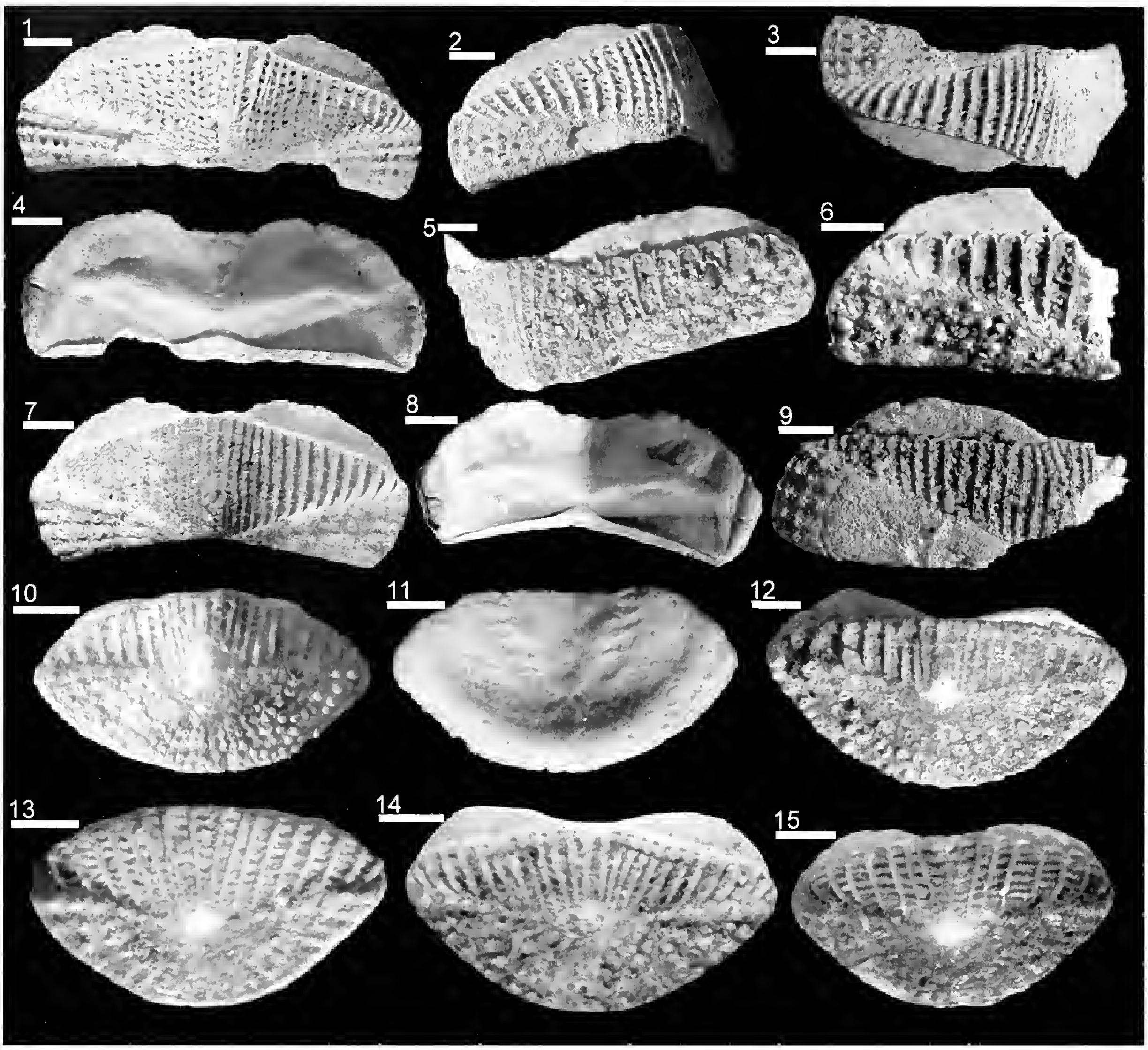

Figure 9 *Lepidozona mertensii* (von Middendorff, 1847): intermediate (1–9) and tail (10–15) valves. 1–6, 10–13, from LACMIP locality 16817 (305C); 7–9, 14–15, from LACMIP locality 305. 1–4, LACMIP 13777; 5, LACMIP 13778; 6, LACMIP 13779; 7–8, LACMIP 13780; 9, LACMIP 13781; 10–11, LACMIP 13782; 12, LACMIP 13783; 13, LACMIP 13784; 14, LACMIP 13785; 15, LACMIP 13786. Scale bars = 1 mm.

having much more distinct longitudinal ridges in central areas of the valves.

Genus *Lepidozona* Pilsbry, 1892

DISTRIBUTION. This genus is best known from the northeastern and northwestern Pacific Ocean, although a few species have been described from the central Indo-Pacific region, one is known from New Zealand, and one deepwater member is thought to range as far south as Chile. One species of *Lepidozona* reported from South Africa (Ferreira, 1974; Strack, 1996) was shown to have been incorrectly assigned to this genus (Schwabe, 2006). The genus is particularly well represented in the northeastern Pacific, with at least 23 species described from temperate and tropical waters, and multiple new species awaiting description (Eernisse et al., 2007; Stebbins and Eernisse, 2009; D.J. Eernisse and A. Draeger, unpublished observations). In fact, this is the most species-rich genus in western North America. One problem for the identification of fossils is that features of the girdle scales are sometimes more diagnostic than valve distinctions, and such girdle elements are generally not available in fossils.

Fossils of *Lepidozona* have been described from numerous Pleistocene marine terrace deposits in Southern California (e.g., Chace and Chace, 1919; Berry, 1926; Hertlein and Grant, 1944; Kanakoff and Emerson, 1959; Valentine, 1961; and Valentine and Meade, 1961), but they have not been reported from older deposits in California. A few specimens assigned to *Lepidozona* have been described from the Pliocene (Oinomikado, 1938) and Miocene of Japan (Itoigawa et al., 1981). One intermediate valve from the latest Eocene or earliest Oligocene of Washington was assigned to this genus (Dell'Angelo et al., 2011).

REMARKS. The sculpture of the valve tegmentum of this genus bears strong similarities to that of *Callistochiton* and *Ischnochiton*, and in fact some more weakly sculptured species of *Lepidozona* were previously included in *Ischnochiton*. *Lepidozona* can be separated from *Callistochiton* based mainly on features of the articulamentum (e.g., in *Callistochiton* but not *Lepidozona* the slits in the head valve generally correspond in number and position to the radial ribs of the tegmentum), and *Lepidozona* can be separated from *Ischnochiton* based mainly on weaker tegmental sculpture (Ferreira, 1974, 1978, 1985). Van Belle (1983) and Kaas and Van Belle (1987) emphasize as a diagnostic character of *Lepidozona* the presence in intermediate valves of a delicately denticulate jugal plate (or lamina) across the sinus, separated from the sutural laminae (or apophyses) on each side by small notch. A molecular analysis (D.J. Eernisse, unpublished) supports the recent reassignments of northeastern Pacific species once considered as *Ischnochiton* to *Lepidozona*, and these are closely aligned with *Tripoplax* Berry, 1919b (*sensu* Clark, 2008). *Lepidozona sinudentata* (Pilsbry, 1892) has recently been shown to be a junior synonym of *L. scrobiculata* (von Middendorff, 1847) (Clark, 2004).

Numerous valves in the Kanakoff collection belong to *Lepidozona*, characterized by lateral valve areas of radial ribs that are often composed of granules or larger, more-isolated tubercles; central areas with longitudinal, often cross-hatched, riblets; and head and tail valves with about 10–12 slits (Ferreira, 1974, 1978). However, the distinctions between species of *Lepidozona* are often quite subtle, and many modern specimens share a mixture of characters used to characterize different species. In addition, for many species of *Lepidozona* from the temperate eastern Pacific, Ferreira (1978) separated them from other species from the region but did not directly compare them to the Panamic and Gulf of California species that occur farther south (Ferreira, 1974, 1985), many of which he remarked were very similar to the temperate species. We have tried to be conservative in assigning specimens to specific species of *Lepidozona* and have set aside a number of specimens at LACMIP as indeterminate *Lepidozona*.

Lepidozona mertensii (von Middendorff, 1847)

Figure 9

Chiton mertensii von Middendorff, 1847:118.
Lepidopleurus mertensii: Cooper, 1867:22.
Ischnochiton mertensii: Pilsbry, 1892:125, pl. 26, figs. 20–26.
Ischnochiton (Lepidozona) mertensii: Berry, 1917:26.
Lepidozona mertensii: Is. Taki, 1938:390, pl. 14, fig. 6, pl. 29, figs. 1–6, pl. 30, figs 6–9, pl. 31, figs 9–10; Ferreira 1978:20, figs. 1–2, 20–21, 34 (contains more complete synonymies); Kaas and Van Belle, 1987:188 (contains more complete synonymies).

DISTRIBUTION. LACMIP localities 305 (200 head, 180 intermediate, and 335 tail valves; 2 figured intermediate valves, LACMIP 13780–13781, and 2 figured tail valves, 13785–13786; all other specimens in unfigured lot, LACMIP 14306), 16817 (305C; 9 head, 51 intermediate, and 14 tail valves; 3 figured intermediate valves, LACMIP 13777–13779, and 3 figured tail valves, 13782–13784; all other specimens in unfigured lot, LACMIP 14307), and 16862 (305A; 2 head, 19 intermediate, and 8 tail valves, all in unfigured lot, LACMIP 14308).

TYPE SPECIMENS. Type specimens were not mentioned and no specimen was illustrated in the original description by von Middendorff (1847). Ferreira (1978) reported that the original type specimens were likely lost, and thus he designated a neotype, LACM 1855, from the original type locality, Fort Ross, Sonoma County, California. Other specimens from the neotype lot (e.g., LACM 1856) are in various institutions worldwide (see Ferreira, 1978).

TYPE LOCALITY. Locality listed in original description as "California" (von Middendorff, 1847). Neotype from intertidal zone, about 1 km south of Fort Ross, Sonoma County, California (Ferreira, 1978).

MATERIAL EXAMINED. Neotype (LACM 1855) and neotype lot (LACM 1856; 10 specimens) of *Lepidozona* (as *Chiton*) *mertensii*.

REMARKS. Ferreira (1978) differentiated *Lepidozona mertensii* from the similar *L. cooperi* (Dall, 1879) based mostly on coloration (reddish in the former; grayish, brownish, or otherwise "dingy" in the latter) and shape of tubercles (rounded in the former, elongated in the latter). The shape of the tubercles in fossils from the Border localities indicates they should be assigned to *L. mertensii*, as the tubercles appear more rounded than elongate and are widely spaced and sporadically occurring, all characters consistent with *L. mertensii* and inconsistent with *L. cooperi*. Ferreira (1978) argued that *L. guadalupensis* Ferreira, 1978, is a southern sibling species to *L. mertensii*, but the largest specimen of the latter species known at the time of its description was 31.0 mm long, including girdle. Intermediate valves here assigned to *L. mertensii* are up to 5 mm long at the midline, corresponding to a chiton about 37.5 mm in length, indicating an animal larger than *L. guadalupensis*. These valves can be differentiated from those of most other species of *Lepidozona* by the presence of tall, isolated tubercles. The tubercles in *L. pectinulata* (Carpenter *in* Pilsbry, 1893) are more densely arranged than the tubercles in these specimens. These specimens differ from valves of *L. willetti* (Berry, 1917) in having larger tubercles and more prominent and widely spaced longitudinal riblets, although these species can be difficult to separate without careful comparison of girdle scales. The specimens differ from *L. golischi* (Berry, 1919a) in having more closely spaced tubercles and in being much larger; from *L. scabricostata* (Carpenter, 1864) in having much more distinct tubercles in lateral areas; from *L. retiporosa* (Carpenter, 1864) in having distinct longitudinal ridges in central areas (instead of a reticulate pattern) and more closely spaced tubercles in lateral areas; and from *L. scrobiculata* (von Middendorff, 1847) in having more rounded tubercles in lateral areas. These fossils differ from *L. interstincta* (Gould, 1852) and *L. radians* (Carpenter *in* Pilsbry, 1892) in having more distinct tegmental sculpture, especially in the central areas of intermediate valves; they differ from *L. clathrata* (Reeve, 1847) in having fewer longitudinal ridges in central areas and more distinct tubercles in lateral areas. They differ from *L. subtilis* Berry, 1956 in having greater prominence of, and more spacing between, tubercles in lateral area and ridges in central area of intermediate valves. Stebbins and Eernisse (2009) described but did not name three species of *Lepidozona* from 30+ m depth off of San Diego. The fossils here differ slightly from their *Lepidozona* sp. A in having relatively larger tubercles; from their *Lepidozona* sp. B in having more distinct sculpture overall, in particular more protruding longitudinal ridges and tubercles; and from their *Lepidozona* sp. C in having larger tubercles.

Lepidozona mertensii occurs from Alaska to northwestern Baja California, and from the intertidal zone to around 100 m (Ferreira, 1978), but is most common to about 8 m in depth on the bottoms and sides of rocks (Eernisse et al., 2007). Stebbins and Eernisse (2009) reported three specimens of *L. mertensii* from the Southern California Bight benthic monitoring programs, from depths between 56 and 85 m. It commonly co-occurs with *Hanleyella oldroydi* (Dall, 1919), *Lepidozona retiporosa*, and *Callistochiton palmulatus*. However, *L. mertensii* is generally rare south of Point Conception, Santa Barbara County, California.

Lepidozona pectinulata (Carpenter *in* Pilsbry, 1893)

Figure 10

Ischnochiton (*Lepidopleurus*) *pectinatus* Carpenter, 1864:612 (*nomen nudum*).

Ischnoplax pectinatus: Keep, 1887:112.

Ishcnochiton pectinulatus: Berry, 1922:412, 414, 421, table 1 (fossil).

Ischnochiton clathratus: Pilsbry, 1892:128.

Lepidozona pectinulata: Ferreira, 1974:165; Ferreira, 1978:25, figs. 5–6, 28 (contains more complete synonymies); Kaas and Van Belle, 1987:203 (contains more complete synonymies).

Ischnochiton bryanti Dall, 1919:503.

Ischnochiton brunneus Dall, 1919:504.

Ischnochiton (*Lepidozona*) *californiensis* Berry, 1931:255, pl. 29, figs. 1–2.

Lepidozona californiensis: Smith, 1960:56, fig. 38.8 (from Pleistocene).

DISTRIBUTION. LACMIP localities 305 (133 head, 502 intermediate, and 298 tail valves; 2 figured head valves, LACMIP 13787–13788, 4 figured intermediate valves, 13789–13792, and 5 figured tail valves, 13794–13798; all other specimens in unfigured lot, LACMIP 14309) and 305C (1 head, 10 intermediate, and 2 tail valves; 1 figured intermediate valve, LACMIP 13793, and 2 figured tail valves, 13799–13800; all other specimens in unfigured lot, LACMIP 14310).

TYPE SPECIMENS. Ferriera (1978) designated a lectotype and two specimens as paralectotypes (PRM 70) based on inferences from the description in Palmer (1958).

TYPE LOCALITY. Ferreira (1978) inferred that the locality attributed to the syntypes ("La Paz") is inaccurate, and he chose to restrict the type locality to Santa Catalina Island, California.

REMARKS. The complicated history of the name *Lepidozona pectinulata* and its taxonomic authority is described in detail by Ferreira (1978).

Valves of *Lepidozona pectinulata* from the San Diego Formation differ from those of *L. mertensii*, *L. cooperi*, *L. willetti*, *L. scabricostata*, *L. retiporosa*, *L. scrobiculata*, and *L. golischi* in having more closely spaced tubercles. In addition, the fossils differ from *L. mertensii* and *L. cooperi* in lacking the slight divergence of longitudinal ridges near the midline of intermediate valves except valve 2, and from *L. retiporosa* in having distinct longitudinal ridges in the central area of intermediate valves. In addition, one of the fossil tail valves (Figure 10.18) has 15 or more slits, consistent with *L. pectinulata* (range 10–17) and inconsistent with the other temperate eastern Pacific species of *Lepidozona*, whose tail valves have up to 14 slits (Ferreira, 1978). Some Panamic species of *Lepidozona* have a similar number of slits, but the San Diego Formation valves differ from those of *L. clathrata* in lacking pronounced ridges in the lateral areas, and from *L. subtilis* in having distinct pustules. These fossils differ from *L. guadalupensis* (endemic to Isla Guadalupe) in having more closely spaced tubercles. These fossils differ from *L. interstincta* and *L. radians* in having more distinct tegmental sculpture, especially in the central area of intermediate valves; they differ from *L. clathrata* in having more distinct tubercles in lateral areas. They differ from *L. subtilis* in having more prominent tubercles in lateral areas and more widely spaced ridges in central area of intermediate valves. The fossils here differ from *Lepidozona* spp. A and C of Stebbins and Eernisse (2009) in having more closely spaced tubercles and longitudinal ridges; and from *Lepidozona* sp. B (Stebbins and Eernisse, 2009) in having more distinct sculpture overall, in particular more protruding longitudinal ridges and tubercles.

In some specimens the longitudinal riblets seem to be more pronounced relative to the cross-hatching compared to most specimens assigned to *L. pectinulata*. However, there is variation in modern specimens of the latter species and specimens of *L. pectinulata* at the SBMNH and LACM from near the type locality share more pronounced longitudinal riblets.

Lepidozona pectinulata occurs from 35°N to 24°N along the coast of California and Baja California, and from the intertidal zone to about 20-m depth (Ferreira, 1978), but most commonly under rocks in the low intertidal and shallow subtidal zones (Eernisse et al., 2007).

Lepidozona sp. cf. *L. rothi* Ferreira, 1983

Figure 11 (1–5)

[*Lepidozona rothi* Ferreira, 1983:316, figs. 19–22.

Lepidozona macleaniana Ferreira, 1985:425, figs. 6–10. (syn. by Kaas and Van Belle, 1987)]

DISTRIBUTION. LACMIP locality 305 (3 intermediate valves; LACMIP 13801–13803).

TYPE LOCALITY. Off of Bahía Sulphur, Isla Clarion, Islas Revillagigedo, Mexico, 82–91 m (Ferreira, 1983).

MATERIAL EXAMINED. Holotype of *L. rothi* (LACM 1818).

REMARKS. The fossil valves share with *Lepidozona rothi* a similar tegmental sculpture of longitudinal riblets with cross-hatching in the central area and rows of merged tubercles in the lateral areas. The lateral areas are highly raised in both as well, and valve 2 has a prominent wedge in the longitudinal riblets in the central area near the midline (see discussion of this character in Ferreira, 1978). These fossils are larger than expected based on the original description of the species ("up to 1.5 cm long"; Ferreira, 1983:316), but Kaas and Van Belle (1987) expanded the description , suggesting that the species ranges up to 2.0 cm in length. The fossil specimens fall within the latter size range.

The fossils differ from *L. clathrata*, *L. cooperi*, *L. golischi*, *L. guadalupensis*, *L. mertensii*, *L. pectinulata*, *L. retiporosa*, *L. scabricostata*, *L. scrobiculata*, *L. willetti*, and *Lepidozona* spp. A–C (Stebbins and Eernisse, 2009) in lacking distinct tubercles on lateral areas of intermediate valves. The San Diego Formation fossils also differ from *L. retiporosa* in having distinct longitudinal ridges in the central area of intermediate valves, and from *L. interstincta* and *L. radians* in having a greater elevation of ridges on the tegmentum, especially in the central area of intermediate valves.

Lepidozona rothi is known only from Isla Clarion, Islas Revillaggedo, Mexico, and Isla del Coco, eastern Pacific, from 55–110 m. It is unknown from the fossil record, and this report is tentative.

Lepidozona sp. cf. *L. radians* (Carpenter *in* Pilsbry, 1892)

Figure 11 (6–10)

[*Ischnochiton radians* Carpenter *in* Pilsbry, 1892:121; Carpenter *in* Pilsbry, 1893:75, pl. 16, figs. 48–49; Thiele, 1909:80; Berry, 1917:231, 235; Dall, 1921:191; Oldroyd, 1927:275.

Lepidozona radians: Eernisse et al., 2007:710; Stebbins and Eernisse, 2009:68, pl. 3, fig. 9).]

DISTRIBUTION. LACMIP localities 305 (1 head, 25 intermediate, and 10 tail valves; 2 figured intermediate valves, LACMIP 13804–13805, and 1 figured tail valve, LACMIP 13806; all other specimens in unfigured lot, LACMIP 14311) and 16817 (305C; 5 intermediate valves, all in unfigured lot LACMIP 14312).

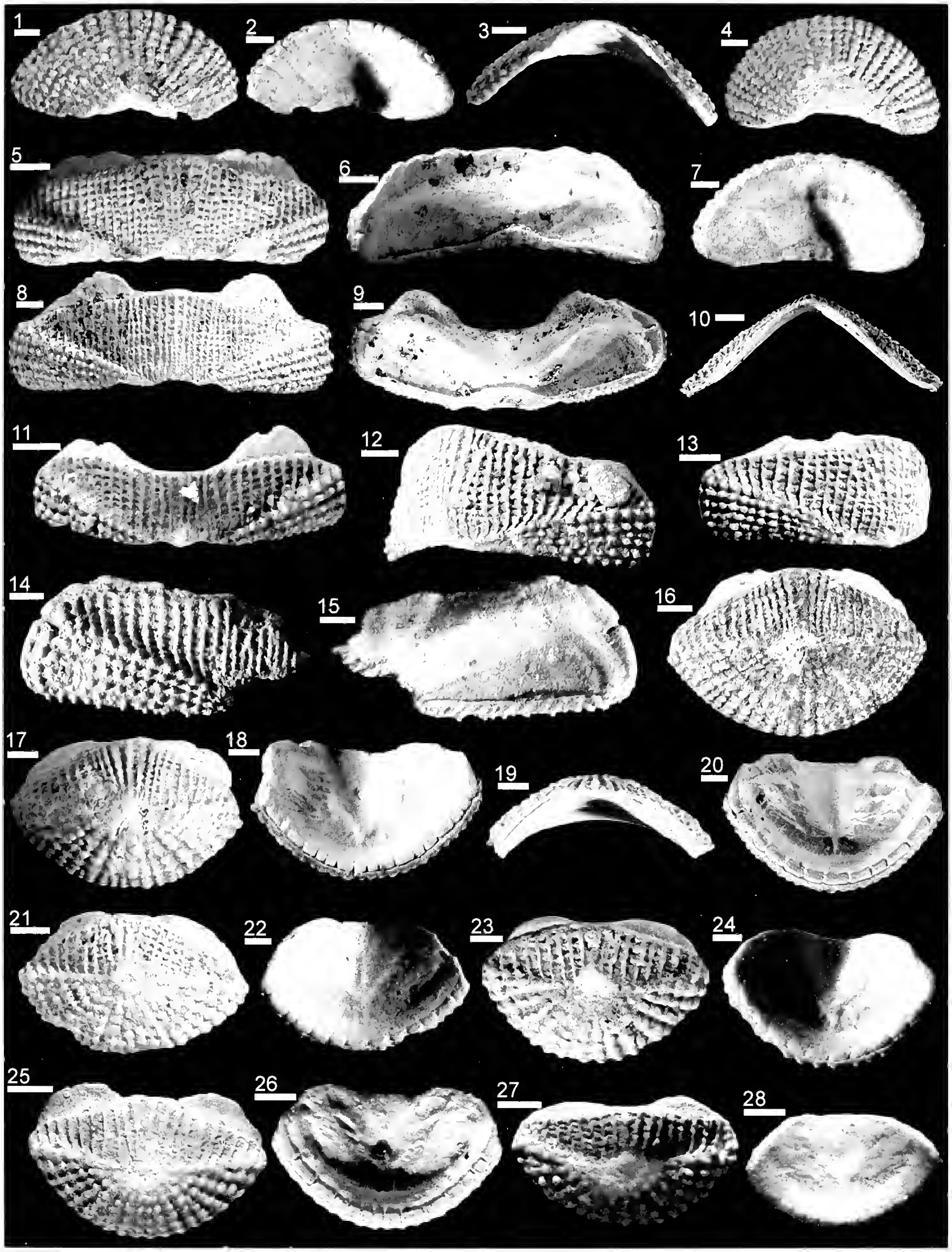

Figure 10 *Lepidozona pectinulata* (Carpenter *in* Pilsbry, 1893): head (1–4, 7), intermediate (5–6, 8–15), and tail (16–28) valves. 1–12, 14–24, from LACMIP locality 305; 13, 25–28 from LACMIP locality 16817 (305C). 1–3, LACMIP 13787; 4, 7, LACMIP 13788; 5–6, LACMIP 13789; 8–10, LACMIP 13790; 11, LACMIP 13791; 12, LACMIP 13792.;13, LACMIP 13793; 14–15, LACMIP 13794; 16, 20, LACMIP 13795; 17–19, LACMIP 13796; 21–22, LACMIP 13797; 23–24, LACMIP 13798; 25–26, LACMIP 13799; 27–28, LACMIP 13800. Scale bars=1 mm.

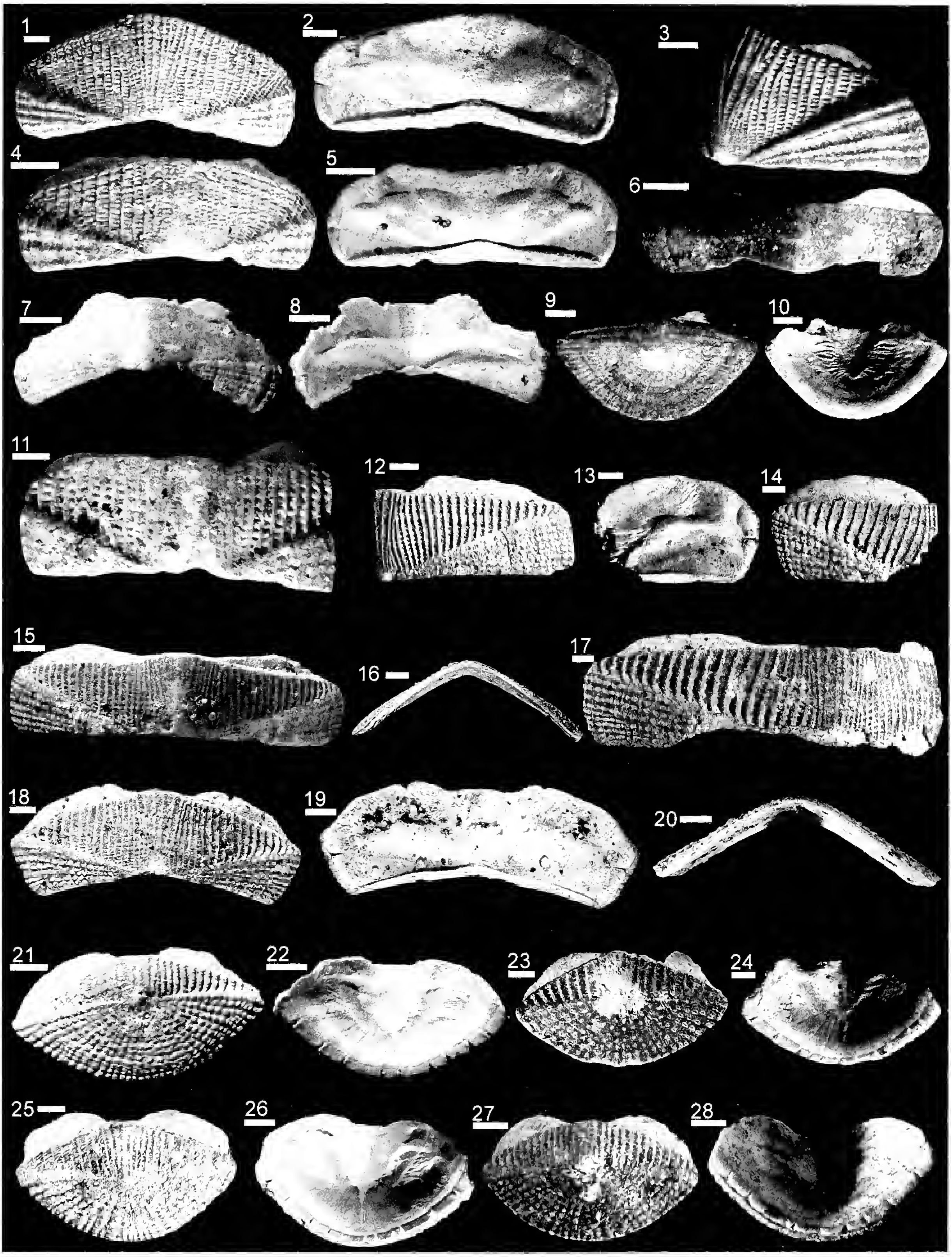

Figure 11 *Lepidozona* spp. 1–20, 23–28, from LACMIP locality 305; 21–22, from LACMIP locality 16817 (305C). 1–5, *Lepidozona* sp. cf. *L. rothi* Ferreira, 1983: intermediate valves. 1–2, LACMIP 13801; 3, LACMIP 13802; 4–5, LACMIP 13803; 6–10, *Lepidozona* sp. cf. *L. radians*: intermediate (6–8) and tail (9–10) valves. 6, LACMIP 13804; 7–8, LACMIP 13805; 9–10, LACMIP 13806; 11–28, *Lepidozona kanakoffi* n. sp.: intermediate (11–20) and tail (21–28) valves. 11, LACMIP 13807, paratype, *L. kanakoffi*; 12, LACMIP 13808, paratype; 13–14, LACMIP 13809, paratype; 15–16, LACMIP 13810, holotype, *L. kanakoffi*; 17, LACMIP 13811, paratype, *L. kanakoffi*; 18–20, LACMIP 13812, paratype; 21–22, LACMIP 13813; 23–24, LACMIP 13814, paratype; 25–26, LACMIP 13815, paratype; 27–28, LACMIP 13816, paratype. Scale bars=1 mm.

TYPE SPECIMENS. The only figured specimen associated with the original description (Carpenter *in* Pilsbry, 1892, pl. 16, figs. 48–49) was a secondary, non–type specimen (USNM 19471; Palmer, 1958). Palmer (1958) found what she believed were Carpenter's original specimens, on which the description was based, and chose one of these as a lectotype and three other valves as paratypes (all PRM 25).

TYPE LOCALITY. Monterey, California (based on label associated with Carpenter's specimens, PRM 25, as reported by Palmer, 1958).

REMARKS. The valves described here share with those of *Lepidozona radians* faint radiating ridges in the central areas; periodic growth increments; wide tail valve with anterior mucro; slightly raised lateral areas with merged granules; and central areas of faint lineations of pores.

Smith (1977) synonymized *Ischnochiton radians* Carpenter *in* Pilsbry, 1892, with *Ischnochiton interstinctus* (Gould, 1846), and Kaas and Van Belle (1990) reassigned it to *Lepidozona interstincta* (Gould, 1846). Eernisse et al. (2007; see also Kelly and Eernisse, 2007; Stebbins and Eernisse, 2009) revised *Lepidozona radians* as distinct from the more northern *L. interstincta*, and emphasized that *L. radians* was much more colorful and variable in its color than the mostly tan to orange *L. interstincta*. Lacking color features and because of the general lack of sculpturing in both species, the isolated valves of the San Diego Formation cannot be separated from either of these species. Thus we have used open nomenclature and choose the species that occurs in California.

These fossils differ from *L. clathrata*, *L. cooperi*, *L. golischi*, *L. guadalupensis*, *L. mertensii*, *L. pectinulata*, *L. retiporosa*, *L. scabricostata*, *L. scrobiculata*, *L. willetti*, and *Lepidozona* spp. A–C (Stebbins and Eernisse, 2009) in lacking distinct tubercles in lateral areas of intermediate valves.

Lepidozona radians ranges from northern Baja California, Mexico, north to at least Port Hardy, British Columbia, Canada (D.J.E., unpublished observations). It normally occurs in the intertidal to shallow subtidal zones, most commonly from 5-to-13-m depth under rocks or on rocky surfaces buried in sand (Eernisse et al., 2007), although it has been found in depths up to 150 m (Stebbins and Eernisse, 2009). To our knowledge neither *L. radians* nor *L. interstincta* has yet been reported as a fossil.

Lepidozona kanakoffi n. sp.

Figure 11 (11–28)

DISTRIBUTION. LACMIP localities 305 (31 intermediate and 25 tail valves; 6 figured intermediate valves, LACMIP 13807–13812, and 3 figured tail valves, 13814–13816; all other specimens in unfigured topotype lot, LACMIP 14313) and 16817 (305 C; 1 intermediate and 2 tail valves; 1 figured tail valve, LACMIP 13813; all other specimens in unfigured lot, LACMIP 14314).

TYPE SPECIMENS. Holotype (Figures 11.15–11.16; LACMIP 13810) and eight figured paratypes (Figures 11.11–11.14, 11.17–11.20, 11.23–11.28, LACMIP 13807–13809, 13811–13812, 13814–13816); 25 intermediate valves and 22 tail valves in topotype lot, LACMIP 14313.

TYPE LOCALITY. LACMIP locality 305.

ETYMOLOGY. Named for the late George P. Kanakoff, whose collecting efforts produced the massive chiton assemblage described herein.

DIAGNOSIS. Intermediate valves with a relatively low aspect ratio; distinct longitudinal ridges in central area of intermediate valves and premucronal area of tail valves; many closely spaced rows of distinct but closely spaced granules in lateral areas of intermediate valves and postmucronal area of tail valves. Typically about 10 rows of granules in lateral areas of intermediate valves and about 30 rows in postmucronal area of tail valves.

DESCRIPTION. Intermediate valves relatively wide; central areas with prominent, somewhat curving longitudinal ridges, about 50 to 60 in one intermediate valve; cross-hatching more or less noticeable in central areas; lateral areas raised somewhat and with about 10 rows of closely spaced but distinct, rounded granules; sutural laminae short and broad, but with distinct jugal sinus, and without a sign of a jugal plate; distinctly carinate in anterior profile, with straight sides; jugal angle about 122° to 127°; 1 slit per side; apical area distinct and broad but short.

Tail valves with mucro at midline (Fig. 15.25) or more commonly just in front of it (Figures 11.21, 11.23, 11.27); premucronal areas with about 30 distinct longitudinal ridges but with cross-hatching also apparent; postmucronal area with about 30 rows of distinct, rounded granules, closely spaced; sutural laminae broad, more or less rounded, with distinct jugal sinus and no sign of an extended jugal plate; about 9 to 11 slits; slit rays distinct; ventral surface of valve shows much sculpturing, including from possible muscle scars.

REMARKS. These valves share a resemblance to other *Lepidozona* species in tegmental sculpture and shape of the projections of the articulamentum. However, they differ from all known members of *Lepidozona* in having a large number of granule rows in the lateral areas (this species has 10 or more, compared to a maximum of eight in all other eastern Pacific species; Ferreira, 1978, 1983, 1985). The fossils also differ from most other members of *Lepidozona* in having a large jugal angle and more prominent longitudinal ridges. In addition, this species is larger than most species of *Lepidozona* and is perhaps most similar to *L. formosa* Ferreira, 1978, but differs from that species in having more rows of granules in the lateral areas and more prominent longitudinal ridges in the central areas. The fossils also differ from *L. retiporosa* in having distinct longitudinal ridges in the central area of intermediate valves, and from *L. interstincta* and *L. radians* in having more distinct tegmentum sculpture. The fossils share with *L. scabricostata* numerous granule rows in the tail valves and lateral areas of intermediate valves, and pronounced longitudinal ridges. However, the granules in the rows and ridges are much more distinct and closely spaced than in *L. scabricostata*.

Genus *Stenoplax* Dall, 1879

DISTRIBUTION. About half of the approximately 22 worldwide living species of *Stenoplax* occur in the temperate or tropical eastern Pacific, but a few New World species occur exclusively in the Caribbean, and one species, *Stenoplax boogii* (Haddon, 1886), is reported in both regions (Kaas and Van Belle, 1987). *Stenoplax* typically inhabits the low intertidal or shallow subtidal zones, typically found under rocks, at least during daylight hours.

A few valves from the Oligocene of Italy were assigned to this genus (Dell'Angelo and Palazzi, 1992) and additional species are known from the Eocene of Europe (Wrigley, 1943; Van Belle, 1981; Bielokrys, 1999). A few valves from the latest Eocene or earliest Oligocene of Washington were assigned to this genus (Dell'Angelo et al., 2011). *Stenoplax conspicua* Pilsbry, 1892, *S. fallax* (Carpenter *in* Pilsbry, 1892), *S. heathiana* Berry, 1946, and *S. magdalenensis* (Hinds, 1845) can be relatively common in Pleistocene marine terrace deposits in California (e.g., Chace, 1916a, 1916b, 1966; Chace and Chace, 1919; Hertlein and Grant, 1944; Kanakoff and Emerson, 1959; Valentine and

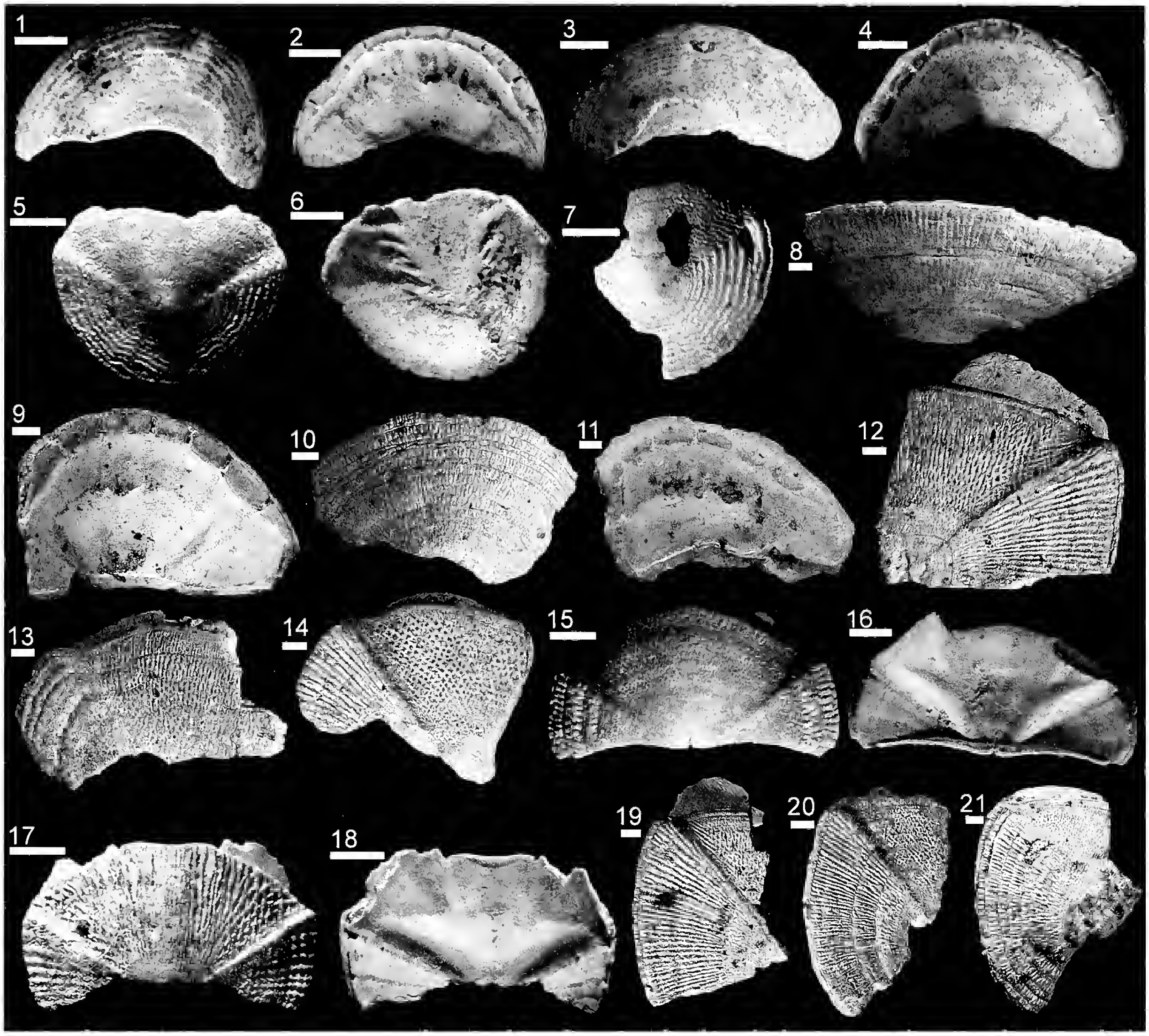

Figure 12 *Stenoplax* spp. 1–4, 8–14, 17–21, from LACMIP locality 305; 5–7, 15–16, from LACMIP locality 16817 (305C). **1–7**, *Stenoplax circumsenta* Berry, 1956: head (1–4) and tail (5–7) valves. 1–2, LACMIP 13817; 3–4, LACMIP 13818; 5–6, LACMIP 13819; 7, LACMIP 13820; **8–21**, *Stenoplax fallax* (Carpenter *in* Pilsbry, 1892): head (8–11), intermediate (12–18), and tail (19–21) valves. 8, LACMIP 13821; 9, LACMIP 13822; 10–11, LACMIP 13823; 12, LACMIP 13824; 13, LACMIP 13825; 14, LACMIP 13826; 15–16, LACMIP 13827; 17–18, LACMIP 13828; 19, LACMIP 13829; 20, LACMIP 13830; 21, LACMIP 13831. Scale bars=1 mm.

Meade, 1961; Marincovich, 1976; Kennedy, 1978; Valentine, 1980).

REMARKS. The most familiar species of *Stenoplax* (e.g., *S. conspicua*, *S. magdalanensis*, and *S. heathiana*), as well as smaller and less well known species, can each have distinctive girdle elements, coloration, or latitudinal distribution, and DNA sequence comparisons are generally effective for distinguishing species (Kelly and Eernisse, 2007; D.J. Eernisse, unpublished data). However, several pairs or complexes of species in this genus overlap substantially in valve morphology. This adds uncertainty to taxonomic hypotheses based on fossil valve material only, but here we point out specific sources of ambiguity in each case.

Stenoplax is a distinct taxon whose members are highly elongate, and whose intermediate valves have prominent sutural laminae and generally raised lateral areas. The much more elongated (relative to other valves) tail valve with prominent diagonal line is diagnostic for this genus.

Stenoplax circumsenta Berry, 1956
Figure 12 (1–7)

Stenoplax circumsenta Berry, 1956:72; Kaas and Van Belle, 1987:151 (contains more complete synonymies).

DISTRIBUTION. LACMIP localities 305 (3 head, 1 intermediate, and 5 tail valves; 2 figured head valves, LACMIP 13817–13818; all other specimens in unfigured lot, LACMIP 14315) and 16817 (305C; 1 head, 1 intermediate, and 3 tail valves; 2 figured tail valves, LACMIP 13819–13820; all other specimens in unfigured lot, LACMIP 14316).

TYPE SPECIMEN. Holotype (SBMNH 34425).

TYPE LOCALITY. Sand flats, Isla Concha, Laguna Ojo de Liebre (Scammon's Lagoon), Baja California Sur, Mexico.

MATERIAL EXAMINED. Holotype (SBMNH 34425) of *Stenoplax circumsenta*.

DESCRIPTION. The fossil tail valves are about 3.7 mm long, 4.8 mm wide, with a 2-mm-long premucronal region and 1.5-mm-long postmucronal area. The sutural laminae are small and widely spaced (0.15 mm long, each about 0.80 mm wide).

REMARKS. The fossil tail valves have an unusual shape in the prominent premucronal area, distinct and somewhat jagged growth lines, prominent change in slope at diagonal line, subdued premucronal sculpture that consists of rows of small pores, and small size, all of which match *Stenoplax circumsenta*. Although *S. circumsenta* was previously synonimized with *S. corrugata* (Pilsbry, 1892) by Ferreira (1983) based on a number of arguments, each of these arguments was refuted by Kaas and Van Belle (1987). In his original description of *S. circumsenta*, Berry (1956:72) noted the similarity between these two species, but stated the difference based on the presence of "curious" acute spines in the girdle of *S. circumsenta*. We maintain the separation of *S. circumsenta* and *S. corrugata* based on a number of characters, including those of tegmental sculpture (Kaas and Van Belle, 1987). In particular, the valves of *S. circumsenta* as well as the tail valves from the San Diego Formation differ from those of *S. corrugata* in having finer, more-jagged growth lines in the postmucronal area. The fossil tail valves differ from those of *S. purpurascens* (Adams, 1845) *sensu* Bullock (1985) in having shorter sutural laminae, a more rounded anterior margin, and a relatively smooth premucronal area (instead of the prominent longitudinal ridges in *S. purpurascens*). These fossils differ from the larger species of *Stenoplax*, *S. fallax*, *S. conspicua*, *S. heathiana*, *S. limaciformis* (Sowerby, 1832), and *S. magdalenensis* in having wavy ridges in the head valve and postmucronal area of the tail valve. These fossils differ from the much smaller *S. mariposa* (Dall, 1919) in having much finer valve sculpture, and from the otherwise similar (and more southern) *S. rugulata* (Sowerby, 1832) in lacking the longitudinal ridges in the premucronal area of the tail valve.

The tail valve length is typically 3.5–4 mm, which is similar to the tail valve length of the holotype of *S. circumsenta* (3.85 mm). The length:width ratio in the tail valve is about 0.7 (ratio in holotype is 0.62); placement of mucro is about 0.5 the valve length (value in holotype is 0.53). Based on their close similarity in form, we cannot see any good reason to exclude these valves from *S. circumsenta*.

Kaas and Van Belle (1987:294, map 48) show an occurrence of *S. circumsenta* off the coast of Los Angeles, California, and the type locality is farther south on the Pacific Coast, but it is possible that the reports farther north should have been for the poorly known *S. corrugata* instead. *Stenoplax circumsenta* is primarily known from Baja California and the Sea of Cortez (Berry, 1956; Ferreira, 1972; Hanselman, 1973; Kaas and Van Belle, 1987; D.J. Eernisse, unpublished observations). The depth range for this species is 0 to 72 m (Kaas and Van Belle, 1987). This is the first known occurrence of this species in the fossil record.

Stenoplax fallax (Carpenter *in* Pilsbry, 1892)

Figure 12 (8–21)

Ischnochiton (*Stenoplax*) *fallax* Carpenter *in* Pilsbry, 1892:59, pl. 16, figs. 17–18.

Stenoplax fallax: Palmer, 1945:101; Kaas and Van Belle, 1987:146 (contains more complete synonymies).

DISTRIBUTION. LACMIP localities 305 (8 head, 13 intermediate, and 13 tail valves; 3 figured head valves, LACMIP 13821–13823, 4 figured intermediate valves, LACMIP 13824–13826, 13827, and 3 figured tail valves, LACMIP 13829–13831; all other specimens in unfigured lot, LACMIP 14317), 16817 (305C; 1 intermediate and 1 tail valve; 1 figured intermediate valve, LACMIP 13827; other specimen 14318), and 16862 (305A; 1 head and 3 intermediate valves, all specimens in unfigured lot, LACMIP 14319).

TYPE SPECIMEN. Holotype (PRM 64), as reported by Palmer (1958).

TYPE LOCALITY. Bodega Bay, Sonoma County, California.

MATERIAL EXAMINED. Numerous topotypes of *Stenoplax fallax* at LACM and SBMNH.

REMARKS. The fossil intermediate valves have a fine, pitted sculpture in the central area, radiating riblets in the lateral areas, and a narrow and elongate valve shape, all characters consistent with *Stenoplax fallax* and inconsistent with the most similar forms *S. magdalenensis* and *S. conspicua* (see Pilsbry, 1892 and Berry, 1922). The fossils differ from *S. heathiana*, *S. limaciformis*, *S. boogii*, *S. purpurascens*, and *S. rugulata* in having distinct pitted sculpture in the central area of intermediate valves. Moreover, the large size also differentiates these fossils from *S. limaciformis*, *S. circumsenta*, *S. rugulata*, and *S. mariposa* (Dall, 1919).

These fossils are very similar to valves of a specimen of the rare species *S. corrugata* at the SBMNH (currently unnumbered) collected by George Hanselman. Although Kaas and Van Belle (1987) mentioned that the holotype of *S. corrugata* is small (13.7 mm long) and claim the species ranges only to 22 mm in length, Hanselman's specimen is 42 mm long. Hanselman's specimen bears the characteristic color markings of *S. corrugata*, different from that in *S. fallax*, so it is likely a member of the former species, as indicated on the specimen label. However, most specimens of *S. corrugata* are much smaller. In his original description of *S. fallax*, Pilsbry (1892) lists a length of 27.5 mm for this species. Kaas and Van Belle (1987), however, refer to *S. fallax* as a large species, ranging up to 75 mm in length. The fossil valves are all more than 5 mm long (in some cases closer to 10 mm), corresponding to a chiton of estimated total length 48 to 76 mm. The specimens here are much larger than what Pilsbry (1892) suggested for *S. fallax* but are within the range suggested by Kaas and Van Belle (1987), and are similar in size to the topotype material (e.g., SBMNH 1002440) of *S. fallax*. The fossils thus have a size range that better matches that of modern *S. fallax* than *S. corrugata*.

Berry (1922) mentions terracing from pronounced growth lines in the lateral areas, and this can be seen in some Border locality specimens (Figures 12.13, 12.16), but not on others. Terracing is likewise present in some extant specimens (e.g., LACM 60-24), but not others assigned to this species from Southern California. The radiating riblets in the head valves, lateral areas of intermediate valves, and postmucronal area of tail valves are more distinct and less wavy than in most modern specimens of *S. fallax*, although there appears to be a high degree of intraspecific variability in this character.

Stenoplax fallax is primarily a subtidal species; adults occur along the sides of rocks buried in sand (Eernisse et al., 2007). This species occurs from Vancouver Island, Canada, to Bahía Todos Santos, Baja California, Mexico (Kaas and Van Belle, 1987).

Stenoplax sp. cf. *S. heathiana* Berry, 1946

Figure 13

[*Stenoplax (Stenoradsia) heathiana* Berry, 1946:161, figs. 1–6, pl. 4, figs. 7–9; Kaas and Van Belle, 1987:128 (contains more complete synonymies).

Stenoplax heathiana: Smith, 1963:148.]

DISTRIBUTION. LACMIP locality 305 (2 head valves, LACMIP 13832–13833, 5 intermediate valves, LACMIP

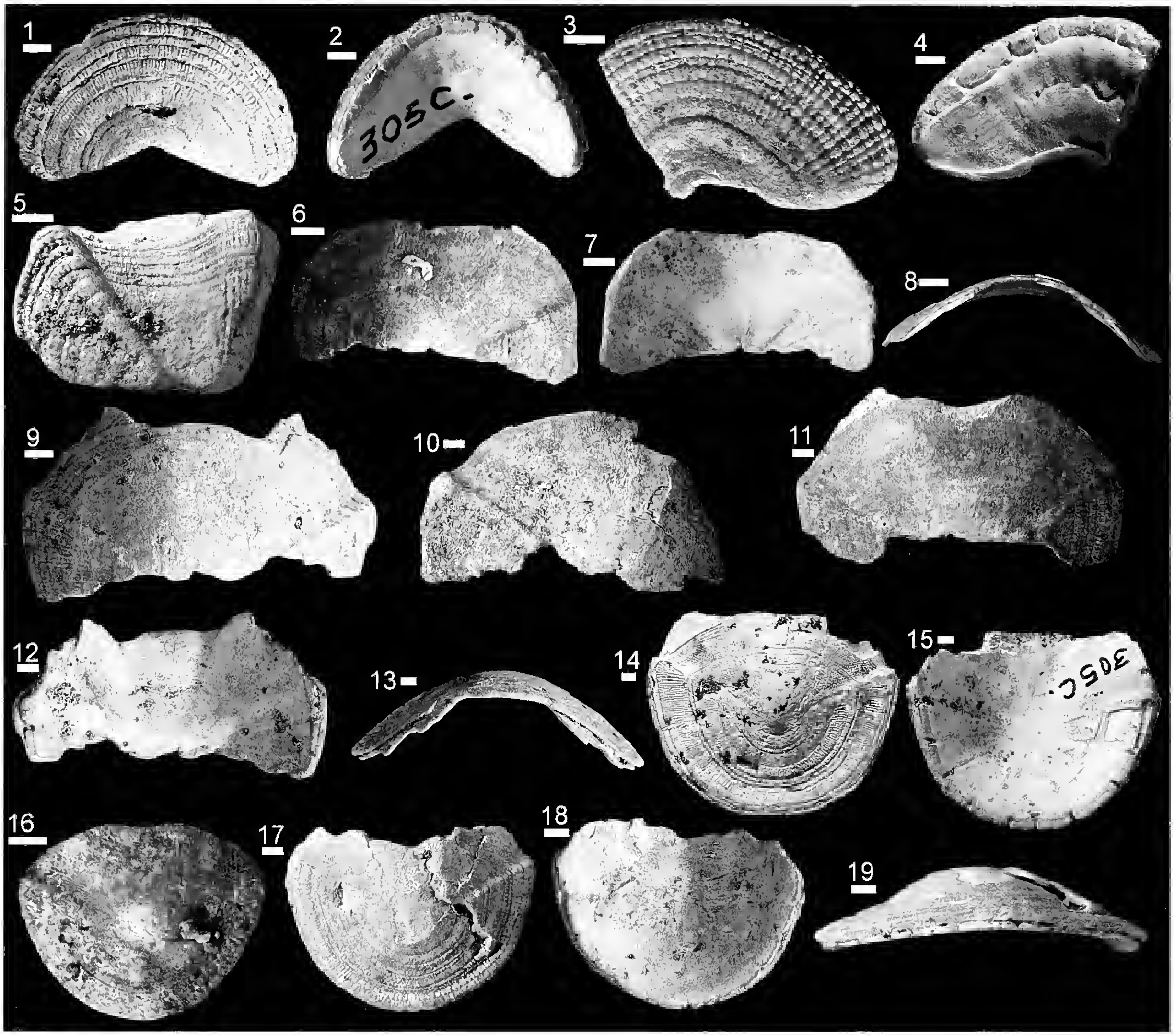

Figure 13 *Stenoplax* sp. cf. *S. heathiana* Berry, 1946: head (1–4), intermediate (5–13), and tail (14–19) valves. 1–13, 16–19, from LACMIP locality 305; 14–15 from LACMIP locality 16817 (305C). 1–2, LACMIP 13832; 3–4, LACMIP 13833; 5, LACMIP 13834; 6–8, LACMIP 13835; 9, 12–13, LACMIP 13836; 10, LACMIP 13837; 11, LACMIP 13838; 14–15, LACMIP 13839; 16, LACMIP 13840; 17–19, LACMIP 13841. Scale bars=1 mm.

13834–13838, and 2 tail valves, LACMIP 13840–13841) and 16817 (305C; 1 tail valve, LACMIP 13839).

MATERIAL EXAMINED. Paratypes of *Stenoplax heathiana* Berry, 1946 (SBMNH 34415–34417).

REMARKS. The fossil intermediate valves are large, with a tegmentum sculpture in the central area of faint growth lines, similar to that of most specimens of *S. heathiana*, but different from that of the similar *S. conspicua* and *S. magdalenensis*, which tend to have more prominent, coarser radiating ridges (but see below), and *S. fallax* and *S. corrugata*, which have a pitted texture. The large size of the fossils differentiates them from *S. limaciformis*, *S. boogii*, *S. circumsenta*, *S. corrugata*, *S. rugulata*, and *S. mariposa*. The lack of somewhat wavy, equally spaced ridges over the entire tegmental surface differentiates these fossils from the Caribbean species *S. purpurascens*.

However, species of *Stenoplax* vary with respect to their tegmentum sculpture (Kaas and Van Belle, 1987; MJV, personal observation) and many species of *Stenoplax* can have 10 slits in the tail valve, as observed in the fossil tail valve, so we only provisionally assign these valves to *S. heathiana*. Some of the fossils may belong to *S. conspicua*, *S. magdalenensis*, or *S. sonorana*, but from abraded and in some cases fragmented valves alone it is difficult to distinguish these species.

Stenoplax heathiana is known from the intertidal to shallow subtidal zones (to 7 m) under rocks buried in sand (Eernisse et al., 2007). It ranges from Fort Bragg, Mendocino County (in northern California), to where it is fairly common in central California. Like several other mostly more northern species, it is absent or rare in the relatively warm Southern California Bight but is found at cooler upwelling-affected localities farther south: it is specifically reported from Punta Santo Tomas, Baja California, Mexico (Kaas and Van Belle, 1987).

Suborder Acanthochitonina Bergenhayn, 1930
Family Mopaliidae Dall, 1889
Genus *Amicula* Gray, 1847a

DISTRIBUTION. Members of this genus are typically found at moderate subtidal depths of about 20 to 100 m, and are

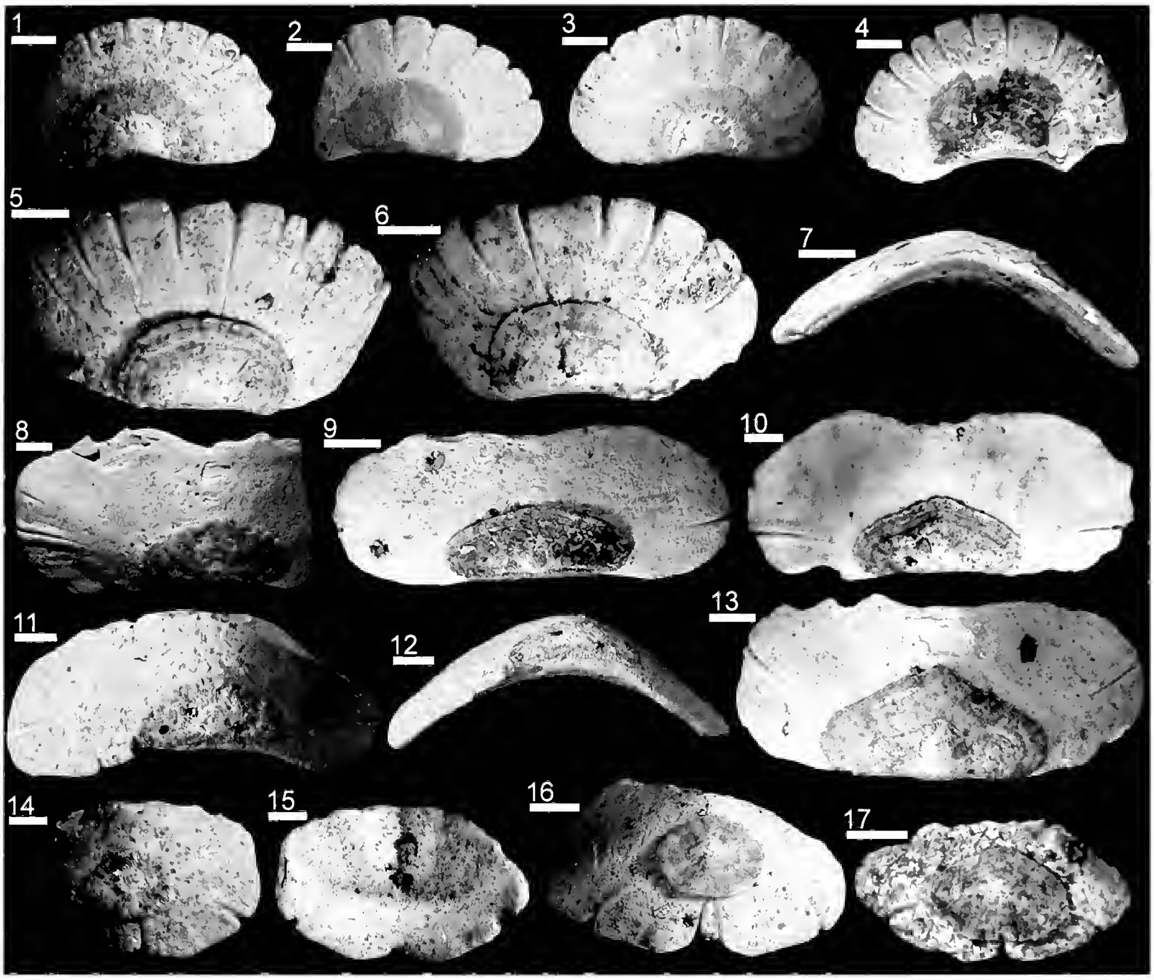

Figure 14 *Amicula solivaga* n. sp.: head (1–7), intermediate (8–13), and tail (14–17) valves. 1–10, 13–17, from LACMIP locality 305; 11–12, from LACMIP locality 16817 (305C). In dorsal views (all except 7, 12), anterior is toward the top of the page. 1, LACMIP 13842, paratype; 2, LACMIP 13843, paratype; 3, LACMIP 13844, paratype; 4, LACMIP 13845, paratype; 5, LACMIP 13846, holotype; 6–7, LACMIP 13847, paratype; 8, LACMIP 13848, paratype; 9, LACMIP 13849, paratype; 10, LACMIP 13850, paratype; 11–12, LACMIP 13851; 13, LACMIP 13852, paratype; 14–15, LACMIP 13853, paratype; 16, LACMIP 13855, paratype; 17, LACMIP 13856, paratype. Scale bars=1 mm.

particularly common in the North Pacific and Arctic but extend also to the cool temperate northwestern Pacific, the Aleutian Islands, and even a few localities in the northwestern Atlantic as far south as Cape Cod, Massachusetts (Jakovleva, 1952; Okutani and Saito, 1987; Kaas and Van Belle, 1994). Besides the occurrence described here, *Amicula vestita* (Broderip and Sowerby, 1829) from the Pleistocene of "Lower Canada" (Pilsbry, 1893:45) is the only member of this genus known with a fossil record.

REMARKS. *Amicula* is characterized by a significant reduction of the tegmentum, medium to large body size, and slit formula 6–8/1/sinus+2 (Kaas and Van Belle, 1994). The sinus in the tail valve is also seen in other mopaliid genera. The taxonomy of *Amicula* is unsettled. Jakovleva (1952) recognized four species: *A. vestita* (including the junior synonym *Amicula amiculata* Pilsbry, 1892), *Amicula pallasii* (von Middendorff, 1847), *Amicula gurjanovae* Jakovleva, 1952, and *A. rosea* Jakovleva, 1952. Okutani and Saito (1987) and Saito (1994) maintained this taxonomy, but Kaas and Van Belle (1994) recognized only two species: *A. amiculata* (with junior synonym *A. gurjanovae*) and *A. vestita*, with junior synomyms *A. rosea* and *A. pallasii*.

Amicula solivaga n. sp.
Figure 14

DISTRIBUTION. Restricted to the San Diego Formation exposures near the U.S.–Mexico border, at LACMIP localities 305 (9 head, 29 intermediate, and 7 tail valves; 6 figured head valves, LACMIP 13842–13847, 4 figured intermediate valves, LACMIP 13848–13850, 13852, and 2 figured tail valves, LACMIP 13853, 13855; all other specimens in unfigured topotype lot, LACMIP 14320), 16817 (305C; 2 intermediate valves; 1 figured, LACMIP 13851 and 1 unfigured, LACMIP 14321), and 16862 (305A; 1 head, 1 intermediate, and 1 tail valve, all in unfigured lot, LACMIP 14322).

TYPE SPECIMENS. Holotype (LACMIP 13846; Figure 14.5; head valve) and 11 figured paratypes (5 head, 4 intermediate, and 2 tail valves; LACMIP 13842–13845, 13847–13850, 13852–13853, 13855); 3 head, 25 intermediate, and 5 tail valves in the topotype lot, LACMIP 14320; all from LACMIP locality 305.

TYPE LOCALITY. LACMIP locality 305.

DIAGNOSIS. Valves of relatively large size, between 0.5 and 1 cm in width; length:width ratio of intermediate valves ~0.36;

tegmentum covers about 1/4 of dorsal surface of valves, suboval, with faint ornamentation of growth lines; posterior margin of valves straight or bent only slightly posteriorly; tail valve with three slits and with only a tiny sinus in the region of the middle slit.

DESCRIPTION. Head valves with shallow posterior sinus; 8–9 slits (n=2); insertion slits deep; tegmentum covers about 1/4 of dorsal surface.

Intermediate valves about 3.5–4 times wider than long; shallow anterior sinus; rounded edges of valves; 1 slit, groove from slit extends far towards apex; prominent slit rays on ventral surface of valve; pronounced v-shaped ridge on undersurface of valve, extending from the midpoint of the lateral margins of the valves to the apex.

Tail valves subhexagonal in outline; 3 slits, middle slit occurring in a shallow sinus; slight raised triangular area from mucro to anterior margin.

ETYMOLOGY. From *solus*, Latin for "alone," and *vagus*, Latin for "wandering," so named because this species of *Amicula* lived far from modern representatives of the genus.

REMARKS. The reduced tegmentum, presence of two slits total (one on each side) in each intermediate valve, and overall shape indicate this is a species of *Amicula*. However, some prominent characters are unique to this species, in particular the presence of eight or nine slits in head valves, as opposed to six to eight that were previously reported for the genus (Jakovleva, 1952). Also, the tegmentum, although reduced, is proportionally larger than that in other species of *Amicula*. In addition, the lack of an anterior embayment in the tail valve of this species differentiates it from others in the genus.

This species is distinct from *A. vestita* (Broderip and Sowerby, 1829) and *A. amiculata* (Pallas, 1787), and all of their putative synonyms, in having a much greater valve surface coverage by tegmentum; a typically suboval, less heart-shaped tegmentum; relatively straight posterior margins; three slits in the tail valve; and a much shallower anterior sinus in the tail valve.

Amicula is today found in the cold, boreal regions, mostly from the North Pacific and Artic (Jakovleva, 1952; Okutani and Saito, 1987), but it also ranges as far south as Hokkaido, Japan, in the northwestern Pacific (Saito, 1994). The complete absence of the genus from western North America, and the warmer-water affinities of some of the other chitons reported here, make its discovery in the San Diego Formation of Southern California a surprise.

Genus *Mopalia* Gray, 1847a

DISTRIBUTION. This genus occurs in the temperate eastern and western Pacific but is particularly common in the temperate northeastern Pacific, with a remarkable diversity of species there (Kelly and Eernisse, 2008). *Mopalia* tends to occur in intertidal to shallow subtidal environments.

This genus has been reported from Miocene rocks in Japan (Itoigawa et al., 1981, 1982). Those fossils consist of only four intermediate valve fragments so their identification as *Mopalia* is problematic. However, a Miocene occurrence is consistent with molecular dating of a Miocene divergence between northwestern and northeastern Pacific species, and it is inconsistent with a Late Pliocene origin of the genus (Kelly and Eernisse, 2008). Fossils in the San Diego Formation therefore represent among the oldest northeastern Pacific records of *Mopalia*, but the genus is expected to have been in the northeastern Pacific since the Miocene. *Mopalia* has previously been reported from a few specimens from the Pliocene by Davis (1998:21), who listed the rare (<10 specimens) occurrence of "?*Mopalia ciliata*" from the Pico Formation in downtown Los Angeles, and Berry (1922:452), who listed one intermediate valve of "*Mopalia*, sp. indet." from the "Santa Barbara" Formation in Santa Monica, and suggested that its age is Pliocene. The latter locality is likely the same (same general area) as what Hoots (1931) referred to as the "San Diego" Formation, which appears to be Pliocene based on the occurrence of the bivalve *Patinopecten healeyi*. Fossils of *Mopalia* also have been reported from the Pleistocene of the eastern Pacific (e.g., Arnold, 1903; Chace and Chace, 1919; Kennedy, 1978; Roth, 1979; and Valentine, 1980) and western Pacific (Itoigawa et al., 1978).

REMARKS. *Mopalia* species are often differentiated by aspects of girdle setae. Although they typically have the same slit pattern of 8/1/sinus+2 (Kaas and Van Belle, 1994), most species have a somewhat unique tegmental sculpture. However, the range of tegmental sculpture does overlap in some species, and this, plus the small sample size for each species of *Mopalia* here, prompted us to choose an open nomenclature for most of the species.

Mopalia sinuata Carpenter, 1864

Figure 15 (1–3)

Mopalia sinuata Carpenter, 1864:603, 648; Palmer, 1958:282, pl. 33, figs. 6–13 (contains more complete synonymies); Kaas and Van Belle, 1994:240 (contains more complete synonymies).
Placiphorella (Osteochiton) sinuata: Dall, 1879:303, 306.
Osteochiton sinuata: Dall, 1886:211.
Mopalia goniura Dall, 1919:513.

DISTRIBUTION. LACMIP localities 305 (13 head, 42 intermediate, and 4 tail valves; 1 figured head valve, LACMIP 13894, and 1 figured intermediate valve, LACMIP 13895; all other specimens in unfigured lot, LACMIP 14323) and 16862 (305A; 2 head and 1 intermediate valve, all in unfigured lot, LACMIP 14324).

TYPE SPECIMENS. Syntypes, USNM 4473 and PRM 58 (Palmer, 1958).

TYPE LOCALITY. Puget Sound, Washington.

MATERIAL EXAMINED. Numerous specimens from at or near the type locality at SBMNH and LACM.

REMARKS. Characteristics of *M. sinuata* seen in the fossils include pores arranged in slightly curving rows, a single, prominent ridge separating central from lateral areas of the intermediate valves, and intermediate valves with a straight posterior margin that is angled backwards from the apex.

The fossils share with *Mopalia imporcata* Carpenter, 1864, the same size and length:width ratio, and the same tegmentum sculpture in the lateral area consisting of two prominent rows of granules and central area sculpture of gently curving longitudinal ridges overlying a less prominent cross-pattern. However, the granules in the major valve-delineating ridges are much more distinct and the longitudinal ridges in the central areas much more prominent in modern specimens of *M. imporcata* than in these fossils. These fossils share with *M. sinuata* a similar, unique shape of the intermediate valve with straight posterior margins that trend posteriorly, a tegmental sculpture of cross-hatching, and a prominent, straight ridge that separates the lateral from central areas.

These fossils differ from *M. middendorffii* (von Schrenck, 1861) in being narrower, having a slightly more prominent ridge delineating valve areas, and having narrower lateral areas; from *M. retifera* Thiele, 1909, *M. schrencki* Thiele, 1909, and *M. seta* Jakovleva, 1952, in having much finer sculpture; from *M. ciliata* (Sowerby, 1840) in lacking longitudinal ridges in the central areas; from *M. lignosa* (Gould, 1846) in lacking distinct granules

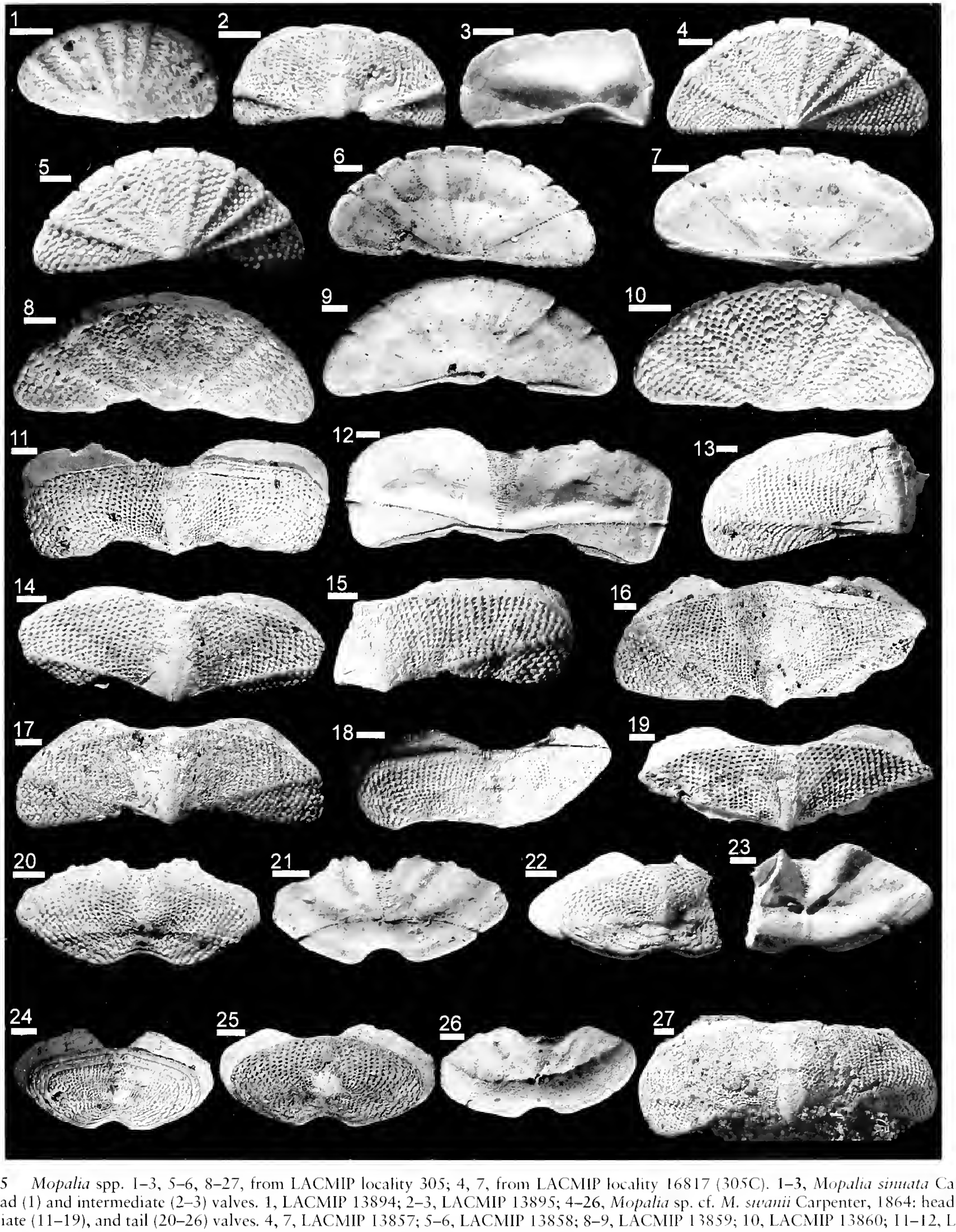

Figure 15 *Mopalia* spp. 1–3, 5–6, 8–27, from LACMIP locality 305; 4, 7, from LACMIP locality 16817 (305C). 1–3, *Mopalia sinuata* Carpenter, 1864: head (1) and intermediate (2–3) valves. 1, LACMIP 13894; 2–3, LACMIP 13895; 4–26, *Mopalia* sp. cf. *M. swanii* Carpenter, 1864: head (4–10), intermediate (11–19), and tail (20–26) valves. 4, 7, LACMIP 13857; 5–6, LACMIP 13858; 8–9, LACMIP 13859; 10, LACMIP 13860; 11–12, LACMIP 13861; 13, LACMIP 13862; 14, LACMIP 13863; 15, LACMIP 13864; 16, LACMIP 13865; 17, LACMIP 13866; 18, LACMIP 13867; 19, LACMIP 13868; 20–21, LACMIP 13869; 22–23, LACMIP 13870; 24, LACMIP 13871; 25–26, LACMIP 13872; 27, *Mopalia* sp. indeterminate: 27, intermediate valve. LACMIP 13873. Scale bars=1 mm.

in lateral areas and in being less wide; from *M. muscosa* (Gould, 1846) in lacking prominent rows of granules in the central area; from *M. hindsii* (Reeve, 1847) in having pores instead of merged granule rows in the central area; from *M. vespertina* (Gould, 1852) in having more prominent tegmental sculpturing; from *M. acuta* (Carpenter, 1855), *M. plumosa* Carpenter in Pilsbry, 1893, and *M. swanii* Carpenter, 1864, in being wider and with more prominent ridges separating central area from lateral areas; from *M. lowei* Pilsbry, 1918, in having finer pores and less of a beak to intermediate valves; from *M. lionata* Pilsbry, 1918, and *M. cirrata* Berry, 1919a, in having much finer sculpture; from *M. egretta* Berry, 1919a, in having finer sculpture, narrower lateral areas, and in being less wide; from *M. phorminx* Berry, 1919a, in lacking prominent ridges in central area; from *M. spectabilis* Cowan and Cowan, 1977, in lacking granules in central area but having distinct pores instead; and differ slightly from *M. ferreirai* Clark, 1991, in lacking a prominent beak on intermediate valves and with less prominent longitudinal ridges in central areas of intermediate valves and less curving posterior margin of intermediate valves.

Mopalia sinuata ranges from Cook Inlet, Alaska, to Avila Beach, San Luis Obispo County, California, and occurs from the intertidal zone to 200-m depth (Kaas and Van Belle, 1994), but is subtidal (8 m or deeper) in central California (Eernisse et al, 2007). *Mopalia sinuata* has been described from the fossil record previously only by Berry (1922) who noted the occurrence of *Mopalia* sp. cf. *M. sinuata* from the Pleistocene of Deadman Island, San Pedro, California.

Mopalia sp. cf. *M. swanii* Carpenter, 1864
Figure 15 (4–26)

[*Mopalia kennerleyi swanii* Carpenter, 1864:648.
Mopalia muscosa swanii: Dall, 1921:195.
Mopalia swanii: Berry, 1951:214, pl. 26, fig. 15; Palmer, 1958:283; Kaas and Van Belle, 1994:238 (contains more complete synonymies).]

DISTRIBUTION. LACMIP localities 305 (142 head, 212 intermediate, and 46 tail valves; 3 figured head valves, LACMIP 13858–13860, 8 figured intermediate valves, 13861–13868, and 4 figured tail valves, 13869–13872; all other specimens in unfigured lot, LACMIP 14325), 16817 (305C; 5 head and 4 intermediate valves; 1 figured head valve, LACMIP 13857; all other specimens in unfigured lot, LACMIP 14326), and 16862 (305A; 1 head, 4 intermediate, and 1 tail valve, all in unfigured lot, LACMIP 14327).

MATERIAL EXAMINED. Numerous topotypes of *Mopalia swanii* at SBMNH and LACM; type locality for *M. swanii* is Tatoosh Island, Washington.

REMARKS. The fossils have the same reticulate pattern in the central areas and isotropic granulose pattern in the lateral areas as seen in specimens of *Mopalia swanii*. The fossil valves fall easily within the size range for this species (listed as "up to 5 cm"; Clark, 1991:309).

The following members of the species-rich genus *Mopalia* have much coarser valve sculpturing than the San Diego Formation fossils and are not further compared here: *M. cirrata*, *M. egretta*, *M. lionata*, *M. lowei*, *M. phorminx*, *M. porifera*, *M. retifera*, *M. schrencki*, and *M. seta*. These fossils differ from valves of *M. middendorffii* in having wider valves with smaller pores; from *M. ciliata* in lacking longitudinal ridges in the central area and having pores instead; from *M. lignosa* in lacking distinct granules in lateral areas of intermediate valves, and in having more prominent pattern of pores in central area; from *M. muscosa* in lacking prominent rows of granules in central area; from *M. hindsii* in having pores instead of merged granule rows in the central area; from *M. vespertina* in having more prominent tegmental sculpture; from *M. sinuata* in being wider and with a much less prominent ridge separating valve areas; from *M. imporcata* in being wider and with less prominent ridges dividing valve areas; from *M. spectabilis* in lacking granules in central area but having distinct pores instead; and from *M. ferreirai* in lacking prominent longitudinal ridges in central area or so prominent major ridges dividing valve areas.

The fossil head valve has a tegmental sculpture dominated by a reticulate pattern of pores throughout the central areas of intermediate valves, and such sculpturing is typical for modern specimens of *M. swanii*. However, such reticulate pores can also be found to varying degrees in certain congeners, including *M. ciliata*, *M. kennerleyi*, *M. ferreirai*, and *M. spectabilis* (all closely related to *M. swanii* based on molecular results of Kelly and Eernisse, 2008), and occasional specimens of *M. egretta* and *M. muscosa*. However, the fossil intermediate valves also appear similar to those of modern *M. acuta* and the closely related *M. plumosa* (Eernisse et al., 2007; Kelly and Eernisse, 2008), although the tail valves have more prominent ridges than is typical for *M. acuta* or *M. plumosa*. However, because of the overlaps in valve form among species of *Mopalia*, and because extant *M. swanii* are uncommon south of Oregon, our identification remains tentative.

Mopalia swanii occurs in the intertidal zone from Alaska to Los Angeles, California (Kaas and Van Belle, 1994), but is uncommon south of Oregon (Eernisse et al., 2007). *Mopalia swanii* has not been previously recorded as a fossil.

Mopalia sp. indeterminate
Figure 15 (27)

DISTRIBUTION. LACMIP locality 305 (1 well-preserved intermediate valve embedded in matrix; LACMIP 13873).

REMARKS. This valve has a uniform, lattice-like sculpture in the central area. The lateral areas also have a lattice sculpture, although with a greater development of granules in between the spaces of the lattice. The two areas are separated by a row of larger granules. This sculpture is similar to that of a number of *Mopalia* species, including *M. ferreirai*, *M. spectabilis*, and *M. swanii*. The sutural laminae extend nearly to the valve midline, and the valve is large, both consistent with assignment to this genus.

Genus *Placiphorella* Dall, 1879

DISTRIBUTION. This genus occurs primarily in the northeastern to northwestern Pacific (Clark, 1994).

A single isolated intermediate valve of *Placiphorella* from the Miocene of Japan was illustrated by Itoigawa et al. (1981). It is also known from the Pleistocene of Japan (Itoigawa et al., 1978). In North America, the oldest previous record of *Placiphorella* is from the Pleistocene (e.g., Chace and Chace, 1919; Valentine and Meade, 1961; Marincovich, 1976; Kennedy, 1978).

REMARKS. *Placiphorella* is characterized by a prominent anterior extension of the girdle with scaled bristles, and short and wide valves embedded in a circular or oval body (Clark, 1994).

Placiphorella velata Dall, 1879
Figure 16 (1–8)

Placiphorella velata Dall, 1879:298, pl. 2, fig. 36; Clark, 1994:291, figs. 1–3, 26, 27 (contains more complete synonymies).
Placiphorella stimpsoni Dall, 1921:197.
Placiphorella sp.: Kohl, 1974:214.

DISTRIBUTION. LACMIP localities 305 (1 figured tail valve, LACMIP 13878, and 1 unfigured intermediate valve, LACMIP 14328), 16817 (305C; 1 head, 4 intermediate, and 1 tail valve; 1 figured head valve, LACMIP 13874, 2 figured intermediate valves, LACMIP 13875–13876, and 1 figured tail valve, LACMIP 13877; other specimens in unfigured lot, LACMIP 14329), and 16862 (305A; 1 head and 1 tail valve, in unfigured lot, LACMIP 14330).

TYPE SPECIMENS. Lectotype and two paralectotypes (collection numbered ANSP 35756) designated by Clark (1994).

TYPE LOCALITY. Bahía Todos Santos, Baja California, Mexico.

MATERIAL EXAMINED. Numerous specimens from at or near the type locality, at SBMNH and LACM.

REMARKS. *Placiphorella velata* is similar to both *P. hanselmani* Clark, 1994, and *P. mirabilis* Clark, 1994. The characters that Clark (1994) used to separate these species do not include tegmental sculpture, and in fact many *Placiphorella* species have a tegmental sculpture similar to these fossils. However, the large size of the fossil valves (many greater than 5 mm in length at the midline) is consistent only with *P. velata. Placiphorella velata* has a combined tegmental length up to 6 cm whereas the other *Placiphorella* species have a maximum size of 5 cm, and all species of the genus have a girdle that extends anteriorly (Clark, 1994). The distinct growth lines and slightly raised lateral areas are also consistent with *P. velata.* Otherwise these fossils are similar also to *P. rufa* Berry, 1917, although the holotype of *P. rufa* has two ridges in the lateral areas of intermediate valves, separated by a shallow sulcus, whereas the Pliocene fossils and *P. velata* have one sharp change in slope in the lateral areas.

These fossils also differ from *P. borealis* Pilsbry, 1893, in lacking the prominent ridges at the posterior margin of the valves; from *P. blainvillii* (Broderip, 1832) in being less wide; from *P. mirabilis* in having more prominent growth lines and major ridges delineating valve areas and in having relatively longer intermediate valves; and from *P. hanselmani* in having more delicate and distinct valve sculpture.

Placiphorella velata occurs from Alaska to central Baja California in depths from 0 to 20 m (Clark, 1994), but it is more commonly found from 5-to-10-m depths on sides and bottoms of rocks (Eernisse et al., 2007). This species has not been previously recorded from rocks older than the Pleistocene.

Placiphorella sp. cf. *P. mirabilis* Clark, 1994
Figure 16 (9–15)

[*Placiphorella mirabilis* Clark, 1994:303, figs. 20–22, 34, 35 (contains more complete synonymy).]

DISTRIBUTION. LACMIP locality 305 (3 head, 14 intermediate, and 5 tail valves; 4 figured intermediate valves, LACMIP 13879–13882, and 1 figured tail valve, LACMIP 13883; all other specimens in unfigured lot, LACMIP 14331).

MATERIAL EXAMINED. Holotype of *Placiphorella mirabilis* (LACM 2703) and paratypes of *P. mirabilis* (LACM 2704–2706).

REMARKS. These fossil valves are much smaller than those identified as *P. velata* (see above), and these valves share with *P. mirabilis* Clark, 1994 intermediate valves with a sharp beak, lateral margins that curve gently anteriorly, and a faint diagonal rib. Open nomenclature is used here, however, because the valves of *P. mirabilis* are similar to those of both *P. rufa* and *P. hanselmani.* The characters that Clark (1994) used to separate *P. mirabilis* from all other species are all nonvalve features.

The fossils differ from *P. borealis* in lacking the prominent ridges at the posterior margin of the valves and from *P. blainvillii* in being less wide. These fossils are difficult to separate absolutely from *P. hanselmani*, but the overall shape of valves, in particular the tail valve, and fine tegmental sculpture of the fossils are more similar to those of *P. mirabilis.* The fossils are also similar to *P. rufa*, although they have less raised lateral areas than is typical for the latter species.

Placiphorella mirabilis occurs between Gaviota, Santa Barbara County, California, and Isla Asuncion, Baja California Sur, Mexico, at depths from 28 to 155 m on rocks (Clark, 1994). *Placiphorella mirabilis* has not been previously reported in the paleontological literature.

Genus *Tonicella* Carpenter, 1873

DISTRIBUTION. This genus occurs in the North Pacific, Arctic, and North Atlantic oceans (Kaas and Van Belle, 1985b). In North America it occurs from Arctic Alaska to Baja California, Mexico (Clark, 1999).

The fossil record of *Tonicella* extends back to the Eocene in Europe (Bielokrys, 1999), the Miocene in Japan (Itoigawa et al. 1981), and the Pleistocene of North America (e.g., Chace and Chace, 1919; Zullo, 1969; Kennedy, 1978; Roth, 1979).

REMARKS. The valves in this genus are characterized by a smooth tegmental surface that is ornamented at most by tiny granules, and with weakly defined lateral areas (Ferreira, 1982).

Tonicella sp. cf. *T. venusta* Clark, 1999
Figure 16 (16–30)

[*Tonicella venusta* Clark, 1999:41, figs. 25–32, 34 (contains more complete synonymies).]

DISTRIBUTION. LACMIP locality 305 (2 head, 55 intermediate, and 3 tail valves; 6 figured intermediate valves, LACMIP 13884–13889, and 2 figured tail valves, 13890–13891; all other specimens in unfigured lot, LACMIP 14332).

REMARKS. Although lacking color, the fossil specimens appear to show some remnant patterns that are indicative of *Tonicella* (Figure 20.20), in particular the *Tonicella lineata* species complex (*sensu* Clark, 1999). The sharp beak, posteriorly curved lateral margins, indistinct tegmental sculpture of faint growth lines, broad W-shaped posterior margin of valves, rounded sutural laminae with broad jugal sinus, anterior mucro and concave postmucronal area of tail valve, and presence of one insertion tooth on each side of the intermediate valve are all consistent with the range in modern *Tonicella venusta.*

Without the color patterns and details of the girdle, it is difficult to classify these fossils with certainty. However, some species can be excluded. For example, the fossils differ from *T. undocaerulea* Sirenko, 1973, and *T. lineata* (Wood, 1815) in having a concave, not straight, postmucronal area of tail valve. The fossils differ from *T. lokii* Clark, 1999, in having more rounded sutural laminae on intermediate valves, and from *T. insignis* (Reeve, 1847) in having a dark band along jugum flanked by pale strips, compared with a lateral wavy pattern in that region of the *T. insignis* intermediate valves. The remnant color pattern (Figure 20.20), although faint, shows a dark triangle at the jugum with apex at valve apex, adjacent white bands, and an apparent splotchy pattern elsewhere. The splotchy pattern is consistent with *T. venusta* and also with the Arctic/circumboreal *T. submarmorea* (von Middendorff, 1847) and *T. marmorea* (Fabricius, 1780), which have been considered to be species complexes by some (e.g., Clark, 1999). The splotchy pattern is inconsistent with the other species of *Tonicella.* It is more difficult to differentiate these fossil intermediate valves from those of *T. marmorea* and *T. submarmorea.* However, the mucro very near


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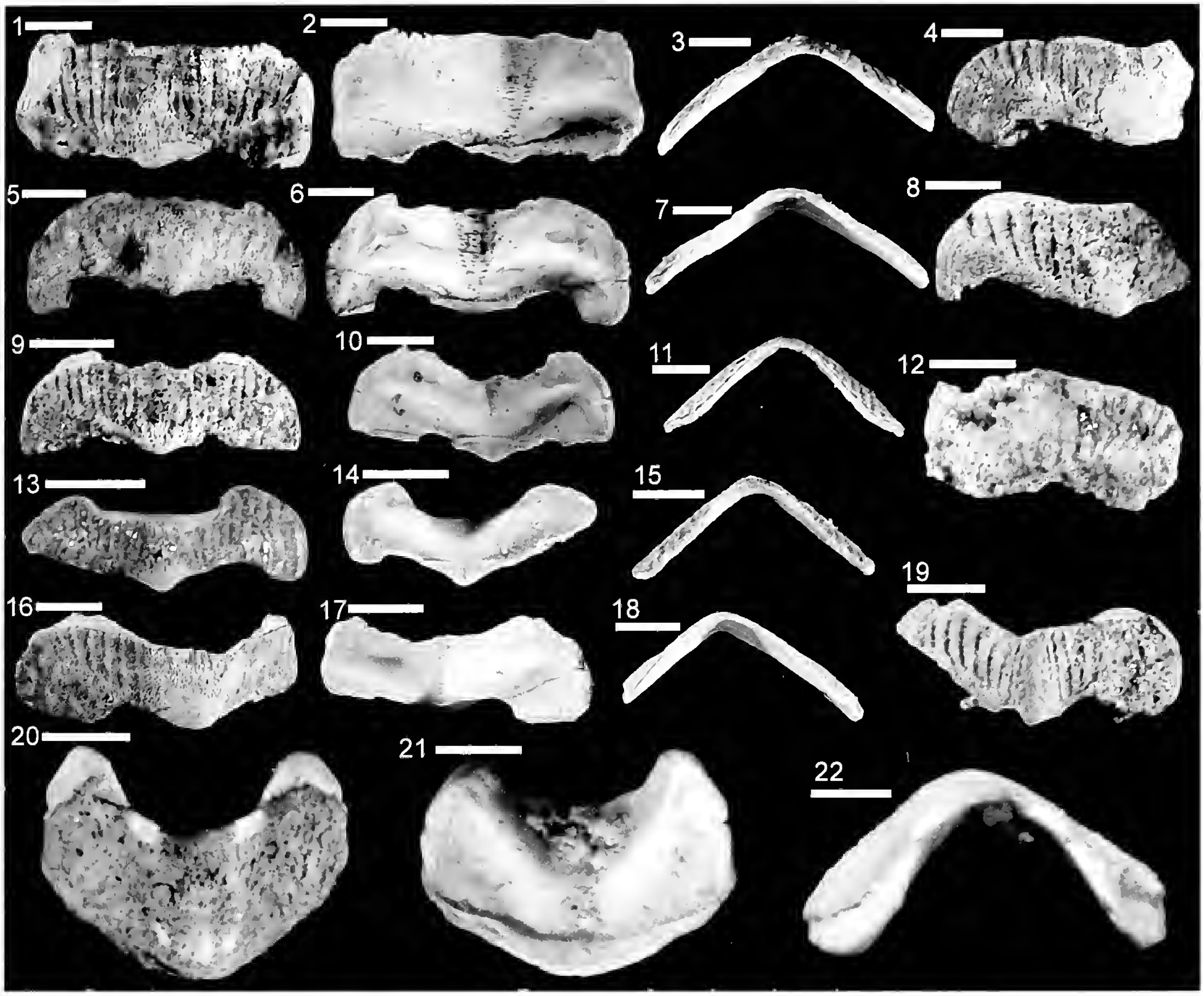

Figure 17 *Dendrochiton* sp. indeterminate (Berry, 1911) and *Nuttallina* sp. indeterminate. 1–15, 19, from LACMIP locality 305; 16–18 from LACMIP locality 16882 (305A); 20–22 from LACMIP locality 16817 (305C). 1–19, *Dendrochiton* sp.: 1–19, intermediate valves. 1–3, LACMIP 14285; 4, LACMIP 14288; 5–7, LACMIP 14286; 8, LACMIP 14289; 9–11, LACMIP 14287; 12, LACMIP 14290; 13–15, LACMIP 14292; 16–18, LACMIP 14293; 19, LACMIP 14291. 20–22, *Nuttallina* sp.: 20–22, intermediate valves. LACMIP 13892. Scale bars=1 mm.

the anterior margin of the tail valve is not seen in *T. submarmorea*. Some modern *T. marmorea* individuals have an anterior mucro, but it is not usually as close to the anterior margin as in these fossils. Of the two well-preserved tail valves in this assemblage, one has nine slits and the other 10, close to, but not the same as in modern *T. venusta* with 11 slits. *Tonicella marmorea* has five to 11 slits (Kaas and Van Belle, 1985b), consistent with our fossils.

Boreochiton Sars, 1878 bears similarities with *Tonicella*, and in fact has been synonymized with the latter by Ferreira (1982) and Kaas and Van Belle (1985b). Sirenko (2000), in contrast, demonstrated that *Boreochiton* is distinct from *Tonicella*. These fossils differ from the three species of *Boreochiton*, *Boreochiton ruber* (Linnaeus, 1767), *B. beringensis* (Jakovleva, 1952), and *B. granulata* (Jakovleva, 1952), in that the tail valve has a shorter premucronal area and the sutural laminae are more rounded and less subquadrate.

Because of the mixture of characters and because some of the distinguishing characters between species of *Tonicella* are missing

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Figure 16 *Placiphorella* spp. and *Tonicella* cf. *venusta* Clark, 1999. 1–6 from LACMIP locality 16817 (305C); 7–30, from LACMIP locality 305. 1–8, *Placiphorella velata* Dall, 1879: head (1–2), intermediate (3–4), and tail (5–8) valves. 1–2, LACMIP 13874; 3, LACMIP 13875; 4, LACMIP 13876; 5–6, LACMIP 13877; 7–8, LACMIP 13878; 9–15, *Placiphorella* sp. cf. *P. mirabilis* Clark, 1994: intermediate (9–14) and tail (15) valves. 9–10, LACMIP 13879; 11–12; LACMIP 13880; 13, LACMIP 13881; 14, LACMIP 13882; 15, LACMIP 13883; 16–30, *Tonicella* cf. *venusta*: intermediate (16–26) and tail (27–30) valves. 16, LACMIP 13884; 17–18, LACMIP 13885; 19, LACMIP 13886; 20–22, LACMIP 13887; 23, LACMIP 13888; 24–26, LACMIP 13889; 27–28, LACMIP 13890; 29–30, LACMIP 13891. Scale bars=1 mm.

in the fossils, we identify them with some uncertainty as *Tonicella* sp. cf. *T. venusta.* These fossils are also very similar to the Arctic/circumboreal *T. marmorea*, but that species does not occur in the eastern Pacific south of the Aleutian Islands, Alaska (Kaas and Van Belle, 1985b). *Tonicella marmorea* is sometimes recognized as a separate species, *T. submarmorea* (von Middendorff, 1847), in the North Pacific. *Tonicella venusta*, however, ranges as far south as Baja California.

Tonicella venusta occurs from south-central Alaska to Isla Cedros, Baja California, Mexico, in depths from the intertidal zone to 140 m (Clark, 1999). It is more common off of central California and farther north, and only four of the 137 reported specimens were collected from Baja California (Clark, 1999). Stebbins and Eernisse (2009) recorded one specimen from 15-m depth off of San Miguel Island (Channel Islands), California, which has a cool-water fauna more typical of central rather than Southern California. *Tonicella marmorea*, the other species that these fossils might represent, is most common in the Arctic and circumboreal regions where it ranges from 0-to-230-m depths (Kaas and Van Belle, 1985b). *Tonicella venusta* was previously unknown from the fossil record.

Genus *Dendrochiton* Berry, 1911

DISTRIBUTION. This genus of small, brightly colored chitons is restricted to the northeastern Pacific, occurring between the latitudes 49°N and 26°N (Ferreira, 1982). The only previously published reference to a fossil representative of this genus is from Vedder and Norris (1963), who listed *Dendrochiton* cf. *D. thamnoporus* from a Pleistocene terrace on San Nicholas Island, California.

REMARKS. Berry (1911) initially proposed this name as a subgenus of *Mopalia*, but later he (Berry, 1917) considered it a full genus. Based on the presence of girdle bristles and eight slits in the head valve, *Dendrochiton* was first considered to be a member of the Mopaliidae (Berry, 1911, 1917; Smith, 1960; Thorpe *in* Keen, 1971). Ferreira (1982) later transferred the genus to the Lepidochitonidae, noting that the radula, tegmentum sculpture, and lack of a sinus in the tail valve of *Dendrochiton* were all more similar to lepidochitonids than to mopaliids. The outline of the intermediate valves of *Dendrochiton* is likewise very similar to that of lepidochitonids such as *Cyanoplax* and *Lepidochitona*. Kaas and Van Belle (1985) seconded the classification of this genus in the Lepidochitonidae, proposing *Dendrochiton* as a subgenus of *Lepidochitona*. More recently, however, Kelly and Eernisse (2008) proposed returning *Dendrochiton* to the Mopaliidae based primarily on high genetic similarity between *Mopalia* and *Dendrochiton*.

Dendrochiton sp. indeterminate
Figure 17 (1–19)

DISTRIBUTION. LACMIP localities 305 (11 intermediate valves; 8 figured intermediate valves, LACMIP 14285–14292; other valves in unfigured lot, LACMIP 14333) and 16862 (305A; 1 intermediate valve; LACMIP 14293).

REMARKS. The fossil intermediate valves are small, relatively short, have posterio-lateral edges curved back, and a central area tegmental sculpture of thick but flat faintly curving longitudinal ridges. All of these characters are consistent with *Dendrochiton*.

The central area tegmental sculpture is the diagnostic character allowing assignment of these valves to *Dendrochiton*, consisting of more or less broad, flat-topped, somewhat sinuous ridges separated laterally from each other by deep grooves. This tegmental sculpture indicates that these valves are not from *Dendrochiton flectens*, which has smooth sculpture, but the characters preserved in these fossils do not allow distinguishing between the other species of *Dendrochiton*. *Dendrochiton thamnoporus* (Berry, 1911), *D. lirulatus* Berry, 1963, *D. semilirulatus* Berry, 1927, and *D. gothicus* (Carpenter, 1864) all are small and have longitudinal ridges in the central area of intermediate valves (see Ferreira, 1982). Similarly, the distinguishing characters between *D. thamnoporus* and *D. semiliratus* listed by Stebbins and Eernisse (2009) in their identification key all relate to girdle ornament and tail valve shape, features that do not occur in these fossils.

Family Lepidochitonidae Iredale, 1914
Genus *Nuttallina* Dall, 1871

DISTRIBUTION. This genus occurs only in western North America, mostly restricted to the region from central California south to the Gulf of California. Ferreira (1982) recognized only two of the nominal species in this genus: *Nuttallina californica* (Reeve, 1847) and *N. crossota* (Berry, 1956). Eernisse et al. (2007) and others have continued to recognize the more southern *N. fluxa* (Reeve, 1847), which has broader valves, is genetically distinct (Kelly and Eernisse, 2007), and is by far the most common chiton species in Southern California. Eernisse et al. (2007) also recognized a fourth distinct species first documented in a Ph.D. dissertation but not yet formally described, referred to as "*Nuttallina* sp. of Piper, 1984." The valves of the latter are very similar to *N. californica*, but this species is generally more southern in its distribution, although all three species are known from Southern California and northern Baja California.

This genus is widely known from Pleistocene marine terrace deposits of Southern California (e.g., Berry, 1922; Chace, 1966; Marincovich, 1976; Valentine, 1980), but this is the first Pliocene record of *Nuttallina*.

REMARKS. Valves of *Nuttallina* are distinct and characterized by a granulose tegmentum (when not eroded), well-developed sutural laminae, spongy eaves, and elongate form with insertion teeth directed anteriorly especially in the tail valve, (Ferreira, 1982). In addition, *Nuttallina* valves have a relatively extensive apical area on the ventral surface.

Nuttallina sp. indeterminate
Figure 17 (20–22)

DISTRIBUTION. LACMIP locality 16817 (305C; one well-preserved intermediate valve; LACMIP 13892).

DESCRIPTION. Intermediate valve triangular in overall shape, with prominent rounded sutural laminae and an extensive jugal sinus. Valve areas difficult to discern, but do not appear to be well delineated. Anterio-lateral regions of valve rounded. Broad emargination in anterior margin. Apical area relatively large, 1 slit per side, jugal area about 90°.

REMARKS. This valve has all the trademark features of *Nuttallina*, but with only one shell plate known it is difficult to identify the species. *Nuttallina* occurs exclusively in the intertidal or shallowest subtidal zone (Eernisse et al., 2007), whereas the fossil beds appear to have formed in deeper water (~25 m), perhaps explaining the paucity of *Nuttallina* therein.

DISCUSSION

DIVERSIFICATION OF CHITONS ON THE PACIFIC COAST OF NORTH AMERICA

Chitons are abundant and diverse on the Pacific Coast of North America, a pattern that Jakovleva (1952) noted for the Oregonian Province and one that prompted E.M. Chace (1940)

Table 2 List of chitons from the San Diego Formation, LACMIP localities 305, 16862 (305A), and 16817 (305C), and biological data on modern representatives of those species. Key: AK=Alaska; BC=Baja California, Mexico; CA=California; CAN=Canada; MX=Mexico.

Species	LACMIP Localities	Depth (m)	Geographic range	Sources
Leptochiton nexus	305, A, C	0–140 (median 50)	AK to Punta Abrejos, BC	Ferreira 1979a; Stebbins and Eernisse, 2009
Leptochiton rugatus	305	0–458 (mostly 8–12)	AK to Bahía Magdalena, BC	Ferreira 1979a; Eernisse et al., 2007; Stebbins and Eernisse, 2009
Oldroydia percrassa	305, A, C	0–730 (median 40)	Monterey, CA, to Sea of Cortez, MX	Ferreira 1979a; Stebbins and Eernisse, 2009
Callistochiton palmulatus	305, A, C	0–80; common shallow subtidal	Mendocino, CA, to Punta San Pablo, BC	Ferreira 1979b; Eernisse et al., 2007; Stebbins and Eernisse, 2009
Callistochiton sphaerae n. sp.	305, A, C	N/A		
Lepidozona sp. cf. *L. rothi*	305	55–110	Clarion Island, MX, and Isla Cocos	Ferreira 1983
Lepidozona sp. cf. *L. radians*	305, C	Common 5–13, occurs deeper	Southeastern AK to northern BC	Eernisse et al., 2007; Stebbins and Eernisse, 2009
Lepidozona pectinulata	305, C	0–20	CA to southern BC (24°N to 35°N)	Ferreira 1978
Lepidozona mertensii	305, A, C	0–100 (most common to ~8)	AK to BC (30°N to 58°N)	Ferreira 1978; Eernisse et al., 2007; Stebbins and Eernisse, 2009
Lepidozona kanakoffi n. sp.	305, C	N/A		
Stenoplax sp. cf. *S. heathiana*	305, C	Intertidal	Fort Bragg, CA, to Punto Santo Tomas, BC	Kaas and Van Belle 1987
Stenoplax fallax	305, A, C	Intertidal to shallow subtidal	Vancouver Island, CAN, to Bahía Todos Santos, BC	Kaas and Van Belle 1987
Stenoplax circumsenta	305, C	0–72	Los Angeles, CA, to Sea of Cortez, MX	Kaas and Van Belle 1987
Amicula solivaga n. sp.	305, A, C	N/A		
Mopalia sinuata	305, A	0–200 (8+ in southern CA)	Cook Inlet, AK, to Avila Beach, central CA	Kaas & Van Belle 1994; Eernisse et al., 2007
Mopalia sp. cf. *M. swanii*	305, A, C	Intertidal	Aleutian Islands, AK, to Malibu, CA	Kaas and Van Belle 1994
Mopalia sp. indeterminate	305	N/A		
Placiphorella velata	A, C	0–20	AK to Central BC	Clark 1994
Placiphorella sp. cf. *P. mirabilis*	305	28–155	Gaviota, CA, to Isla Asuncion, BC	Clark 1994; Stebbins and Eernisse, 2009
Tonicella sp. cf. *T. venusta*	305	0–140	South-central AK to Isla Cedros, BC	Clark 1999; Stebbins and Eernisse, 2009
Dendrochiton sp. indeterminate	305, A	N/A		
Nuttallina sp. indeterminate	C	N/A		

to call the Pacific Coast of North America "the metropolis of chitons" with more than 150 of the world's ~950 known species occurring there. Thorpe (1962) estimated that chiton diversity along the California coast is second only to that of southern Australia. However, the early to middle Cenozoic history of Pacific Coast Polyplacophora is largely unknown. In part the poor fossil record of chitons may be due to the low preservation potential of chiton valves (Puchalski and Johnson, 2009) and because chiton fossils are often fragmentary and rare in sedimentary deposits and so are often overlooked by collectors and researchers (Puchalski et al., 2008). Even chitons in calm-water aquaria rapidly disarticulate after death, and sometimes their valves break just before then (M.J.V., personal observation). But oddly, known chiton diversity was far greater in the Paleozoic than in the Mesozoic (Smith, 1973) or earliest Cenozoic (Puchalski et al., 2008). Perhaps this is because chitons suffered major mass extinctions at the Permo-Triassic and Cretaceous-Tertiary boundaries. Nevertheless, our knowledge of global chiton diversity is greatest for the late Cenozoic (Vendrasco, 1999), based mostly on the Holocene and Pleistocene records. A great proportion of this modern chiton diversity is on the Pacific Coast of North America.

The collective fauna described here reveals that chitons were relatively diverse on the Pacific Coast by the Pliocene. This diversity is in stark contrast to that of the Miocene of western North America, which has so far yielded very few chitons. Only a few chitons are known from the Eocene of Southern California, but as yet these remain unidentified (G. Kennedy, personal communication, 2010). A possible explanation for the apparent increase in chiton diversity there is that chitons diversified as food for them increased. Beginning in the middle Miocene, seawater temperatures in the eastern Pacific began to drop. This trend was interrupted by a Pliocene warm period from about 4.6 to 3 Ma, and then the cool temperatures returned (Lyle et al., 2008). The cool middle Miocene has been inferred as the time when fleshy algae like kelp first became abundant along the coast of western North America (Estes and Steinberg, 1988, 1989), increasing the primary productivity of the region and providing more food for grazing mollusks (Estes et al., 2005). In addition, upwelling is thought to have begun along midlatitude west coasts during the late middle Miocene (15 to 12 million years ago), perhaps due to increased polar cold deep-water production at that time, which strengthened shore-parallel winds at midlatitudes that produced the upwelling (Jacobs et al., 2004). Increased upwelling is correlated with higher primary productivity and a more diverse rocky shore invertebrate fauna due to more food for filter feeders and organic matter for detritivores (Jacobs et al., 2004). Grazers such as chitons would also benefit from the increased organic matter and primary producers on the rocks. Overall, higher productivity can correlate with more diverse marine ecosystems (Vermeij, 1989; Leigh and Vermeij, 2002), although this is not always the case (e.g., coral reefs in the tropics that have high diversity in a low productivity zone, and the Arctic Ocean, which has high productivity but apparently low diversity). This increase in productivity was followed by the development of a heterogeneous coastline (late Miocene) with abundant rocky shores (Pliocene to Pleistocene) (Jacobs et al., 2004), all factors that should have increased the diversification rate of chitons and other organisms in the rocky intertidal zone. Along a similar line of reasoning, Tsuchi (2002) documented an increase in the rate of evolution of mollusks on both sides of the Pacific that correlated with a stepwise cooling that began in the middle Pliocene. So perhaps the pattern inferred from the chiton fossil record is in large part real—the spread of upwelling and fleshy algae along the Pacific Coast beginning in the late Miocene combined with the increased heterogeneity of the coastline from tectonic activity in the Pliocene and Pleistocene (Jacobs et al., 2004) may have promoted increases in chiton abundance and diversity throughout the region during the Neogene.

The San Diego Formation provides the earliest known detailed view of the "modern" chiton fauna in the temperate eastern Pacific Ocean. This assemblage records the first appearance of many genera and species that are now common along the Pacific Coast of North America (Figure 3; Table 2). One common Pacific Coast chiton genus is *Mopalia*, and current information indicates it diversified in the North Pacific relatively recently. Kelly and Eernisse (2008) used molecular data to infer a middle Miocene (~16 Ma) spread across the North Pacific for *Mopalia*, and noted many other rocky-shore taxa in the Pacific probably spread across the North Pacific at the same time. They inferred that *Mopalia* experienced a major diversification in the northeastern Pacific beginning about 5 Ma (Kelly and Eernisse, 2008). This contrasts with the known range of *Mopalia* from the fossil record (back to ~3.2 Ma; Figure 3).

Another genus that likely diversified relatively recently in the North Pacific is *Lepidozona*, which is mostly restricted to that region. The greatest diversity of *Lepidozona* is in the northeastern Pacific (Stebbins and Eernisse, 2009), with the oldest fossils apparently being from the Miocene of Japan (Itoigawa and Nishimoto, 1975) and one valve from the latest Eocene or earliest Oligocene of Washington (Dell'Angelo et al., 2011). *Lepidozona* is abundant and relatively diverse in the San Diego Formation, providing evidence that the genus also diversified in the North Pacific since the Miocene.

The fact that early to middle Cenozoic chitons are largely missing from the fossil record of western North America is surprising given the abundance of marine nearshore sedimentary rocks in the region from that time. One possible explanation for this pattern is that the rocky intertidal environments, where chitons are abundant, are erosional environments that have been less likely to be preserved (Johnson, 2006). In fact, the excellent fossil record of the rocky shore on the Pacific Coast over the past million years or so is mainly due to tectonic uplift and emergence of marine terraces (Jacobs et al., 2004). However, chiton valves are common in bioclastic subtidal sediment today (cf. LACM collections), and the combined evidence indicates that the San Diego Formation sediments were deposited in a moderately deep subtidal environment. The San Diego Formation collections show that a diverse assemblage and abundance of chitons can be preserved seaward from rocky shore environments, in predominantly depositional rather than erosional situations, further highlighting the discrepancy between the lack of early–mid-Cenozoic chitons and their striking abundance in the Border beds of the San Diego Formation.

CHITON MIGRATION

The chiton fauna from the San Diego Formation extends the stratigraphic range of many chiton species along the Pacific Coast into the middle Pliocene (Figure 3). The data can be used to help assess hypotheses about the origin and timing of migration of some chiton species. Some of the eastern Pacific chiton genera have a slightly older fossil record in the western Pacific (e.g., to the Miocene for *Mopalia* and *Placiphorella*). The northeastern Asian (e.g., Hokkaido, Japan) and western North American chiton faunas share some genera in common (Jakovleva, 1952), including *Mopalia*, *Lepidozona*, *Tonicella*, *Placiphorella*, *Amicula*, *Schizoplax*, *Cryptochiton*, *Leptochiton*, *Tripoplax*, and *Boreochiton*. This similarity reflects the overall pattern for mollusks on both sides of the northern Pacific (Keen, 1941).

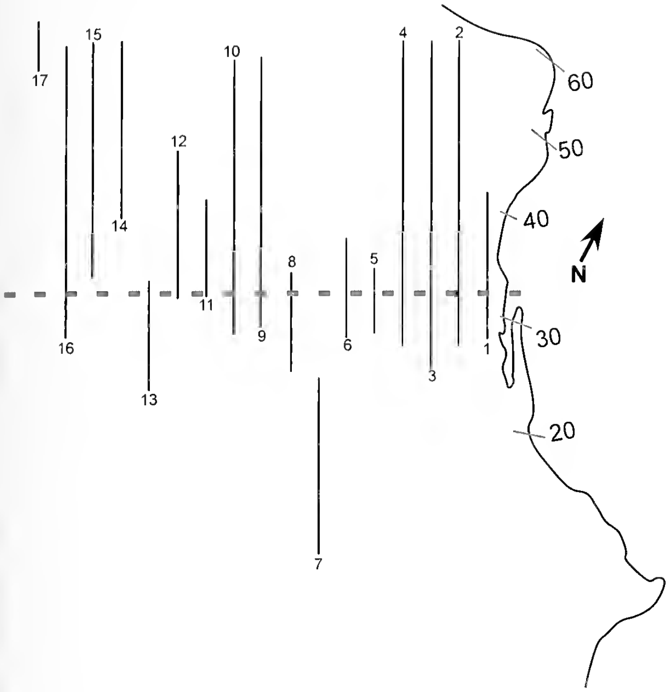

Figure 18 Modern geographic ranges of chitons from the Border localities—LACMIP localities 305, 16862 (305A), and 16817 (305C)—of the San Diego Formation. Dashed line shows current latitude of the San Diego Formation Border beds. Key: 1, *Callistochiton palmulatus*; 2, *Leptochiton nexus*; 3, *L. rugatus*; 4, *Placiphorella velata*; 5, *P.mirabilis* (San Diego Formation representative: *Placiphorella* sp. cf. *P. mirabilis*); 6, *Oldroydia percrassa*; 7, *Lepidozona rothi* (as *Lepidozona* sp. cf. *L. rothi*); 8, *L. pectinulata*; 9, *L. mertensii*; 10, *L. radians* (as *Lepidozona* sp. cf. *L. radians*); 11, *Stenoplax heathiana* (as *Stenoplax* sp. cf. *S. heathiana*); 12, *S. fallax*; 13, *S. circumsenta*; 14, *Mopalia sinuata*; 15, *M. swanii* (as *Mopalia* sp. cf. *M. swanii*); 16, *Tonicella venusta* (as *Tonicella* sp. cf. *T. venusta*); 17, *Amicula* (as *Amicula solivaga* n. sp.).

Amano (2005) compiled evidence from the fossil record for Cenozoic molluscan migrations through or to the cool North Pacific, documenting apparent cases of migration westward (*Penitella*, *Platyodon*, *Panomya*, *Littorina*, *Liracassis*, *Nucella*, *Ceratostoma*, *Macoma*, *Kaneharaia*, and *Lirabuccinum*), eastward (*Mya*, *Neptunea*, *Mizuhopecten*, Turritelloidea, and Buccinoidea), and from the Arctic to the North Pacific (e.g., *Cyrtodaria*). Vermeij (2001) previously suggested that many of these eastward or westward migrating mollusks originated during the late Eocene to early Oligocene cooling, and Squires (2003) documented an influx of cool-water taxa along the coast of Washington to California during this time period. Amano (2005) classified North Pacific mollusks into subgroups and inferred that (1) most of the taxa that appear to have originated in the northwestern Pacific migrated eastward (21 of 25 genera or subgenera), and of the migrating taxa, eight genera first appear in the fossil record during the late Eocene in Asia and most migrated during the Oligocene or Miocene and (2) most of the taxa thought to have originated in the northeastern Pacific migrated westward (22 of 26 genera or subgenera), mostly originating during the late Eocene or early Oligocene and a vast majority migrating during the early or early middle Miocene.

Among chitons that exclusively or predominantly occur in the North Pacific, some genera only have a fossil record in the northeastern Pacific: *Amicula* (from Pliocene—this paper; modern distribution trans-Pacific); *Cryptochiton* (from Pliocene—Arnold, 1903; Berry, 1922; modern distribution trans-Pacific); *Nuttallina* (from Pliocene—this paper; modern distribution northeastern Pacific only); *Cyanoplax* (from Pleistocene—Berry, 1922; modern distribution northeastern Pacific only); *Katharina* (from Pliocene—Berry, 1922; modern distribution northeastern Pacific only); *Dendrochiton* (from Pliocene—this paper; modern distribution northeastern Pacific only); and *Oldroydia* (from Pliocene—this paper; modern distribution northeastearn Pacific only). Other North Pacific chitons have a trans-Pacific fossil record and modern distribution, but with earlier records in the western Pacific: *Mopalia* (from Miocene—Itiogawa and Nishimoto, 1975); and *Placiphorella* (from Miocene—Itiogawa and Nishimoto, 1975).

The very high diversity of chitons endemic to the North Pacific indicates diversification in the region. A large proportion of species of many chiton genera occur in the northeastern Pacific and some chiton genera have a slightly earlier fossil record in the western Pacific than in the eastern Pacific. If the fossil record is taken at face value, these observations indicate an eastward or southeastward migration for genera such as *Mopalia* and *Placiphorella* prior to their apparent diversification along the Pacific Coast of North America. Sirenko and Clark (2008) inferred a similar migration pattern for *Deshayesiella*.

A marine connection has existed between the Arctic and Pacific basins at different times since the late Miocene (Marincovich and Gladenkov, 1999), and hence it is possible that some eastern Pacific chiton genera originated in the Arctic and spread to the eastern and western Pacific. However, this migration path could not have been common, as many Pacific chiton genera are known from the earlier Miocene of Japan before the Arctic opened to the Pacific. As another alternative, chitons may have migrated northward along the Pacific Coast of North America from tropical regions during these time intervals, but migrations of mollusks northward during this time appear to have been much less common than southward migrations (Roy et al., 1995). Nevertheless, some chiton genera that occur off the San Diego coast today, such as *Stenoplax*, *Callistochiton*, *Acanthochitona*, and *Chaetopleura*, do not occur north of California and appear to have greater affinities with the warm-tropical Panamic rather than the cool-temperate Oregonian chiton faunas.

Patchy local upwelling localities extend to across the equator along the eastern Pacific margin, allowing for a potential interchange of temperate faunas on either side of the equator (Lindberg, 1991). This potential, however, does not seem to have impacted chiton evolution much, as the chiton fauna of the northeastern Pacific is quite different from that of the southeastern Pacific, with the exception of some quite deep-dwelling species in a few genera (e.g., *Placiphorella*, *Tripoplax*, *Leptochiton*).

PALEOCLIMATE

The Border localities have a rich fauna of at least 264 molluscan species (102 bivalve, 136 gastropod, 22 chiton, and four scaphopod species; Appendix 2). Appendix 2 is mainly compiled from collections at LACMIP, and in part from the unpublished manuscript of Hertlein and Grant and from field observations (M.J.V., C.Z.F., D.J.E., Scott Rugh). Modern ecological data for these mollusks (e.g., Morris, 1966; Keen, 1971; Rice, 1973; Abbott, 1974; Keen and Coan, 1975; McLean, 1978; Bernard, 1983; McLean and Gosliner, 1996; Coan et al., 2000) indicate that most of the fossil species currently live off the San Diego coast, although a few are extralimital northern or extralimital southern in their distribution (Figures 18–19). Extralimital northern species include the bivalves *Chlamys hastata* (Sowerby,

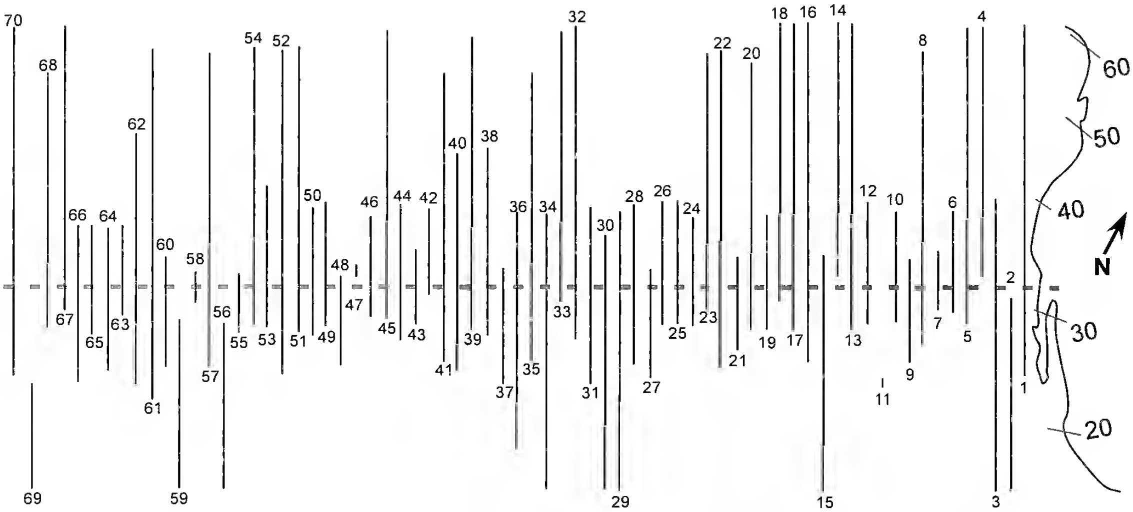

Figure 19 Modern geographic ranges of other (nonchiton) species that are abundant from the Border localities—LACMIP localities 305, 16862 (305A), and 16817 (305C)—of the San Diego Formation. Dashed line shows current latitude of the San Diego Formation Border beds. Includes 1–17, bivalves; 18–64, gastropods; 65–66, scaphopods; 67–68, corals; 69, echinoderm; 70, crustacean. 1, *Acila castrensis*; 2, *Barbatia illota*; 3, *Chama arcana*; 4, *Chlamys hastata*; 5, *Cyclocardia ventricosa*; 6, *Ensis myrae*; 7, *Gari fucata*; 8, *Glycymeris septentrionalis*; 9, *Here excavata*; 10, *Lucinisca nuttalli*; 11, *Miltha xantusi*; 12, *Nuculana taphria*; 13, *Nutricola tantilla*; 14, *Panopea abrupta*; 15, *Parvilucina approximata*; 16, *Pododesmus macrochisma*; 17, *Thracia trapezoides*; 18, *Acmaea mitra*; 19, *Alvania oldroydae*; 20, *Amphissa versicolor*; 21, *Barbarofusus barbarensis*; 22, *Callianax biplicata*; 23, *Calliostoma annulatum*; 24, *C. gemmulatum*; 25, *C. supragranosum*; 26, *Cancellaria cooperi*; 27, *Cerithiopsis pedroana*; 28, *Conus californicus*; 29, *Crepidula aculeata*; 30, *C. onyx*; 31, *Crossata californica*; 32, *Cylichnia attonsa*; 33, *Diadora arnoldi*; 34, *Epitonium minuticostata*; 35, *Epitonium sawinae*; 36, *Eulima raymondi*; 37, *Glossaulax reclusianus*; 38, *Haliotis rufescens* (as *Haliotis* sp. cf. *H. rufescens*); 39, *Halistylus pupoides*; 40, *Hipponix tumens*; 41, *Hirtoscala tinctum*; 42, *Homalopoma radiatum*; 43, *Kelletia kelletii*; 44, *Lacuna unifasciata*; 45, *Ligacalliostoma canaliculatum*; 46, *Lirobittium rugatum*; 47, *Lirularia optabilis*; 48, *Megastraea turbanica*; 49, *Megasurcula carpenteriana* (as *Megasurcula* sp. cf. *M. carpenteriana*); 50, *Megathura crenulata*; 51, *Micranellum crebricinctum*; 52, *Alia* (*Mitrella*) *tuberosa*; 53, *Nassarius perpinguis*; 54, *Opalia montereyensis*; 55, *Ophiodermella inermis*; 56, *Parviturbo stearnsii* (as *Parviturbo* sp. cf. *P. stearnsii*); 57, *Pomaulax gibberosa*; 58, *Pseudomelatoma grippi*; 59, *Scalina brunneopicta*; 60, *Shaskyus festivus*; 61, *Solariella peramabilis*; 62, *Tricolia pulloides* (as *Tricolia* sp. cf. *T. pulloides*); 63, *Triphora pedroana*; 64, *Turritella cooperi*; 65, *Cadulus fusiformis*; 66, *Dentalium neohexagonum*; 67, *Balanophyllia elegans*; 68, *Paracyathus stearnsii*; 69, *Eucidaris thouarsii* (as *Eucidaris* sp. cf. *E. thouarsii*); 70, *Cancer productus*.

1842), *Clinocardium nuttallii* (Conrad, 1837), *Dermatomya tenuiconcha* (Dall, 1913), *Ensis myrae* Berry, 1953a, *Miodontiscus prolongatus* (Carpenter, 1864), *Modiolus sacculifer* (Berry, 1953b), *Panopea abrupta* (Conrad, 1849), *Tellina idae* Dall, 1891, *Thyasira flexuosa* (Montagu, 1803), and the gastropod *Haliotis walallensis* Stearns, 1899. In addition, some species occur in the San Diego area and perhaps a bit southward but are much more common to the north, such as *Ligacalliostoma canaliculatum* (Lightfoot, 1786) (McLean and Gosliner, 1996). Southern extralimital species include the bivalves *Barbatia illota* (Sowerby, 1833), *Cyclopecten pernomus* (Hertlein, 1935), *Dosinia ponderosa* (Gray, 1838), *Macoma medioamericana* Olsson, 1942, *Miltha xantusi* (Dall, 1905), and the gastropods *Acirsa cerralvoensis* DuShane, 1970, *Architectonica nobilis* Röding, 1798, *Megastraea turbanica* (Dall, 1910), and *Scalina brunneopicta* (Dall, 1908). In addition, living *Diplodonta sericata* (Reeve, 1850) occur north to Santa Cruz Island, California, but Coan et al. (2000) indicate that it is permanently established only as far north as Laguna San Ignacio on the Pacific coast of central Baja California.

Chitons may be particularly useful environmental indicators, as their typically fragile, aragonitic shell plates do not withstand considerable transport or current reworking. Moreover, most of the recovered chiton plates are remarkably well preserved, without much abrasion, corrosion, or bioerosion, all indicating rapid burial near where they lived. Although many of the chiton species from the Border localities currently range along much of the coastline from southeastern Alaska to northern Baja California, the following species indicate a cool-water environment: *Mopalia swanii*, *M. sinuata*, and *Amicula*. These three taxa currently range only north of San Diego; in contrast, by far the most commonly dredged species of *Mopalia* off of San Pedro (~120 km north of San Diego) is *M. imporcata*. Moreover, some common chitons from the Border locality are more similar to those that today dominate the central California coast (e.g., *Stenoplax fallax*, *S. heathiana*, and *Tonicella venusta*). On the other hand, the collections also appear to contain the distant extralimital southern *Lepidozona rothi* (as *Lepidozona* cf. *rothi*), as well as *Stenoplax circumsenta* (as *Stenoplax* cf. *circumsenta*), a species more common south of San Diego, but these fossils are only provisionally identified as such. Overall, however, the chiton fauna is most similar to that presently found off the San Diego coast today. This similarity is also reflected in a recent faunal survey of chitons from 30-to-200-m depths off San Diego (Stebbins and Eernisse, 2009).

Microfossils from the Border localities likewise yield evidence of a mixing of cool- and warm-water taxa, but dominance of taxa that today occur off the San Diego coast. Mandel (1973) suggested a temperature range of 22°C to 26°C (subtropical) based on his study of more than 30 planktonic and benthonic foraminiferans from localities he referred to as 305A and 305C. This temperature range is warmer than sea surface temperatures at the Imperial Beach pier (1 km north of the Border localities), that ranged between 12°C and 24°C during the period from April 2006 to January 2009 (Scripps Institution of Oceanography [SIO]); the maximum temperature at 5-m depth during this same period was only ~20°C (SIO). However, Mandel's (1973) faunal list indicates a mixed warm- and cool-water foraminiferal fauna and it is unclear if he collected the same beds as Kanakoff.

We (M.J.V. and C.Z.F.) examined a collection of foraminifers at LACMIP from LACMIP locality 305 and likewise found some warm-water indicators such as one specimen of *Globorotalia tumida* (Brady, 1877) (Figure 2.10), a typically warm-water species that can be found in waters between ~17°C to 29°C but occurs at highest abundances at ~27°C (Bé and Tolderlund, 1971; Hillbrecht, 1996) and abundant *Globigerinoides ruber* (d'Orbigny, 1839) (Figure 2.9), a species that is commonly found at temperatures between 23°C and 27°C in the Sargasso Sea off Bermuda (Bé, 1960), and only occurs off Southern California during El Niño events (J. Kennett, personal communication to M.J.V., 2006). In addition, Bé (1960) found *Orbulina universa* d'Orbigny, 1839, another abundant planktonic foraminiferan at LACMIP locality 305, to be most abundant in the Caribbean Sargasso Sea during the warmer summer and fall months and preferring water temperatures between 23°C and 27°C. In contrast to the warm-water planktonic foraminiferans, we confirmed the presence of *Globigerina bulloides* d'Orbigny, 1826 (Figure 2.11) from LACMIP locality 305, and this species is very common today in cool, productive waters (Bé and Tolderlund, 1971; Hillbrecht, 1996) off California.

Unlike the planktonic foraminiferal assemblage, the benthonic foraminiferal assemblages from the LACMIP lack warm-water indicators, and instead indicate temperatures similar to those typical of the San Diego coast today. The overall benthonic foraminiferal fauna best matches the *Hanzawaia nitidula* association of Murray (1991). Four species in this assemblage also occur in the San Diego Formation: *Hanzawaia nitidula* (Bandy, 1953) (Figure 2.12); *Quinqueloculina lamarckiana* d'Orbigny, 1839 (Figure 2.13); *Cibicides fletcheri* Galloway and Wissler, 1927; and *Planulina ornata* (d'Orbigny, 1839). These species prefer sand and are characteristic of some regions between Nicaragua and Panama, with a temperature tolerance between 10°C and 30°C. However, there are also similarities with the *Cibicides fletcheri* fauna of Murray (1991) that prefers a fine-grained sand substrate, which is the primary lithology of the Border beds. Three species, *Cibicides fletcheri*, *Rotorbinella campanulata* (Galloway and Wissler, 1927), and *Cassidulina tortuosa* Cushman and Hughes, 1925, occur in the San Diego Formation and their thermal tolerances are between 13°C and 20°C (Murray, 1991). Although Mandel (1973) and Ingle (1967) suggested that *Hanzawaia nitidula* indicates subtropical temperatures, it nevertheless lives in modern times along the San Diego coast (Uchio, 1960).

Page Valentine (1976) identified more than 50 ostracod species from LACMIP collections associated with locality 305. Using his data on temperature tolerances (Valentine, 1976), all but one of the ostracods in the Border beds have an overlapping temperature tolerance of 13°C to 20°C. The one slightly anomalous record, *Ambolastracon* sp. O, has an inferred temperature tolerance of 13°C to 18°C. This temperature range falls within sea surface temperatures at the Imperial Beach pier (see above).

Although the faunas from the Border localities are dominantly warm-temperate in aspect, and most of the abundant taxa from these beds currently reside in the Californian biogeographic province, there are nevertheless a few cases of both extralimital southern and extralimital northern species. Such a faunal mixture is relatively common in Pliocene (e.g., Groves, 1991) and Pleistocene deposits in western North America (Valentine, 1955; Emerson, 1956; Zinsmeister, 1974; Roy et al., 1995). However, the greatest number of Pleistocene assemblages previously thought to contain both warm and cool species were subsequently shown to be from two different terrace levels and thus to have different ages (Muhs et al., 2002; G. Kennedy, personal communication, 2010).

An understanding of global, regional, and local climate trends may help explain faunal mixing. During the early Miocene the eastern Pacific was overall warmer than today, whereas the middle Miocene through Pleistocene was a time of oscillating sea levels and oceanic temperatures, but with an overall cooling trend (Hall, 2002). Tropical and subtropical mollusks were common in California during the early and middle Miocene (Marincovich, 1984)—even the upper Miocene Castaic Formation of Los Angeles County had a distinct warm-water fauna (Stanton, 1966). A subsequent, gradual cooling trend appears to have begun sometime in the Pliocene between about 4.6 Ma (Leroy et al., 1999) and 4.15 Ma (Tiedemann et al., 1994), culminating in the onset of Northern Hemisphere glaciation at 2.7 Ma (Lyle et al., 2008). This gradual cooling trend contained dramatic fluctuations: for example, a warming trend from an anomalously cold period appears to have occurred from about 3.3 to 3.15 Ma (Leroy et al., 1999; Ravelo et al, 2004). This mid-Pliocene warming event has been documented in both the Atlantic and Pacific oceans and so appears to be a global occurrence (Dowsett et al., 1996). This warming event was followed by a progressive cooling leading to late Pliocene/early Pleistocene glaciations (Tiedemann et al., 1994; Leroy et al., 1999; Ravelo et al., 2004). By the end of the Pliocene, extralimital southern mollusks had almost entirely disappeared from California (Addicott, 1970).

Three hypotheses seem most likely to explain the mixture of northern and southern extralimital taxa in the Border localities: (1) the Border beds were deposited during the mid-Pliocene warm period in an area with strong upwelling (Powell et al., 2009); (2) these beds were deposited at the mouth of a relatively warm bay in cool surrounding waters (*sensu* Addicott, 1970), the latter possibly due to upwelling; and/or (3) the beds are a mixed assemblage from slightly different time periods while climate fluctuated. It is also possible that the Border beds were deposited during the transitional period between the warming event and the beginning of progressive cooling (~3.15 Ma), consistent with the age of the formation based on foraminifera and mollusks.

Upwelling, which is well developed along the marginal eastern Pacific, can transport cool, deep waters from depth into relatively shallower, warm surface waters. For example, extralimital northern species can occur far south of their normal range in areas of upwelling on the south sides of rocky points along much of Baja California, Mexico (Hubbs, 1948, 1960; Emerson, 1956; Stepien et al., 1991). Powell et al. (2009) suggested that the presence of *Architectonica*, *Miltha xantusi* (Dall, 1905), and other extralimital southern taxa at the Border localities indicated deposition during the mid-Pliocene warming event, and that the presence of cool-water species there were due to upwelling. However, the fossil assemblages from the Border beds are not dominated by warm-water taxa.

Addicott (1970) noted faunal mixing in Pliocene deposits in California and suggested the warm-water components likely occurred there because of warm water maintained in the shallow-water embayments that occurred in the present-day San Joaquin Valley, California, with the relatively cooler taxa occurring due to overall climate cooling in the later Pliocene. A similar shallow-water bay characterized deposition of the San Diego Formation (Hall, 2002) and many of the abundant taxa from the Border localities are most common in bay environments, including *Glossaulax reclusianus* (Deshayes, 1839) (see McLean, 1978). Squires et al. (2006) favored this scenario to explain why extralimital southern taxa were present in the Pliocene Pico Formation of Los Angeles County.

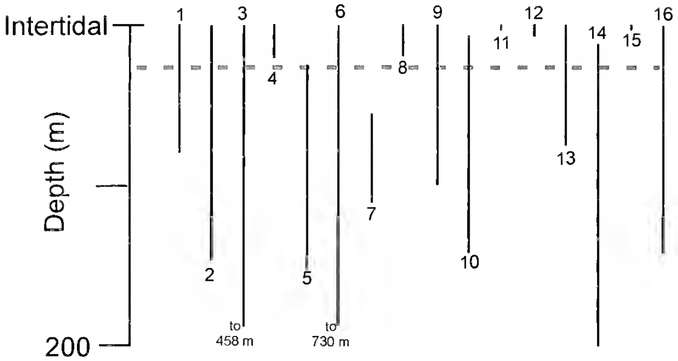

Figure 20 Known depth ranges for modern chiton species with representatives in the San Diego Formation. Dashed line indicates inferred depth of deposition (25 m, based on analysis of the total fauna). Key as in Figure 18.

The oxygen isotope record provides clear evidence that there were many smaller-scale climate shifts related to Milankovitch cycles throughout the Pliocene (Gradstein et al., 2004), and thus it is possible that such shorter time-scale variation in climate could have contributed to the mixed fauna. Similarly, some occurrences of mixing of warm- and cool-water molluscan faunas from Pleistocene marine terraces has been explained by fossils in those collections having slightly different ages, from both cool and warm time periods (Muhs et al. 2002).

Perhaps there was a combination of factors. For example, Ramp et al. (2005) documented the periodic spread of upwelled waters across the mouth of Monterey Bay, California, a geographic feature similar in slope to that of the Pliocene San Diego embayment. Therefore it is possible that the Border beds were deposited in the mouth of a warm shallow bay with upwelling nearby. There are many possible explanations for the presence of these anomalous taxa, and future research may help determine which is most likely. In any case, the climate was similar to what occurs today off the San Diego coast.

PALEOBATHYMETRY

Overall, the paleodepth is clearly neritic, or sublittoral, as defined by Hedgpeth (1957) and Valentine (1961), i.e., from the low-water line to ~150-m depth. The fossils indicate either continental shelf or most likely an inner neritic habitat at depths averaging about 20 to 25 m (Figures 20–21).

The assemblages of chiton valves from the Border localities are quite similar to those seen in modern sediments dredged from ~15 to 30 m off the California coast (based on examination of samples at LACM; Vendrasco, 1999). For example, LACM station 65–35, from ~27 m off San Pedro, California, contains valves of *Callistochiton palmulatus*, *Leptochiton nexus*, *Oldroydia percrassa*, and *Lepidozona* spp., all of which also occur in the Border beds. This assemblage is also similar to that found in rock dredges and trawls at similar depths off San Pedro, Los Angeles County, California (D.J.E., personal observation). The most conspicuous chitons along the central and Southern California coast, *Nuttallina fluxa*, *Cyanoplax hartwegii* (Carpenter, 1855), and *Mopalia muscosa* (Seapy and Littler, 1993; Liff-Grieff, 2006; MJV and DJE, personal observation), are missing from this assemblage (except for one specimen of *Nuttallina*). This is explained by the relatively deeper-water deposition of the Border beds.

Nevertheless, there is also a minor shallow-water component to the assemblage of the Border beds. For example, several of the chitons in this study are found in the intertidal to shallow subtidal zones (*Placiphorella velata*, *Lepidozona pectinulata*, *Stenoplax fallax*, *Nuttallina* sp., and species questionably identified here such as *S. heathiana*, and *Mopalia swanii*). Likewise, the gastropod *Calliostoma gemmulatum* is abundant in the Border beds and today occurs only in the lower intertidal zone (McLean, 1978). In addition, the bivalve *Penitella penita* typically lives in water depths of less than 10 m and the mussel *Modiolus rectus* (Conrad, 1837) lives in depths of less than 15 m (Coan et al., 2000). In addition to the shallow-water species, a deeper-water (>25-m depth) component to the assemblage of the Border beds is also present. For example, the abundantly occurring *Miltha xantusi* occurs today no shallower than 55 m (but see above), and the species *Eulima raymondi* Rivers, 1904, *Lirobittium rugatum* (Carpenter, 1864), and *Solariella peramabilis* Carpenter, 1864 have only been recorded from water depths of more than 30 m.

Overall, overlapping depth ranges of all species in this assemblage indicate a depth of deposition of the fossils averaging about 20 to 25 m, with a few species migrating or washing in from shallower and deeper water.

CHITON VALVE SORTING

Chitons have three distinct types of valves: head, intermediate, and tail (Figure 4). Normal individuals possess one head valve, six intermediate valves, and one tail valve. Modern chiton individuals with fewer or greater than eight valves are known but are extremely rare. For example, less than half a percent of 3,483

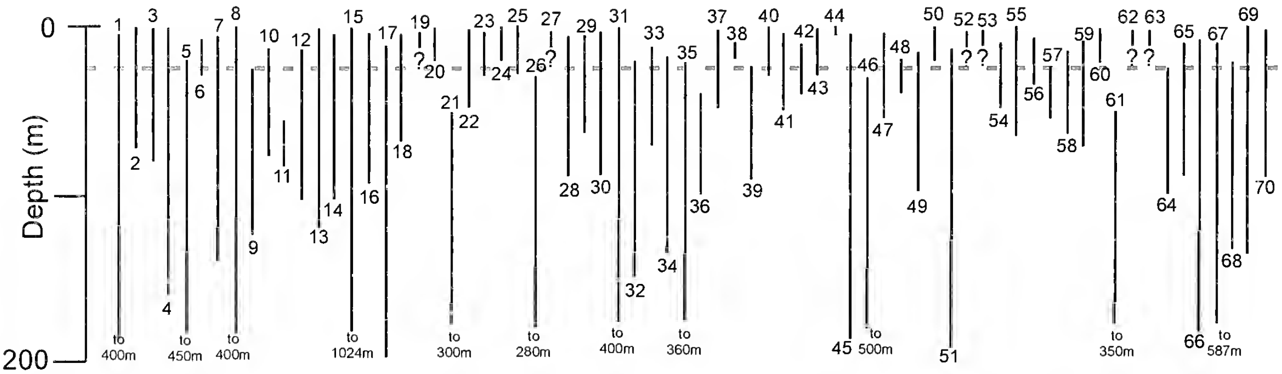

Figure 21 Known depth ranges for other molluscan (nonchiton) species with representatives in the San Diego Formation. Dashed line indicates inferred depth of deposition (25 m). Key as in Figure 19.

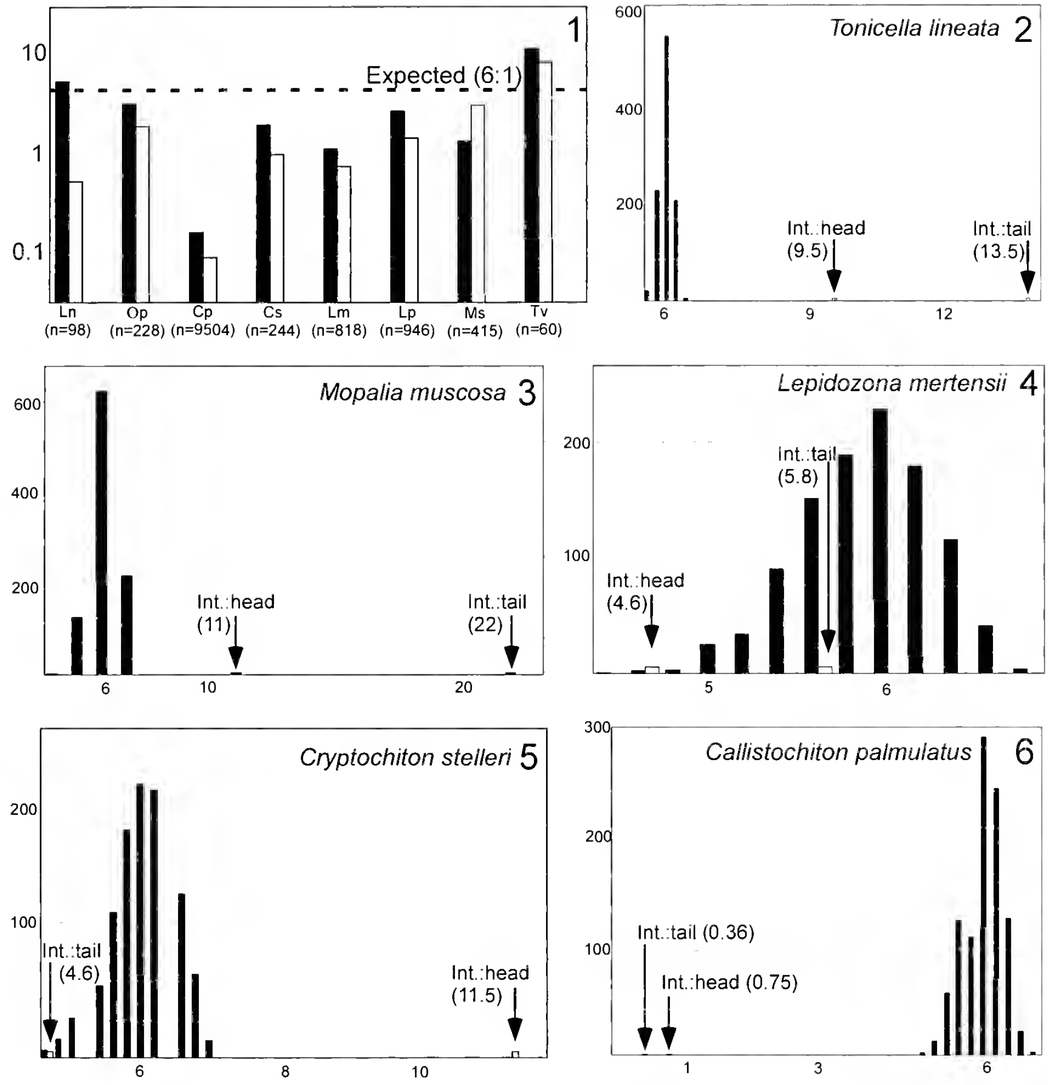

Figure 22 Ratios of valve types in the San Diego Formation (1) and in modern sediments (2–6). 1, Ratios of numbers of intermediate-to-head valves (filled bars) and intermediate-to-tail valves (unfilled bars) in fossil chiton assemblages from LACMIP localities 305, 16862 (305A), and 16817 (305C). The expected valve ratio of 6:1 is indicated by the darker dashed line. Only species with 60 or more total valves known from these deposits were included in this analysis. Abbreviations. Ln=*Leptochiton nexus*; Op=*Oldroydia percrassa*; Cp=*Callistochiton palmulatus*; Cs=*Callistochiton sphaerae* n. sp.; Lm=*Lepidozona mertensii*; Lp=*Lepidozona pectinulata*; Ms=*Mopalia* sp. cf. *M. swanii*; Tv=*Tonicella* sp. cf. *T. venusta*. 2–6, Ratios of intermediate-to-end valves of chiton species in specific Holocene accumulations. Histogram in each case shows the results of a statistical simulation repeated 1,000 times using the same sample size, revealing the expected range of valve ratios if there is no bias. 2, *Tonicella lineata*, n=302; 3, *Mopalia muscosa*, n=25; 4, *Lepidozona mertensii*, n=32; 5, *Cryptochiton stelleri*, n=30; 6, *Callistochiton palmulatus*, n=61.

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individuals of three chiton species examined were aberrant with an unexpected number of valves (Langer, 1978).

Fossil and modern assemblages of chiton valves typically show a deviation from the 1:6:1 expected ratio of valve types (Vendrasco, 1999; Puchalski and Johnson, 2009). A number of factors may bias chiton valve ratios in fossil assemblages. The valve types in chiton individuals have physical differences (in many size and shape parameters; Vendrasco, 1999), they tend to live in the rocky intertidal or shallow subtidal zones where currents can be strong and destructive, and their valves are typically delicate, especially for subtidal species. Valves of all chitons so far examined are composed of the mineral aragonite (Carter and Hall, 1990), which is more prone to dissolution than is calcite (Brenchley and Harper, 1998).

The extensive collection of chiton valves in this assemblage allows a robust analysis of chiton valve sorting, which shows a statistically significant deviation from the expected 1:6:1 ratio (Vendrasco, 1999). The results are shown in Figure 22.1. All species in this assemblage had a different ratio from the expected, and in some cases (e.g., *Callistochiton* spp.) the ratio is dramatically skewed from the expected. Overall, the deposit is dominated by *Callistochiton* valves (which make up more than 80% of the total chiton valves in the LACMIP collections), in particular *C. palmulatus*. A similar domination by this species has been seen in Pleistocene deposits (Chace, 1916a). This domination is due in part to the robust nature of the tail valve, which is subspherical and massive, and so resists degradation far better than nearly all other chiton valves. The head valve of C.

palmulatus is also thicker than the central area of the intermediate valves. The ratio of valve types (head, intermediate, and tail) in this species from the San Diego Formation is highly skewed from the expected 1:6:1, biased toward the end valves, particularly the tail valve, at a ratio of 12.2:1:34.7.

These ratios typically show greater bias than similar assemblages of chiton valves from modern sediments (cf. LACM collections; Figures 22.2–22.6). The modern assemblages were collected from sediments that lacked clear signs of strong currents (e.g., no ripple marks) (J.H. McLean, personal communication to M.J.V., 2009), and so might be expected to have chiton valves in a ratio closer to the expected 1:6:1. Again, with modern *Callistochiton palmulatus*, there is a distinct bias toward the tail valve (ratio 1:1.43:2; 143 valves from seven localities), indicating that the unequal dispersal and destruction of chiton valves occurs soon after the death of individuals. However, in general, the valve ratios in modern sediments show less deviation from the expected than the ratios of chitons from the Border beds. This higher level of deviation in the San Diego Formation was probably not due to collection bias because bulk matrix samples were processed in a laboratory setting where volunteers were instructed to "save everything" (Marincovich, 1974), as evidenced by the high number of small fragments of shells in the collections at LACMIP. However, because samples were presorted for us we cannot be absolutely certain that the biases are neutral with respect to which valves ended up in the collections. The greater divergence from the expected 1:6:1 ratio in the Border beds than in modern sediments is more likely due to exposure to a greater extent of current activity (for a longer time and/or slightly faster currents) that caused greater sorting due to different valve shapes and sizes and greater rates of destruction of the less robust valve types.

CONCLUSIONS

The San Diego Formation has produced the most diverse and abundant fossil chiton assemblage known. The LACMIP collections from the Border localities of this formation contain three new species (*Callistochiton sphaerae*, *Lepidozona kanakoffi*, and *Amicula solivaga*) and 19 additional species in 11 genera in four families. The stratigraphic ranges of six genera in the eastern Pacific are extended into the Pliocene, helping to fill a substantial gap in information on the Cenozoic history of chitons. This assemblage also contains a thermally anomalous record of the cold-water genus *Amicula* far south of its current range, as represented by a new extinct species.

The Border localities of the San Diego Formation are regarded as Pliocene in age, and evidence discussed here indicates an age between 3.25 and 2.5 Ma. Data on modern taxa represented here indicate deposition in a mixed silty/rocky habitat perhaps averaging about 20-to-25-m depths, possibly near the mouth of a large bay. There is a mixture of relatively cool- and warm-water species in the assemblage although most species currently occur in the nearby shallow marine habitat off of San Diego, and the average temperature range in which these fossil individuals lived appears to have been roughly similar to what occurs off of San Diego now. Upwelling, warm shallow bay habitat, and deposition of fossils during a time period of fluctuating temperatures may all have contributed to the faunal mixing.

The massive chiton assemblage allows detailed analysis of valve ratios, revealing consistent differences from the expected ratio of 1:6:1 for head:intermediate:tail valves. The divergence from the expected pattern is on average greater than for chiton valves in Holocene sediments, providing evidence that taphonomic factors occurring long after valve disarticulation can exert a strong influence on the proportions of chiton valve types in the fossil record.

This fossil deposit provides the oldest view of the late Cenozoic diversification of chitons along the Pacific Coast of North America. The diversification appears to have intensified from the middle Miocene to Pleistocene, in part because of regional increases in productivity and environmental heterogeneity during that time.

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Appendix 1

LOCALITY DESCRIPTIONS

Locality data are based on records and original field notes at LACMIP. Some original landmarks (e.g., a house, ranch) no longer exist and the extent of fossiliferous exposures may have changed since Kanakoff made his original collections.

305: Exposure of 18 m, 0.3 to 0.6 m thickness, exactly 89 m from the international U.S./Mexican border. South of Knox Ranch (as of 1957). 731 m east and 411 meters south of the northwest corner of Section 8, T 19 S, R 2 W, shown on the U.S. Geological Survey (USGS) Imperial Beach, California 7½′ (1:24,000) topographic map. On the hand-drawn map that George Kanakoff made of the localities, he wrote that the fossil-bearing deposit 305 is 10 feet (3.0 m) above the road. Collectors: William Emerson and George Kanakoff; collecting dates: July 20, 1956, and December 9, 1957.

16862 (305A): On the west side of a gulley east of 305; 686 m east and 347 m south of the northwest corner of Section 8, T 19 S, R 2 W, San Bernadino Baseline and Meridian (SBBM), USGS Imperial Beach, California 7½′ (1:24,000) topographic map, in the Tijuana River basin. In Kanakoff's locality record, he wrote that locality 305 A is at the "same elevation" as 305. Moreover, Mandel (1973) regarded these beds to be "at the same stratigraphic horizon" as those of 305C. On the hand-drawn map that George Kanakoff made of the localities, he wrote that the fossil-bearing deposit 305A is 8 feet (2.4 m) above the road. Collectors: William Emerson and George Kanakoff (1957); L. Marincovich, P. Oringer, R. Lane, B. Savic, and F. Wolfson (1959). Collecting dates: December 13, 1957, and August 3–10, 1959.

16817 (305C): An exposure 18 m long at the base of the hill on the west side of the gully east of locality 305; same elevation; in the Tijuana River basin. 30 m west and 134 m south of the northeast corner of Section 8, T 19 S, R 2 W, SBBM, USGS Imperial Beach, California 7½′ (1:24,000) topographic map. On the hand-drawn map that George Kanakoff made of the localities, he wrote that the fossil-bearing deposit 305C is 30 feet (9.1 m) above the road. Collectors: George Kanakoff and others; collecting dates: October 1964; May 11–13, 1965; June 1965.

Appendix 1 [Continued]
LIST OF FOSSILS FROM THE SAN DIEGO FORMATION BORDER BEDS

Faunal list from LACMIP localities 305, 16862 (305A), and 16817 (305C). Faunal list compiled primarily from Hertlein and Grant (1960, 1972, unpublished manuscript [*MS*]) and specimens at LACMIP.

Species	Frequency and locality	Depth range (m)	Geographic range in Eastern Pacific	Sources
Mollusca				
Bivalvia				
Acila castrensis (Hinds, 1843)	a; 305	5–400	Bering Sea, AK, to Sea of Cortez, MX	*2b*, C
Aligena diegoana Hertlein & Grant, 1972[1]	c; 305, A, C	N/A		*2b*
Anadara trilineata (Conrad, 1856b)[1]	a; 305, A	N/A		*2b*
Anomia peruviana d'Orbigny, 1846	r; 305, A, C	IT to 120	Monterey, CA, to Sechura, Peru	*2b*, C
Arca sisquocensis Reinhart, 1937[1]	c; 305, A	N/A		*2b*
Argopecten callida (Hertlein, 1925)[1] [fide Moore, 1984]	?; 305	N/A		*2b*
Argopecten ventricosus Sowerby, 1842 [as *Chlamys* (*Argopecten*) *circularis*]	r; 305, A	1–55	Santa Barbara, CA, to Bayovar, Peru	*2b*, C
Axinopsida serricata (Carpenter, 1864)	vr; 305, A	low IT to 275	Point Barrow, AK, to Punta San Pablo, BC	*2b*, C
Barbatia illota (Sowerby, 1833)[2]	a; 305, A	IT to 73	Punta Peñasco, MX, to Lobitos, Peru	*2b*, K
Basterotia hertleini Durham, 1950[1]	vr; C	N/A		
Brachidontes adamsianus (Dunker, 1857) (as *Aeidimytilus adamsianus*]	vr; C	IT	Anacapa Island, CA, to Islas Galapagos	*2b*, C
Cardiomya pectinata (Carpenter, 1864) [as *Cuspidaria pectinata*]	vr; A	5–1,000	Prince William Sound, AK, to Isla la Plata, Ecuador	*2b*, C
Chama arcana Bernard, 1976 [as *C. pellucida*]	a; 305, A	IT to 80	Santa Cruz County, CA, to Costa Rica	*2b*, C
Chlamys hastata (Sowerby, 1842)[3]	a; 305, A, C	IT to 160	Afognak Island, AK, to San Diego, CA	*2b*, C
Chlamys hastata ellisi Hertlein & Grant, 1972[1]	vr; 305	N/A		
Chlamys jordani (Arnold, 1903)[1]	?; 305	N/A		*2b*
Chione sp. cf. *C. undatella* (Sowerby, 1835)	?; 305	IT to 40	Goleta, CA, to Paita, Peru	*2b*, C
Clinocardium nuttalli (Conrad, 1837)[3]	vr; 305	IT to 180	Punuk Islands, AK, to San Diego, CA	*2b*, C
Compsomyax subdiaphana (Carpenter, 1864)	r; 305, A	2–500	Prince William Sound, AK, to Bahía San Quintin, BC	*2b*, C
Crassadoma gigantea (Gray, 1825) [as *Hinnites giganteus*]	vr; 305	IT to 80	Prince William Sound, AK, to Bahía Magdalena, BC	*2b*, C
Crassinella pacifica (Adams, 1852) [as *Crassinella branneri*]	r; 305, C	IT to 160	Santa Cruz Island, CA, to Zorritos, Peru	*2b*, C
Crenella decussata (Montagu, 1808) [as *C. inflata*]	vr; 305, A, C	IT to 200	Beaufort Sea, AK, to Peru	*2b*, C
Cryptomya californica (Conrad, 1837) [also as *C. californica magna*]	c; 305, A	IT to 80	Montague Island, AK, to Bayovar, Peru	*2b*, C
Cumingia sp. cf. *C. californica* Conrad, 1837	r; 305, C	IT to 65	Crescent City, CA, to Bahía San Juanico, BC	*2b*, C
Cyathodonta sp.	vr; 305			
Cyclocardia occidentalis (Conrad, 1855)[1]	vr?; A	N/A		
Cyclocardia ventricosa (Gould, 1850)	a; 305, A, C	20–450	Prince William Sound, AK, to Punta Rompiente, BC	*2b*, C
Cyclopecten pernomus (Hertlein, 1935)[2]	r; A, C	2–1,720	Isla Cedros, BC, to La Libertad, Ecuador	*2b*, K
Dendostrea? *vespertina* (Conrad, 1854)[1] [=*Myrakeena veatchii*]	?; 305, A	N/A		*2b*, S
Dermatomya tenuiconcha (Dall, 1913)[3]	vr; 305	293–2,200	Aleutian Islands, AK, to La Jolla, CA	*2b*, C
Diplodonta orbella (Gould, 1851)	vr; 305	IT to 46	Monterey, CA, to Isla Espíritu Santo, BC	*2b*, C
Diplodonta sericata (Reeve, 1850)[2?] [as *D. cornea*]	r; 305, C	IT to 75	Santa Cruz, Island, CA, to Laguna San Ignacio, BC	*2b*, C
Dosinia ponderosa diegoana Hertlein and Grant, 1972[1]	r; 305, A	N/A		
Ensis myrae Berry, 1953a	a; 305,A,C	5–25	Monterey Bay, CA, to Punta San Pablo, BC	*2b*, C
Epilucina californica (Conrad, 1837) [as *Lucina* (*Epilucina*) *californica*]	c; 305, A, C	IT to 80	Crescent City, CA, to Rocas Alijos, BC	*2b*, C
Euvola stearnsii (Dall, 1874)[1] [as *Pecten* (*Flabellipecten*) stearnsi]	a; 305, A, C	N/A		
Gari fucata (Hinds, 1845) [as *Gobraeus edentulus*]	a; 305,A,C	5 to 137	Santa Cruz Island, CA, to Isla Cedros, BC	*2b*, C
Glans carpenteri (Lamy, 1922) [as *G. subquadrata*]	r?; 305, A	IT to 100	Frederick Island, CAN, to Punta Rompiente, BC	*2b*, C
Glycymeris septentrionalis (von Middendorff, 1849) [as *G. profunda* and *G. grewingki*]	a; 305, A	IT to 400	Cook Inlet, AK, to Rocas Alijos, BC	*2b*, C
Gregariella chenui (Récluz, 1842)	vr; C	IT to 100	Monterey, CA, to Callao, Peru	*2b*, C
Here excavata (Carpenter, 1857) [as *Lucina* (*Here*) *excavata*]	a; 305, A, C	25–125	Santa Barbara, CA, to Bahia Santa Maria, BC	*2b*, C
Hiatella arctica (Linnaeus, 1767)	r; 305, C	IT to 1,190	Point Barrow, AK, to Chile	*2b*, C
Juliacorbula luteola (Carpenter, 1864) [as *Corbula luteola*]	c; 305, A	low IT to 60	Monterey Bay, CA, to Cabo San Lucas, BC	*2b*, C
Kellia suborbicularis (Montagu, 1803) [as *K. laperousii*]	r; 305, A, C	IT to 20	Prince William Sound, AK, to Zorritos, Peru	*2b*, C
Leporimetis obesa (Deshayes, 1855) [as *Florimetis biangulata*]	vr; 305	ST to 40	Point Conception, CA, to Magdalena Bay, BC	*2b*, C

Appendix 1 [Continued]

Species	Frequency and locality	Depth range (m)	Geographic range in Eastern Pacific	Sources
Leukoma staminea (Conrad, 1837) [as *Protothaca staminea*]	vr; 305	IT to 10	Attu Island, AK, to Bahia Santa Maria, BC	*2b*, C
Limaria orcutti (Hertlein & Grant, 1972)[1] [as *Lima* (*Limaria*) *orcutti*]	vr; 305, C	N/A		
Lucinisca nuttalli (Conrad, 1837) [as *Lucina* (*Lucinoma*) *nuttalli*]	a; 305,A,C	10 to 75	Monterey Bay, CA, to Laguna Ojo de Libre, BC	*2b*, C
Lucinoma annulatum (Reeve, 1850) [as *Lucina* (*Lucinoma*) *annulata*]	c; 305,A,C	IT to 665	Kodiak Island, AK, to Guaymas, MX	C
Lyropecten cerrosensis (Gabb, 1866)[1]	vr; C	N/A		
Macoma indentata Carpenter, 1864	r; 305, A, C	IT to 100	Humboldt Co., CA, to Isla Santa Margarita, BC	*2b*, C
Macoma medioamericana Olsson, 1942[2]	vr?; A	IT to 80	Sea of Cortez, MX (31° N) to Caleta la Cruz, Peru	*2b*, B, K
Mactromeris catilliformis (Conrad, 1867) [as *Spisula* (*Mactromeris*) *catilliformis*]	vr?; 305, A	5 to 20	Duxbury Point, CA, to Laguna Ojo de Libre, BC	*2b*, C
Mactromeris hemphilli (Dall, 1894b) [as *Spisula* (*Mactromeris*) *hemphilli*]	c; 305,A,C	IT to 50	Cayucos, CA, to Punta Pequeña, BC	*2b*, C
Milneria minima (Dall, 1871)	vr; 305	IT to 30	Vancouver Island, CAN, to Rocas Alijos, BC	*2b*, C
Miltha xantusi (Dall, 1905)[2]	a; 305,A,C	55–80	Mostly off Cabo San Lucas, BC, southern Sea of Cortez, MX	*2b*, K, B
Miodontiscus prolongatus (Carpenter, 1864)[3]	vr; 305	5–210	Prince William Sound, AK, to Point Loma, CA	*2b*, C
Modiolus rectus (Conrad, 1837)	?; 305, A	IT to 15	Queen Charlotte Islands, CAN, to Paita, Peru	*2b*, C
Modiolus sacculifer (Berry, 1953b)	c; 305, A	IT to 100	Moss Beach, CA, to Punta Banda, BC	*2b*, C
Myrakeena veatchii (Gabb, 1866)[1] [as *Ostrea vespertina* and *O. veatchii*]	?; 305, A	N/A		*2b*
Mysella pedroana Dall, 1899	c; 305, A	IT to 30	San Francisco, CA, to Playa Rosarito, BC	C
Nemocardium centifilosum (Carpenter, 1864)	vr; A	30–150	Portlock Bank, AK, to Punta Rompiente, BC	*2b*, C
Nuculana taphria (Dall, 1896)	a; 305, A, C	10–100	Fort Bragg, CA, to Isla Cedros, BC	*2b*, C
Nutricola ovalis (Dall, 1902) [as *Psephidia ovalis*]	r; C	20–150	Fort Bragg, CA, to Punta Rompiente, BC	C
Nutricola tantilla (Gould, 1853) [as *Transenella tantilla*]	a; 305, A, C	IT to 120	Prince William Sound, AK, to Isla Cedros, BC	*2b*, C
Pandora bilirata Conrad, 1855	vr; 305	ST to 250	Prince William Sound, AK, to Sea of Cortez, MX	*2b*, C
Pandora punctata Conrad, 1837	vr; C	IT to 50	Vancouver Island, CAN, to Punta Pequeña, BC	*2b*, C
Panomya sp. cf. *P. priapus* (Tilesius, 1822) [as *P.* sp. cf. *P. beringiana*][3]	vr; 305	10–50	Point Barrow, AK, to Cook Inlet, AK	*2b*, C
Panopea abrupta (Conrad, 1849) [as *Panopeagenerosa*][3]	a; 305,A,C	low IT to 100	Kodiak Island, AK, to Newport Bay, CA	*2b*, C
Parvilucina approximata (Dall, 1901) [as *Lucina tenuisculpta intensa*]	a; 305, A, C	IT to 1,024	Santa Barbara, CA, to Panama	*2b*, C
Patinopecten healeyi (Arnold, 1906)[1]	a; 305,A,C	N/A		
Pecten bellus (Conrad, 1856b)[1]	a; 305,A,C	N/A		
Penitella conradi Valenciencces, 1846	vr; 305, C	IT to 20	Vancouver Island, CAN, to Bahia San Bartolome, BC	*2b*, C
Penitella penita (Conrad, 1837)	vr; 305	IT to 10	Prince William Sound, AK, to Punta Pequeña, BC	C
Periploma stenopa Woodring, 1938[1]	vr; A	N/A		
Petricola carditoides (Conrad. 1837)	vr; 305	IT to 46	Sitka, AK, to Punta Pequeña, BC	*2b*, C
Pododesmus macrochisma (Deshayes, 1839)	a; 305,A,C	IT to 90	Bering Sea, AK, to Bahia Magdalena, BC	*2b*, C
Pristes oblongus Carpenter, 1864	r; 305, A, C	IT to 2	Monterey, CA, to Mazatlan, MX	*2b*, C
Protothaca tenerrima (Carpenter, 1857)	c; 305, A, C	IT to 30	Banarof Island, AK, to Bahia Thurloe, BC	*2b*, C
Protothaca tenerrima alta (Waterfall, 1929)[1]	vr; C	N/A		
Rhamphidonta frankiana (Hertlein & Grant, 1972)[1] [as *Bornia (Temblornia) frankiana*]	vr; C	N/A		
Rochefortia tumida (Carpenter, 1864) [as *Mysella tumida*]	?; 305, A	IT to 973	Beaufort Sea, AK, to Sea of Cortez, MX	*2b*, C
Saxidomus nuttalli Conrad, 1837 [as *Saxidomus nuttalli latus* Stewart *in* Woodring, Stewart, and Richards, 1940 [1941]]	vr; A	IT to 10	Humboldt Bay, CA, to Punta Rompiente, BC	*2b*, C
Securella kanakoffi (Hertlein & Grant, 1972)[1] [as *Chione* (*Securella*) *kanakoffi*]	a; 305, A, C	N/A		
Semele rubropicta (Dall, 1871) [also as *S. ashleyi*]	r; 305, C	IT to 100	Seldovia Bay, AK, to Sea of Cortez, MX	*2b*, C
Septifer bifurcatus (Conrad, 1837)	vr; C	IT to 50	Monterey, CA, to Cabo San Lucas, BC	*2b*, C
Siliqua lucida (Conrad, 1837)	r; 305, A, C	low IT to 50	Bodega Harbor, CA, to Boca de Soledad, BC	*2b*, C
Solen sicarius Gould, 1850	c; 305, A	IT	Queen Charlotte Islands, CAN, to Bahia San Quintin, BC	*2b*, C
Sphenia cf. *fragilis* (Adams & Adams, 1854) [as *S.* cf. *luticola*]	vr; 305	IT to 55	Carpinteria, CA, to Ecuador	*2b*, C

Appendix 1 [Continued]

Species	Frequency and locality	Depth range (m)	Geographic range in Eastern Pacific	Sources
Swiftopecten parmeleei (Dall, 1898b)[1] [as *Chlamys* (*Swiftopecten*) *parmeleei*]	a; 305,A,C	N/A		
Tagelus californianus (Conrad, 1837)	vr; A	IT	Humboldt Bay, CA, to Costa Rica	*2b*, C
Tellina bodegensis Hinds, 1845	r; 305, A	IT to 100	Sitka, AK, to Bahía Magdalena, BC	
Tellina carpenteri Dall, 1900	c; 305, A, C	IT to 823	Sitka, AK, to Panama	*2b*, C
Tellina idae Dall, 1891[3]	c; 305, A, C	IT to 100	Santa Barbara, CA, to San Diego, CA	*2b*, C
Tellina nuculoides (Reeve, 1854) [as *T. salmonea*]	c; 305, A, C	IT to 75	Pribilof Islands, AK, to Islas Coronado, BC	
Thracia trapezoides Conrad, 1849 [as *Thracia kanakoffi*]	a; 305, A, C	11–200	Wide Bay, AK, to Isla Cedros, BC	*2b*, C
Thyasira flexuosa (Montagu, 1803) [as *Thyasira gouldii*][3]	vr; 305, A	20–3,000	Beafort Sea, AK, to Point Loma, CA	*2b*, C
Tivela stultorum (Mawe, 1823)	vr; 305, C	IT to 30	Stinson Beach, CA, to Bahía Magdalena, BC	*2b*, C
Trachycardium quadragenarium (Conrad, 1837) [as *Cardium* (*Dallocardia*) *quadragenarium*]	vr; 305, A	IT to 50	Monterey, CA, to Punta Rompiente, BC	*2b*, C
Tresus nuttallii (Conrad, 1837)	r?; 305, A	IT to 80	Kodiak Island, AK, to Bahía Magdalena, BC	*2b*, C
Trigonulina pacifica Jung, 1996 [as *Verticordia ornata*]	r; 305	15–170	Pacific Grove, CA, to Callao, Peru	*2b*, C
Zirfaea pilsbryi Lowe, 1931	vr; 305	low IT to 125	Point Lay, AK, to Bahía Magdalena, BC	*2b*, C
Gastropoda				
Acanthina emersoni Hertlein and Allison, 1959[1]	a; 305, A, C	N/A		
Acirsa cerralvoensis DuShane, 1970[2]	vr; 305	7–38	Isla Angel de la Guarda to Cabo San Lucas, BC	K, Sk
Acmaea mitra Rathke, 1833	a; 305,A,C	IT to 64	Aleutian Islands, AK, to Isla San Martin, northern BC	*MS*, M
Alvania oldroydae Bartsch, 1911	a; 305, A, C	ST	Monterey Bay, CA, to Isla Asuncion, BC	A, M
Amphissa versicolor Dall, 1871	a; 305, A, C	IT to 20; chiefly IT	Graham Island, CAN, to Punta San Pablo, BC	A, M, M3
Angulobittium sp. cf. *A. asperum* (Gabb, 1861)[3] [as *Bittium asperum*]	vr; 305	27–91	Santa Rosa Island, CA, to San Diego, CA	*MS*, M3
Architectonica nobilis Röding, 1798[2]	c; 305, A, C	ST to 250	Bahía Magdalena, BC to Peru	K, Sk
Balcis sp. cf. *B. micans* (Carpenter, 1864)	vr; C	30–100	Kodiak Island, AK, to Punta Abreojos, BC	MG
Balcis oldroydae (Bartsch, 1917)	a; 305, A, C	20–90	Kachemak Bay, AK, to Isla Cedros, BC	MG
Barbarofusus barbarensis (Trask, 1855)	a; 305, A, C	50–300	Santa Barbara, CA, to central BC	MG, M3
Barleeia sp. cf. *B. californica* Bartsch, 1920a	r; 305, A, C	low IT to ST	Santa Cruz Island, CA, to Isla Cedros, BC	A, M, M3
Barleeia sp. cf. *B. subtenuis* Carpenter, 1864	c; 305, A, C	low IT to ST	Afognak Island, AK, to San Ignacio Lagoon, BC	A, M
Brochina occidentale (Bartsch, 1920b)	r; 305, A	?	Kachemak Bay, AK, to Bahía Magdalena, BC	M, M3
Caecum californicum Dall, 1885	c; 305, C	low IT to ST	Monterey Bay, CA, to Bahía Magdalena, BC	M
Caecum dalli Bartsch, 1920b	r; 305	ST	Farallon Islands, CA, to Isla Asuncion, BC	M, M3
Callianax biplicata (Sowerby, 1825) [as *Olivella biplicata*]	a; 305, A, C	low IT to 48	Gulf of AK to Bahía Magdalena, BC	A, M, M3
Calliostoma annulatum (Lightfoot, 1786)	a; 305, A, C	ST in so. CA	Forrester Island, AK, to Isla San Geronimo, BC	M
Calliostoma coalingense catoteron Woodring and Bramlette, 1950[1]	N/A			
Calliostoma gemmulatum Carpenter, 1864	a; C	IT to 20	Cayucos, CA, to Isla de Natividad, BC	M, M3
Calliostoma supragranosum Carpenter, 1864	a; 305, A, C	IT to 30	Monterey Bay, CA, to Isla Asuncion, BC	M, M3
Calyptraea filosa Gabb, 1866[1]	N/A			
Calyptraea inornata (Gabb, 1866)[1]	N/A			
Calyptraea sp.	a; 305, A, C			
Cancellaria arnoldi Dall, 1909[1]	a; 305, A, C	N/A		
Cancellaria cooperi Gabb, 1865	a; 305, A, C	30–280	Monterey Bay, CA, to Punta San Pablo, BC	MG
Cancellaria fergusoni Carson, 1926[1]	r; C	N/A		
Cancellaria lipara Woodring *in* Woodring and Bramlette, 1950[1]	vr; 305, A	N/A		
Cancellaria rapa Nomland, 1917[1]	vr; C	N/A		
Cancellaria sanctaemariae Carson, 1926[1]	c; 305, A, C	N/A		
Cantharus sp.	c; A, C			
Cerithiopsis pedroana Bartsch, 1907	a; 305, A, C	ST	San Pedro, CA, to Estero Todos Santos, BC	M, M3
Cidarina cidaris (Carpenter, 1864)	?; 305	35–300	Prince William Sound, AK, to Isla Cedros, BC	*MS*, MG, M3
Conus californicus Reeve, 1844	a; 305, A, C	low IT to 90	Farallon Islands, CA, to Bahía Magdalena, BC	A, M, M3
Cranopsis cucullata (Gould, 1846) [as *Puncturella cucculata*]	c; 305, A, C	>100 in southern CA	Kodiak Island, AK, to Cabo San Quintin, BC	*MS*, MG
Crawfordiana fugleri (Arnold, 1907)[1]	vr; A	N/A		

Appendix 1 [Continued]

Species	Frequency and locality	Depth range (m)	Geographic range in Eastern Pacific	Sources
Crepidula aculeata (Gmelin, 1791)	a; 305, C	low IT to 60 (most shallow)	Cayucos, CA, to Valparaiso, Chile	A, M, Mo
Crepidula onyx Sowerby, 1824	a; 305, C	low IT to 90	Southern CA, to Peru	A, M
Crepidula princeps Conrad, 1856a[1]	a; 305, A, C			
Crossata californica (Hinds, 1843) [as *Bursa* (*Crossata*) *californica*)	a; 305, A, C	0–400	Monterey Bay, CA, to Costa Rica	A, Sk, M, M3
Crucibulum spinosum (Sowerby, 1824)	a; 305, A, C	IT to 55	San Pedro, CA, to Chile	K, M
Cylichnia attonsa Carpenter, 1864	a; 305, A, C	20–150	Kodiak Island, AK, to central BC	A, M3
Cymatium elsmerense (English, 1914)[1]	c; 305, A, C	N/A		
Cymatosyrinx sp.	a; 305, A, C			
Diodora arnoldi McLean, 1966	a; 305, A, C	9–64	Crescent City, CA, to Isla San Martin, BC	MS, A, M
Diodora aspera (Rathke, 1833)	r; 305, C	IT to 38	Afognak Island, AK, to Cabo San Martin, BC	MS, A, M, M3
Epitonium acrostephanus Dall, 1908	c; 305	27–372	Puget Sound, WA, to Islas Coronado, BC	A
Epitonium cf. *greenlandicum* (Perry, 1811)	vr; 305	18–238	AK to Graham Island, CAN	A
Epitonium (Asperiscala) minuticostata (De Boury, 1912)	a; 305, A, C	18–137	CA to Islas Galapagos	K, KC, R
Epitonium sawinae (Dall, 1903)	a; 305, A, C	18–360	British Columbia, CAN, to Bahía Magdalena, BC Sur	MG, M3
Erato columbella Menke, 1847	r; 305, C	low IT to 90	Monterey, CA, to Isla Cedros, BC	A, M
Eulima raymondi Rivers, 1904	a; 305, A, C	40–100	Monterey Bay, CA, to Bahía Guatulco, MEX	MG, M3
Euspira draconis (Dall, 1903) [as *Polinices draconis*]	r; A	19–48	Mugu Lagoon, CA, to Mazatlan, MX	A, M
Euspira lewisii (Gould, 1847) [as *Polinices* (*Lunatia*) *lewisii*]	r; 305, A	0 to 100	Chukchi Sea, AK, to Isla San Geronimo, BC	M, M3
Ficus sp.	vr; C			
Fissurellidea bimaculata (Dall, 1871) [as *Megatebennus bimaculatus*]	c; 305, C	IT to 37	Forester Island, AK, to Islas Tres Marias, MX	MS, A, R, M, M3
Forreiria wrighti Jordan and Hertlein, 1926[1]	a; 305, A, C	N/A		
Fusitriton sp. cf. *F. oregonense* (Redfield, 1846)[3]	vr; A	ST to 420	Bering Sea, AK, to San Diego, CA	A, M3
Garnotia adunca (Sowerby, 1825)	a; 305, A, C	IT to 37	Queen Charlotte Islands, CAN, to Santo Tomas, BC	A, M, M2
Granulina margaritula (Carpenter, 1857)	vr; A, C	low IT to 76	Afognak Island, AK, to Panama	A, M
Glossaulax reclusianus(Deshayes, 1839) [as *Polinices* (*Glossaulax*) *reclusianus*]	a; 305, A, C	IT to 46; mostly IT	Mugu Lagoon, CA, to Mazatlan, MX	A, M, M3
Haliotis sp. cf. *H. kamtschatkana assimilis* Dall, 1878 [as *Haliotis assimilis*]	?; 305	3–30; 10+ in southern CA	Central CA to central BC	MS, M, M3
Haliotis sp. cf. *H. rufescens* Swainson, 1822	a; 305,A,C	6–16	Sunset Bay, Oregon, to Bahía San Bartolome, BC	MS, A, Mo, M3
Haliotis walallensis Stearns, 1899	vr; C	ST to 32	Coos Bay, Oregon, to Puerto Santo Tomas, BC; uncommon in southern CA	MS, A, M3
Halistylus pupoideus (Carpenter, 1864)	a; 305,A,C	20–90	Forester Island, AK, to Bahía San Bartolome, BC	MS, MG
Hemitoma sp.[2]	vr; C			
Hipponix tumens Carpenter, 1864	a; 305, C	0 to 30	Crescent City, CA, to Bahía Magdalena, BC	A, M, M3
Hirtoscala hindsii (Carpenter, 1856)	r; 305, C	IT to 195	Plumper Sound, CAN, to Peru	MG, M3
Hirtoscala indianorum (Carpenter, 1864)[3] [as *Epitonium* (*Nitidiscala*) *indianorum*]	vr; C	IT to 120 (>30 southern CA)	Forrester Island, AK, to Santa Cruz Island, CA	MG, M3
Hirtoscala tinctum (Carpenter, 1864) [as *Epitonium* (*Nitidiscala*) *tinctum*]	a; 305, C	IT to 46	Vancouver, CAN, to Bahía Magdalena, BC	A, M, Re, M3
Homalopoma grippi (Dall, 1911)	vr; 305, C	60 to 260	Santa Rosa Island, CA, to Islas Revillagigedo, MX	A, M3
Homalopoma paucicostatum (Dall, 1871)	vr; 305, C	exclusively ST	Sonoma County, CA, to Cabo San Quintin, BC	MG
Homalopoma radiatum (Dall, 1918)	a; 305, A, C	10–40	Cordell Bank, CA, to Sacramento Reef, BC	M, M2, M3
Kelletia kelletii (Forbes, 1852)	a; 305, A, C	0–30	Point Conception, CA, to Isla Asuncion, BC	A, M, M3
Lacuna unifasciata Carpenter, 1857	a; 305, A, C	low IT	Moss Beach, CA, to Punta Abreojos, BC	A, M, M3
Lamellaria sp.	vr; 305			
Ligacalliostoma canaliculatum (Lightfoot, 1786) [as *Calliostoma caniculatum*]	a; 305, A, C	IT to 183	Sitka, AK, to Islas San Benito, BC	R, M, M3
Lirobittium rugatum (Carpenter, 1864)	a; 305, A, C	30–500	Off Point Pinos, Monterey County, CA, to Islas San Benito, BC	MG
Lirularia aresta (Berry, 1941)[1]	vr; 305	N/A		

Appendix 1 [Continued]

Species	Frequency and locality	Depth range (m)	Geographic range in Eastern Pacific	Sources
Lirularia optabilis (Carpenter, 1864)[3]	a; 305, A	5–55	Santa Rosa Island, CA, to Laguna Beach, CA	A, M3
Littorina sp. cf. *L. scutulata* Gould, 1849	vr; C	IT	Kodiak Island, AK, to Bahía San Bartolome, BC	M
Macrarene diegensis McLean, 1964[1]	c; A, C	N/A		
Mangelia sp.	a; 305, A, C			
Maxwellia eldridgei (Arnold, 1907)[1]	a; 305, A, C	N/A		
Mediargo mediocris (Dall, 1909)[1]	vr; 305, A, C	N/A		
Megalomphalus sp.	r; 305, C			
Megastraea turbanica (Dall, 1910)[2] [as *Astraea turbanica*]	a; 305, A, C	20–40	Islas Coronado, BC, to Isla Santa Margarita, BC	A, K, M3
Megasurcula sp. cf. *M. carpenteriana* (Gabb, 1865)	a; 305, A, C	16–100	Bodega Bay, CA, to Isla Cedros, BC	M
Megathura crenulata (Sowerby, 1825)	a; 305,A,C	IT to 20	Monterey, CA, to Punta Pequeña, BC	A, M, Re, M3
Metaxia convexa (Carpenter, 1857)	r; 305, A, C	low IT to ST	Monterey Bay, CA, to Mazatlan, MX	M, M3
Micranellum crebricinctum (Carpenter, 1864)	a; 305, A, C	10–200	Kachemak Bay, AK, to Punta Abreojos, BC	MG
Microglyphis sp.	c; C			
Mitra idae Melvill, 1893	c; 305, C	0–100	Crescent City, CA, to Isla Cedros, central BC	M, M3
Mitrella tuberosa (Carpenter, 1864)	a; 305, A, C	ST	Forrester Island, AK, to southern BC	M
Nassarius (Caesia) sp. cf. *N. grammatus* (Dall, 1917)[1]	vr; 305	N/A		
Nassarius perpinguis (Hinds, 1844)	a; 305, A, C	low IT to ST	Point Reyes, CA, to Isla Cedros, central BC	M
Naticidae indeterminate [as *Polinices* spp.]				
Neosimnia sp.	vr; 305			
Niveotectura funiculata (Carpenter, 1864)	c; 305,A,C	20–70	Shumagin Island, AK, to Bahía Magdalena, BC	*MS*, MG
Nodiscala spongiosa (Carpenter, 1864)	c; 305, A, C	18–72	Monterey, CA, to Islas Galapagos	MG
Nucella sp.	vr; 305, A, C			
Ocenebra sp.	a; 305, A, C			
Odostomia sp.	a; 305, A, C			
Opalia montereyensis (Dall, 1907)	a; 305	ST (to 46+)	Forester Island, AK, to Bahía Magdalena, BC	A, M
Opalia varicostata Stearns, 1875[1] [syn. *O. varicostata anomala*]	a; 305, A, C	N/A		
Opalia sp. cf. *O. borealis* Keep, 1881[3]	c; 305, A	IT	Bristol Bay, AK, to San Luis Obispo County, CA	A, M3
Ophiodermella graciosana (Arnold, 1907)[1]	a; 305, A, C	N/A		
Ophiodermella inermis (Reeve, 1843)	a; 305, A, C	IT to 65	Santa Rosa Island, CA, to Isla Asuncion, BC	M, M3
Parviturbo acuticostatus (Carpenter, 1864)	c; 305, A	ST to 30	Monterey Bay, CA, to Sea of Cortez, MX	*MS*, M, M3
Parviturbo sp. cf. *P. stearnsii*[2] (Dall, 1918) [as *P. acuticostatus quaylei*]	a; 305, A, C	3–30	Asuncion Island, BC to Port Utria, Columbia	*MS*, A, K
Pomaulax gibberosa (Dillwyn, 1817)	a; 305, A, C	20–50 in southern CA	Dall Island, AK, to Isla Santa Margarita, BC	A, K, M, Sk, M3
Pseudomelatoma grippi (Dall, 1919)	a; 305	15–65	San Pedro, CA, to Isla San Martin, northern BC	M, M3
Pusula californiana (Gray, 1827)	c; 305, A, C	ST to 76	Crescent City, CA, to Islas Revillagigedos, MX	A, M, M3
Scalina brunneopicta (Dall, 1908)[2]	a; 305, A, C	9–72	Isla Cedros, BC to Costa Rica	A, K, KC
Scelidontoma bella (Gabb, 1865)	c; 305, A, C	>20–110	Forrester Island, AK, to Cabo San Martin, BC	*MS*, MG
Schwartziella sp. cf. *S. bakeri* (Bartsch, 1902)	r; 305, A	ST	Monterey Bay, CA, to Islas Coronado, BC	M, M3
Seila montereyensis Bartsch, 1907	a; 305, A, C	low IT to 67	Monterey Bay, CA, to Punta Abreojos, BC	A, M
Shaskyus festivus (Hinds, 1844)	a; 305, A, C	0–20	Santa Barbara, CA, to Bahía Magdalena, BC	M, M3
Sinezona rimuloides (Carpenter, 1865) [as *Coronadoa simonsae*]	vr; C	IT to 30	Farallon Islands, CA, to Iquique, Chile	K, M
Sinum scopulosum (Conrad, 1849)	r; 305, A	15–150	Monterey Bay, CA, to Todos Santos, BC	M, M3
Skenea sp.	vr; 305			*MS*
Solariella peramabilis Carpenter, 1864	a; 305, A, C	50–350	Forrester Island, AK, to Isla Clarion, MX	MG
Strictispira zizyphus (Berry, 1940)[1]	a; 305, C	N/A		M3
Tegula aureotincta (Forbes, 1852)	r; 305	IT to ST	Ventura County, CA, to Bahía Magdalena, BC	*MS*, M
Tegula gallina multifilosa (Stearns, 1892)	c; 305, A, C	IT	San Francisco, CA, to Sea of Cortez, MX	*MS*, A
Tegula hemphilli Oldroyd, 1921[1]	vr; A, C	N/A		*MS*
Tegula regina (Stearns, 1892)	vr; 305	ST, mostly ~10	Catalina Island, CA, to Isla Asuncion, BC	M
Teinostoma supravallatum (Carpenter, 1864)	c; 305	ST	Los Angeles County, CA, to Isla San Geronimo, BC	M
Terebra martini (English, 1914)[1]	a; 305, A, C	N/A		
Tricolia sp. cf. *T. pulloides* (Carpenter, 1865)	a; A, C	low IT to ST	Puget Sound, WA, to Cabo San Lucas, BC	M
Triphora pedroana Bartsch, 1907	a; 305, A, C	low IT to ST	Monterey Bay, CA, to Isla San Geronimo, BC	M

Appendix 1 [Continued]

Species	Frequency and locality	Depth range (m)	Geographic range in Eastern Pacific	Sources
Trophon sp.	c; 305, A, C			
Turbonilla sp.	a; 305, A, C			
Turcica brevis Stewart *in* Woodring et al. 1940[1941][1]	a; 305, C	N/A		*MS*
Turritella cooperi Carpenter, 1864	a; 305, A, C	25–100	Point Piños, CA, to Bahía Magdalena, BC	MG, M3
Vitrinella oldroydi Bartsch, 1907	c; 305, A, C	0–20	British Columbia, CAN, to Bahía Magdalena, BC Sur	A, M, M3
Zonaria (Neoberraya) spadicea (Swainson, 1823)	r; 305	low IT to 48	Monterey, CA, to Isla Cedros, BC (rare north of Point Conception, CA)	A, M
Polyplacophora: See Table 2				
Scaphopoda				
Cadulus fusiformis Pilsbry and Sharp, 1898	a; 305, A, C	10–90	Monterey, CA, to BC	O
Dentalium neohexagonum Sharp and Pilsbry in Pilsbry and Sharp, 1897	a; 305, A, C	9–182	Monterey, CA, to Sea of Cortez, MX	*MS*, K, M
Dentalium sp. cf. *D. semipolitum* Broderip and Sowerby, 1829	c; C	IT to 18	Monterey, CA, to Costa Rica	A
Siphodentalium quadrifissatum (Pilsbry and Sharp, 1898)	vr; A, C	4–365	Monterey, CA, to BC	A
Nonmollusks				
Porifera				
Cliona celata Grant, 1825	r; 305		AK to British Columbia, CAN	G
Cnidaria				
Astrangia sp. cf. *A. insignifica* Nomland, 1916	r; 305	0–53	San Luis Obispo, CA, to Isla Santa Margarita, BC	*2a*
Balanophyllia elegans Verrill, 1864	a; 305, A, C	0–587 (>10 in southern CA)	Snipe Bay, AK, to Sacramento Reef, north BC	*2a*
Dendrophyllia sp. cf. *D. oldroydi* Faustino, 1931	vr; 305	183–366	San Pedro, CA, to San Diego, CA	*2a*
Paracyathus stearnsii Verrill, 1869	a; 305, A, C	20–134	Queen Charlotte Islands, CAN, to Bahía Asuncion, BC	*2a*
Bryozoa				
Reptadeonella violacea (Johnston, 1847)[2]	vr; 305	9–110	Sea of Cortez, MX	*2a*, CB
Callopora corniculifera (Hincks, 1882)[3]	?; 305	IT to 96–126	British Columbia, CAN, to Channel islands, CA	*2a*, So
Cellaria diffusa Robertson, 1905	?; 305	IT to 216	Puget Sound WA, to Islas Galapagos	*2a*, So
Cellaria mandibulata Hincks, 1882	?; 305	IT to >140	British Columbia to Point San Eugenio	*2a, So*
Chapperia patula (Hincks, 1881)	r; 305	ST to 90	Frequently found in British Columbia, CAN, but ranges to BC	*2a*, So
Coleopora gigantea (Canu and Bassler, 1923)	vr; 305	ST to >200	Monterey Bay, CA, to BC	*2a*, So2
Conopeum commensale Kirkpatrick and Metzelaar, 1922	?; 305			*2a*
Diaperoforma californica (d'Orbigny, 1852) [as *Diaperoecia californica*]	?; 305	ST to 200	British Columbia, CAN, to Islas Coronados, MX	*2a*, So
Disporella californica (d'Orbigny, 1853)	?; 305			*2a*
Eurystomella bilabiata (Hincks, 1884)	vr; 305	IT to 237	Nootka Island, AK, to Tenacatita, MX (perhaps an area of cool water upwelling)	*2a*, So
Heteropora pacifica Borg, 1933	?; 305	low IT to 27	AK to central CA	*2a*
Hippopodinella adpressa (Busk, 1854)	?; 305			*2a*
Hippoporella gorgonensis Hastings, 1930	?; 305			*2a*
Hippothoa (*Celleporella*) *hyalina* (Linnaeus, 1767)	r; 305	IT to 130.5	AK to CA (possibly Galapagos)	*2a*, So
Lagenipora (*Lagenicella*?) *punctulata* (Gabb and Horn, 1862)	?; 305	ST to 200	Northern CA to BC and Sea of Cortez, MX	*2a*, So
Microporella californica (Busk, 1856)[3]	vr; 305	IT to 150	AK to southern CA	*2a*, So
Microporella cribrosa Osburn, 1952	vr; 305	ST to 126	Mussel Point, central CA, to Sea of Cortez, MX	So
Microporella umbonata (Hincks, 1884)	?; 305			*2a*
Microporelloides sp. [as *Microporella ciliata* (Pallas, 1766)]	vr; 305			*2a*
Mucronella major (Hincks, 1884)	r; 305			*2a*
Parasmittina trispinosa (Johnston, 1838)	r; 305			*2a*
Porella porifera (Hincks, 1884)[3]	?; 305	ST to 250	British Columbia, CAN, to Channel Islands CA	*2a*, So
Puellina californiensis Soule, Soule, and Chaney, 1995 [as *Colletosia radiata*]	?; 305	ST to 180	Channel Islands, CA, possibly to Sea of Cortez, MX	*2a*, So
Reginella mucronata (Canu and Bassler, 1923)	c; 305			*2a*

Appendix 1 [Continued]

Species	Frequency and locality	Depth range (m)	Geographic range in Eastern Pacific	Sources
Rhynchozoon rostratum (Busk, 1856)	?; 305	ST to 200	AK to South America	2*a*, So
Schizoporella? cornuta (Gabb and Horn, 1862) [as *Schizoporella cornuta*]	vr; 305	ST to >200	Southern AK to Panama (some citations doubtful)	2*a*, So
Thalamoporella californica (Levinsen, 1909)	vr; 305	IT to 15	Monterey Bay, CA, and south	2*a*, So2
Tubulipora tuba (Gabb & Horn, 1862)	vr; 305	IT to 235	British Columbia, CAN, to BC	2*a*, So
Brachiopoda				
Glottidia albida (Hinds 1844)	r; 305, C	IT to 110	Monterey Bay, CA, to Bahía Acapulco, MX	2*a*
Echinodermata				
Dendraster ashleyi ynezensis Hertlein and Grant, 1960[1]	c; 305	N/A		
Eucidaris sp. cf. *E. thouarsii* (Valenciennes, 1846)	a; 305	IT to 140	Catalina Island, CA, to Ecuador	2*a*, D
Strongylocentrotus franciscanus (Agassiz, 1863)	?; 305	IT to 90	Kodiak Island, AK, to Isla Cedros, BC	2*a*, D
Strongylocentrotus purpuratus (Stimpson, 1857)	?; 305	IT to 160	Vancouver Island, CAN, to Isla Cedros, MX	2*a*, D
Arthropoda: Crustacea				
Robustaurila jollaensis (LeRoy, 1943)	c; 305		Cape Flattery, WA, to BC	N
Balanus gregarius (Conrad, 1856b)[1]	a; 305, A, C	N/A		
Balanus nubilus Darwin, 1854	vr; 305	low IT to 90	Southern AK to La Jolla, CA	G, N, N2
Balanus proinus Woodring *in* Woodring and Bramlette, 1950[1] [as *Balanus hesperinus proinus*]	c; 305	N/A		
Paraconcavus sp. cf. *Ppacificus* (Pilsbry, 1916)	vr; 305	ST to 73	Monterey Bay, CA, to Baja, CA	N, N2
Cancer antennarius Stimpson, 1856	c; 305, A, C	low IT to 91	Queen Charlotte Sd., CAN, to Cabo San Lucas, MX	G, Se
Cancer anthonyi Rathbun, 1897	c; 305, A, C	ST to 48	Humboldt Bay, CA, to Bahía Magdalena, CA	G
Cancer branneri Rathbun, 1926	vr; 305	ST to 30	AK to Southern, CA	G
Cancer gracilis Dana, 1852	r; C	ST to 105	AK to Bahía Playa Maria, BC	G, Ku
Cancer oregonensis (Dana, 1852)	r; C	IT to 435	Pribilof Islands, AK, to Los Angeles, CA	*Se*
Cancer sp. cf. *C. polyodon* Poeppig, 1836[2]	vr; C	4–8	Ecuador to Chile	W
Cancer productus Randall, 1840	a; 305, C	low IT to 90	AK to BC	G, Se
Caudites fragilis LeRoy, 1943	vr; 305		Cambria, CA, to Isla Asuncion, BC	V
Cetolepas hertleini Zullo, 1969[1]	r; C	N/A		
Coquimba schencki (LeRoy, 1943)	vr; 305		Oxnard, CA, to Isla Cedros, BC	V
Coronula sp.	r; A			
Loxorhynchus crispatus Stimpson, 1857	r; C	low IT to 180	Redding Rock, Humboldt County, CA, to BC	G
Metacarcinus jenniferae (Nations, 1975)[1]	vr; 305	N/A		
Munseyella pedroensis Triebel, 1957	vr; 305		Point Conception, CA, to Isla Cedros, BC	V
Palmanella californica Triebel, 1957[1]	r; 305	N/A		
Randallia ornata (Randall, 1840)	c; 305, A	IT to 21	Monterey Bay, CA, to BC	G

Footnotes.

[1] extinct taxa,

[2] southern extralimital taxa,

[3] northern extralimital taxa.

Abbreviations. Frequency and locality: a=abundant (>100 large fragments to complete specimens at LACMIP or otherwise reported as such by Hertlein and Grant, unpublished manuscript [*MS*]), c=common (20–100), r=rare (5–20), vr=very rare (<5), ?=no clear abundance data from Hertlein and Grant (1960, 1972, *MS*) nor specimens at LACMIP, 305=found at LACMIP locality 305, A=found at 16862 (305A), C=found at 16817 (305C). Depth range: IT=intertidal, ST=subtidal. Geographic locality: AK=Alaska, BC=Baja California, CA=California, CAN=Canada, MX=Mexico; WA=Washington. Sources: 2*a*=species included in Hertlein and Grant, 1960; 2*b*=species included in Hertlein and Grant, 1972; *MS*=species described in Herlein and Grant, *MS*; A=Abbott, 1974; B=Bernard, 1983; C=Coan et al., 2000; Ca=Cairns, 1994; CB=Canu and Bassler, 1928; D=Durham et al., 1980; G=Gotshall, 1994; K=Keen, 1971; KC=Keen and Coan, 1975; Ku=Kuris et al, 2007; M=McLean, 1978; M2=McLean, 2007; M3=J. McLean, personal communication; MG=McLean and Gosliner, 1996; Mo=Morris, 1966; N=Newman, 2007; N2=Newman and Abbott, 1980; O=Oldroyd, 1927; R=Rice, 1973; Re=Rehder, 1981; S=Squires et al., 2006; Se=Sept, 2002; Sk=Skoglund, 2002; So=Soule et al., 1995; V=Valentine, 1976; W=Wolff and Soto, 1992. Where there are conflicts about information on modern taxa from different sources, information from the more recent source took precedence; otherwise the most detailed information is shown.

Appendix 2

SPECIMEN NUMBERS FOR CHITON FOSSILS DESCRIBED IN THIS PAPER

Specimen number	Species	Type specimen	Locality	Valve type (head, intermediate, tail)	Figure
13730	*Leptochiton rugatus*		305	Head	5.1–5.3
13731	*Leptochiton rugatus*		305	Head	5.4, 5.7
13732	*Leptochiton rugatus*		305	Head	5.5–5.6
13733	*Leptochiton rugatus*		305	Intermediate	5.8–5.10
13734	*Leptochiton rugatus*		305	Intermediate	5.11–5.12
13736	*Leptochiton rugatus*		305	Intermediate	5.13
13737	*Leptochiton rugatus*		305	Tail	5.14–5.15
13738	*Leptochiton rugatus*		305	Tail	5.16–5.17
13739	*Leptochiton nexus*		305	Intermediate	5.18–5.20
13740	*Leptochiton nexus*		305	Intermediate	5.21
13741	*Leptochiton nexus*		305	Intermediate	5.22, 5.26
13742	*Leptochiton nexus*		305	Intermediate	5.23–5.25
13743	*Leptochiton nexus*		305	Tail	5.27–5.29
13744	*Leptochiton nexus*		305	Tail	5.30
13745	*Leptochiton nexus*		305	Tail	5.31–5.32
13746	*Leptochiton nexus*		305	Tail	5.33–5.34
14294	*Leptochiton nexus*		305	3 head, 25 intermediate, and 60 tail valves	
14295	*Leptochiton nexus*		16817 (305C)	Tail	
14296	*Leptochiton nexus*		16862 (305A)	Tail	
13747	*Oldroydia percrassa*		305	Head	6.1–6.2
13748	*Oldroydia percrassa*		305	Head	6.3–6.4
13749	*Oldroydia percrassa*		305	Head	6.5–6.6
13750	*Oldroydia percrassa*		305	Intermediate	6.7
13751	*Oldroydia percrassa*		305	Intermediate	6.8–6.9
13752	*Oldroydia percrassa*		16817 (305C)	Intermediate	6.10, 6.13
13753	*Oldroydia percrassa*		16817 (305C)	Intermediate	6.11–6.12
13754	*Oldroydia percrassa*		16817 (305C)	Tail	6.14–6.15
13755	*Oldroydia percrassa*		305	Tail	6.16
13735	*Oldroydia percrassa*		305	Tail	6.17
14297	*Oldroydia percrassa*		305	23 head, 130 intermediate, and 50 tail valves	
14298	*Oldroydia percrassa*		16817 (305C)	2 head, 7 intermediate, and 4 tail valves	
14299	*Oldroydia percrassa*		16862 (305A)	1 head and 1 tail valve	
13756	*Callistochiton palmulatus*		16817 (305C)	Head	7.1–7.2
13757	*Callistochiton palmulatus*		305	Head	7.3–7.4
13758	*Callistochiton palmulatus*		16817 (305C)	Head	7.5–7.6
13759	*Callistochiton palmulatus*		16817 (305C)	Head	7.7–7.8
13760	*Callistochiton palmulatus*		16817 (305C)	Intermediate	7.9–7.11
13761	*Callistochiton palmulatus*		16817 (305C)	Intermediate	7.12–7.14
13762	*Callistochiton palmulatus*		16817 (305C)	Intermediate	7.15–7.17
13763	*Callistochiton palmulatus*		16817 (305C)	Tail	7.18–7.19
13764	*Callistochiton palmulatus*		305	Tail	7.20–7.21
13765	*Callistochiton palmulatus*		305	Tail	7.22–7.23
13766	*Callistochiton palmulatus*		305	Tail	7.24–7.25
1300	*Callistochiton palmulatus*		305	~2,500 head, 193 intermediate, and ~6,100 tail	
14301	*Callistochiton palmulatus*		16817 (305C)	122 head, 12 intermediate, and 448 tail valves	
14302	*Callistochiton palmulatus*		16862 (305A)	23 head, 31 intermediate, and 65 tail valves	
13767	*Callistochiton sphaerae* n. sp.	Paratype	305	Head	8.1–8.2
13768	*Callistochiton sphaerae* n. sp.	Paratype	305	Head	8.3–8.4
13769	*Callistochiton sphaerae* n. sp.	Holotype	305	Intermediate	8.5–8.7
13770	*Callistochiton sphaerae* n. sp.	Paratype	305	Intermediate	8.8–8.10
13771	*Callistochiton sphaerae* n. sp.	Paratype	305	Intermediate	8.11–8.13
13772	*Callistochiton sphaerae* n. sp.	Paratype	305	Intermediate	8.14–8.16
13773	*Callistochiton sphaerae* n. sp.	Paratype	305	Intermediate	8.17–8.18
13854	*Callistochiton sphaerae* n. sp.		16817 (305C)	Tail	8.19
13774	*Callistochiton sphaerae* n. sp.	Paratype	305	Tail	8.20–8.22
13775	*Callistochiton sphaerae* n. sp.	Paratype	305	Tail	8.23, 8.27
13776	*Callistochiton sphaerae* n. sp.	Paratype	305	Tail	8.24–8.26
14303	*Callistochiton sphaerae* n. sp.	Unfigured topotype lot	305	33 head, 87 intermediate, and 83 tail valves	

Appendix 2 [Continued]

Specimen number	Species	Type specimen	Locality	Valve type (head, intermediate, tail)	Figure
14304	*Callistochiton sphaerae* n. sp.		16817 (305C)	3 head, 9 intermediate, and 10 tail valves	
14305	*Callistochiton sphaerae* n. sp.		16862 (305A)	2 head and 6 tail valves	
13777	*Lepidozona mertensii*		16817 (305C)	Intermediate	9.1–9.4
13778	*Lepidozona mertensii*		16817 (305C)	Intermediate	9.5
13779	*Lepidozona mertensii*		16817 (305C)	Intermediate	9.6
13780	*Lepidozona mertensii*		305	Intermediate	9.7–9.8
13781	*Lepidozona mertensii*		305	Intermediate	9.9
13782	*Lepidozona mertensii*		16817 (305C)	Tail	9.10–9.11
13783	*Lepidozona mertensii*		16817 (305C)	Tail	9.12
13784	*Lepidozona mertensii*		16817 (305C)	Tail	9.13
13785	*Lepidozona mertensii*		305	Tail	9.14
13786	*Lepidozona mertensii*		305	Tail	9.15
14306	*Lepidozona mertensii*		305	200 head, 178 intermediate, and 333 tail valves	
14307	*Lepidozona mertensii*		16817 (305C)	9 head, 48 intermediate, and 11 tail valves	
14308	*Lepidozona mertensii*		16862 (305A)	2 head, 19 intermediate, and 8 tail valves	
13787	*Lepidozona pectinulata*		305	Head	10.1–10.3
13788	*Lepidozona pectinulata*		305	Head	10.4, 10.7
13789	*Lepidozona pectinulata*		305	Intermediate	10.5–10.6
13790	*Lepidozona pectinulata*		305	Intermediate	10.8–10.10
13791	*Lepidozona pectinulata*		305	Intermediate	10.11
13792	*Lepidozona pectinulata*		305	Intermediate	10.12
13793	*Lepidozona pectinulata*		16817 (305C)	Intermediate	10.13
13794	*Lepidozona pectinulata*		305	Tail	10.14–10.15
13795	*Lepidozona pectinulata*		305	Tail	10.16, 10.20
13796	*Lepidozona pectinulata*		305	Tail	10.17–10.19
13797	*Lepidozona pectinulata*		305	Tail	10.21–10.22
13798	*Lepidozona pectinulata*		305	Tail	10.23–10.24
13799	*Lepidozona pectinulata*		16817 (305C)	Tail	10.25–10.26
13800	*Lepidozona pectinulata*		16817 (305C)	Tail	10.27–10.28
14309	*Lepidozona pectinulata*		305	131 head, 498 intermediate, and 293 tail valves	
14310	*Lepidozona pectinulata*		16817 (305C)	1 head and 9 intermediate valves	
13801	*Lepidozona*sp. cf. *L. rothi*		305	Intermediate	11.1–11.2
13802	*Lepidozona*sp. cf. *L. rothi*		305	Intermediate	11.3
13803	*Lepidozona*sp. cf. *L. rothi*		305	Intermediate	11.4–11.5
13804	*Lepidozona* sp. cf. *L. radians*		305	Intermediate	11.6
13805	*Lepidozona* sp. cf. *L. radians*		305	Intermediate	11.7–11.8
13806	*Lepidozona* sp. cf. *L. radians*		305	Tail	11.9–11.10
14311	*Lepidozona* sp. cf. *L. radians*		305	1 head, 23 intermediate, and 9 tail valves	
14312	*Lepidozona* sp. cf. *L. radians*		16817 (305C)	5 intermediate valves	
13807	*Lepidozona kanakoffi* n. sp.	Paratype	305	Intermediate	11.11
13808	*Lepidozona kanakoffi* n. sp.	Paratype	305	Intermediate	11.12
13809	*Lepidozona kanakoffi* n. sp.	Paratype	305	Intermediate	11.13–11.14
13810	*Lepidozona kanakoffi* n. sp.	Holotype	305	Intermediate	11.15–11.16
13811	*Lepidozona kanakoffi* n. sp.	Paratype	305	Intermediate	11.17
13812	*Lepidozona kanakoffi* n. sp.	Paratype	305	Intermediate	11.18–11.20
13813	*Lepidozona kanakoffi* n. sp.		16817 (305C)	Tail	11.21–11.22
13814	*Lepidozona kanakoffi* n. sp.	Paratype	305	Tail	11.23–11.24
13815	*Lepidozona kanakoffi* n. sp.	Paratype	305	Tail	11.25–11.26
13816	*Lepidozona kanakoffi* n. sp.	Paratype	305	Tail	11.27–11.28
14313	*Lepidozona kanakoffi* n. sp.	Unfigured Topotype lot	305	25 intermediate and 22 tail valves	
14314	*Lepidozona kanakoffi* n. sp.		16817 (305C)	1 intermediate and 1 tail valve	
13817	*Stenoplax circumsenta*		305	Head	12.1–12.2
13818	*Stenoplax circumsenta*		305	Head	12.3–12.4
13819	*Stenoplax circumsenta*		16817 (305C)	Tail	12.5–12.6
13820	*Stenoplax circumsenta*		16817 (305C)	Tail	12.7
14315	*Stenoplax circumsenta*		305	1 head, 1 intermediate, and 5 tail valves	

Appendix 2 [Continued]

Specimen number	Species	Type specimen	Locality	Valve type (head, intermediate, tail)	Figure
14316	*Stenoplax circumsenta*		16817 (305C)	1 head, 1 intermediate, and 1 tail valve	
13821	*Stenoplax fallax*		305	Head	12.8
13822	*Stenoplax fallax*		305	Head	12.9
13823	*Stenoplax fallax*		305	Head	12.10–12.11
13824	*Stenoplax fallax*		305	Intermediate	12.12
13825	*Stenoplax fallax*		305	Intermediate	12.13
13826	*Stenoplax fallax*		305	Intermediate	12.14
13827	*Stenoplax fallax*		16817 (305C)	Intermediate	12.15–12.16
13828	*Stenoplax fallax*		305	Intermediate	12.17–12.18
13829	*Stenoplax fallax*		305	Tail	12.19
13830	*Stenoplax fallax*		305	Tail	12.20
13831	*Stenoplax fallax*		305	Tail	12.21
14317	*Stenoplax fallax*		305	5 head, 9 intermediate, and 10 tail valves	
14318	*Stenoplax fallax*		16817 (305C)	1 tail valve	
14319	*Stenoplax fallax*		16862 (305A)	1 head and 3 intermediate valves	
13832	*Stenoplax* sp. cf. *S. heathiana*		305	Head	13.1–13.2
13833	*Stenoplax* sp. cf. *S. heathiana*		305	Head	13.3–13.4
13834	*Stenoplax* sp. cf. *S. heathiana*		305	Intermediate	13.5
13835	*Stenoplax* sp. cf. *S. heathiana*		305	Intermediate	13.6–13.8
13836	*Stenoplax* sp. cf. *S. heathiana*		305	Intermediate	13.9, 13.12–13.13
13837	*Stenoplax* sp. cf. *S. heathiana*		305	Intermediate	13.10
13838	*Stenoplax* sp. cf. *S. heathiana*		305	Intermediate	13.11
13839	*Stenoplax* sp. cf. *S. heathiana*		16817 (305C)	Tail	13.14–13.15
13840	*Stenoplax* sp. cf. *S. heathiana*		305	Tail	13.16
13841	*Stenoplax* sp. cf. *S. heathiana*		305	Tail	13.17–13.19
13842	*Amicula solivaga* n. sp.	Paratype	305	Head	14.1
13843	*Amicula solivaga* n. sp.	Paratype	305	Head	14.2
13844	*Amicula solivaga* n. sp.	Paratype	305	Head	14.3
13845	*Amicula solivaga* n. sp.	Paratype	305	Head	14.4
13846	*Amicula solivaga* n. sp.	Holotype	305	Head	14.5
13847	*Amicula solivaga* n. sp.	Paratype	305	Head	14.6–14.7
13848	*Amicula solivaga* n. sp.	Paratype	305	Intermediate	14.8
13849	*Amicula solivaga* n. sp.	Paratype	305	Intermediate	14.9
13850	*Amicula solivaga* n. sp.	Paratype	305	Intermediate	14.10
13851	*Amicula solivaga* n. sp.		16817 (305C)	Intermediate	14.11–14.12
13852	*Amicula solivaga* n. sp.	Paratype	305	Intermediate	14.13
13853	*Amicula solivaga* n. sp.	Paratype	305	Tail	14.14–14.15
13855	*Amicula solivaga* n. sp.	Paratype	305	Tail	14.16
14320	*Amicula solivaga* n. sp.	Unfigured Topotype lot	305	3 head, 25 intermediate, and 5 tail valves	
14321	*Amicula solivaga* n. sp.		16817 (305C)	1 intermediate valve	
14322	*Amicula solivaga* n. sp.		16862 (305A)	1 head, 1 intermediate, and 1 tail valve	
13894	*Mopalia sinuata*		305	Head	15.1
13895	*Mopalia sinuata*		305	Intermediate	15.2–15.3
14323	*Mopalia sinuata*		305	12 head, 42 intermediate, and 4 tail valves	
14324	*Mopalia sinuata*		16862 (305A)	2 head and 1 intermediate valve	
13857	*Mopalia* sp. cf. *M. swanii*		16817 (305C)	Head	15.4, 15.7
13858	*Mopalia* sp. cf. *M. swanii*		305	Head	15.5–15.6
13859	*Mopalia* sp. cf. *M. swanii*		305	Head	15.8–15.9
13860	*Mopalia* sp. cf. *M. swanii*		305	Head	15.10
13861	*Mopalia* sp. cf. *M. swanii*		305	Intermediate	15.11–15.12
13862	*Mopalia* sp. cf. *M. swanii*		305	Intermediate	15.13
13863	*Mopalia* sp. cf. *M. swanii*		305	Intermediate	15.14
13864	*Mopalia* sp. cf. *M. swanii*		305	Intermediate	15.15
13865	*Mopalia* sp. cf. *M. swanii*		305	Intermediate	15.16
13866	*Mopalia* sp. cf. *M. swanii*		305	Intermediate	15.17
13867	*Mopalia* sp. cf. *M. swanii*		305	Intermediate	15.18
13868	*Mopalia* sp. cf. *M. swanii*		305	Intermediate	15.19
13869	*Mopalia* sp. cf. *M. swanii*		305	Tail	15.20–15.21
13870	*Mopalia* sp. cf. *M. swanii*		305	Tail	15.22–15.23
13871	*Mopalia* sp. cf. *M. swanii*		305	Tail	15.24
13872	*Mopalia* sp. cf. *M. swanii*		305	Tail	15.25–15.26

Appendix 2 [Continued]

Specimen number	Species	Type specimen	Locality	Valve type (head, intermediate, tail)	Figure
14325	*Mopalia* sp. cf. *M. swanii*		305	139 head, 204 intermediate, and 42 tail valves	
14326	*Mopalia* sp. cf. *M. swanii*		16817 (305C)	4 head and 4 intermediate valves	
14327	*Mopalia* sp. cf. *M. swanii*		16862 (305A)	1 head, 4 intermediate, and 1 tail valve	
13873	*Mopalia* sp.		305	Intermediate	15.27
13874	*Placiphorella velata*		16817 (305C)	Head	16.1–16.2
13875	*Placiphorella velata*		16817 (305C)	Intermediate	16.3
13876	*Placiphorella velata*		16817 (305C)	Intermediate	16.4
13877	*Placiphorella velata*		16817 (305C)	Tail	16.5–16.6
13878	*Placiphorella velata*		305	Tail	16.7–16.8
14328	*Placiphorella velata*		305	1 intermediate valve	
14329	*Placiphorella velata*		16817 (305C)	2 intermediate valves	
14330	*Placiphorella velata*		16862 (305A)	1 head and 1 tail valve	
13879	*Placiphorella* sp. cf. *P. mirabilis*		305	Intermediate	16.9–16.10
13880	*Placiphorella* sp. cf. *P. mirabilis*		305	Intermediate	16.11–16.12
13881	*Placiphorella* sp. cf. *P. mirabilis*		305	Intermediate	16.13
13882	*Placiphorella* sp. cf. *P. mirabilis*		305	Intermediate	16.14
13883	*Placiphorella* sp. cf. *P. mirabilis*		305	Tail	16.15
14331	*Placiphorella* sp. cf. *P. mirabilis*		305	3 head, 10 intermediate, and 4 tail valves	
13884	*Tonicella* sp. cf. *T. venusta*		305	Intermediate	16.16
13885	*Tonicella* sp. cf. *T. venusta*		305	Intermediate	16.17–16.18
13886	*Tonicella* sp. cf. *T. venusta*		305	Intermediate	16.19
13887	*Tonicella* sp. cf. *T. venusta*		305	Intermediate	16.20–16.22
13888	*Tonicella* sp. cf. *T. venusta*		305	Intermediate	16.23
13889	*Tonicella* sp. cf. *T. venusta*		305	Intermediate	16.24–16.26
13890	*Tonicella* sp. cf. *T. venusta*		305	Tail	16.27–16.28
13891	*Tonicella* sp. cf. *T. venusta*		305	Tail	16.29–16.30
14332	*Tonicella* sp. cf. *T. venusta*		305	2 head, 49 intermediate, and 1 tail valve	
14285	*Dendrochiton* sp. indeterminate		305	Intermediate	17.1–17.3
14288	*Dendrochiton* sp. indeterminate		305	Intermediate	17.4
14286	*Dendrochiton* sp. indeterminate		305	Intermediate	17.5–17.7
14289	*Dendrochiton* sp. indeterminate		305	Intermediate	17.8
14287	*Dendrochiton* sp. indeterminate		305	Intermediate	17.9–17.11
14290	*Dendrochiton* sp. indeterminate		305	Intermediate	17.12
14292	*Dendrochiton* sp. indeterminate		305	Intermediate	17.13–17.15
14293	*Dendrochiton* sp. indeterminate		16862 (305A)	Intermediate	17.16–17.18
14291	*Dendrochiton* sp. indeterminate		305	Intermediate	17.19
14333	*Dendrochiton* sp. indeterminate		305	3 intermediate valves	
13892	*Nuttallina* sp. indeterminate		16817 (305C)	Intermediate	17.20–17.22

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LATE PLIOCENE MEGAFOSSILS OF THE PICO FORMATION, NEWHALL AREA, LOS ANGELES COUNTY, SOUTHERN CALIFORNIA[1]

RICHARD L. SQUIRES[2]

ABSTRACT. Taxonomic composition and stratigraphic distribution of megafossils in the Pico Formation south of Newhall, northern Los Angeles County, Southern California, are described in detail. Eighty-three taxa, from 15 localities, were found: one brachiopod, 36 bivalves, 40 gastropods, one scaphopod, one crab, one barnacle, one sea urchin, one shark, and one land plant. All are illustrated here. The pectinid bivalve *Argopecten invalidus* (Hanna, 1924) is put into synonymy with *A. subdolus* (Hertlein, 1925) and *A. callidus* (Hertlein, 1925). Rare specimens of the gastropods *Calliostoma* and *Ocinebrina* might be new species.

The mollusks, which are indicative of a late Pliocene age, lived in waters of inner sublittoral depths and normal marine salinity. Most of the 41 extant species indicate warm-temperate waters similar to those occurring today off the adjacent coast, although a few species, both extant and extinct, indicate a southerly warmer water component. The fauna lived predominantly in, or on, soft sands, but a few lived on other shells or possibly on large rock clasts.

Geologic field mapping done as part of this present study revealed that the Pico Formation south of Newhall was deposited at the site where a braided river entered the marine environment (i.e., braid delta). Initially, the river gravel and coarse sand interfingered with relatively deep offshore silts, barren of megafauna, in the lower and middle parts of the formation. Eventually, the delta built up, and the resulting shoaling conditions in the upper part of the formation were conducive for the megafauna to live in, or immediately adjacent to, the deltaic shoreface fine sands. Storm waves raked the delta and concentrated the shells of the megafauna, along with cobbles of igneous and metamorphic basement rocks, into channelized deposits. Postmortem transport distance was short, as evidenced by many paired-valved bivalve shells.

INTRODUCTION

During the Pliocene, the Pico Formation was deposited for a distance of approximately 92 km along the axis of the Ventura Basin, which trends parallel to the present course of the modern Santa Clara River in Southern California (Fig. 1). The formation has its broadest extent of outcrops in the Ventura area, and the outcrop pattern narrows significantly eastward toward the Newhall area. The Pico Formation represents the youngest marine deposits in the eastern Ventura Basin. Throughout most of this basin, the Pico Formation is an offshore-marine sequence consisting of siltstone, mudstone, and claystone with some minor amounts of sandstone and conglomerate. Megafossils are sparse, but relatively deep-water benthic foraminifera are common. To the east, toward Val Verde and Valencia (Fig. 1), the formation becomes increasingly sandier and conglomeratic, and shallow-marine gastropods and bivalves are locally common in the upper part (Grant and Gale, 1931; Squires et al., 2006). The purposes of this present study are to 1) determine how far east the shallow-marine megafossiliferous beds continue beyond the Valencia area into the stratigraphically and structurally complex Newhall area, 2) tabulate and illustrate the taxonomic composition of the megafauna, and 3) establish its age, depositional environment, and zoogeographic implications.

All preexisting geologic maps (e.g., Winterer and Durham, 1958, 1962; Dibblee, 1991a, 1992a) of the Newhall area are inconsistent in regard to 1) the differentiation of the Pico Formation from the other Neogene stratigraphic units in the area (i.e., Towsley Formation, Saugus Formation, and Sunshine Ranch Member of the Saugus Formation), 2) the structural geology of the area, and 3) the depositional environments the Pico Formation. Also, no previous detailed megafossil investigations were done. It was necessary, therefore, to do my own geologic mapping in order to understand the fundamental geologic relationships of the easternmost Pico Formation in the Ventura Basin. The outcome is that the Pico Formation in the Newhall area is recognized for the first time as having been deposited in a braid-delta environment. This study is important because it affords the unusual opportunity to observe the complex interfingering between the fluvial and marine components of a Tertiary-age, predominantly marine formation in Southern California. The study area encompasses where the two environments interfinger for a lateral distance of approximately 5 km, and the lateral-fluvial component extends eastward for an additional 3 km (Fig. 2).

There might be a few small outcrops of the Pico formation just south and southeast of the study area in the San Fernando Valley (e.g., Lopez Canyon) (Chen, 1988) and, possibly, a fault-bounded, small outcrop approximately 22 km southeast of Newhall (Berry et al., 2009) in Gold Creek, a tributary of Big Tujunga Canyon.

PREVIOUS WORK

The earliest work on fossils from the study area was by Gabb (1869:49), who described a few species of Pliocene mollusks from an area originally referred to as Fremont Pass, later known as San Fernando Pass, and now known as Newhall Pass, located just north of the junction of U.S. Interstate 5 and California State Highway 14. Ashley (1895:338) listed some mollusks from the same general area. None of his specimens were illustrated nor were they assigned a museum catalog number; they could not be located.

Eldridge and Arnold (1907:22) used the name "Fernando" for an enormous section of siliciclastics, largely of Pliocene age, that crops out over a considerable area of Southern California, including the study area. Instead of basing the section on lithology, they improperly based it on three megafossil zones (collectively of Pliocene age). They erroneously lumped fossils found in Newhall Pass and Elsmere Canyon, but they listed only the fossils from Elsmere Canyon. The former beds belong to the

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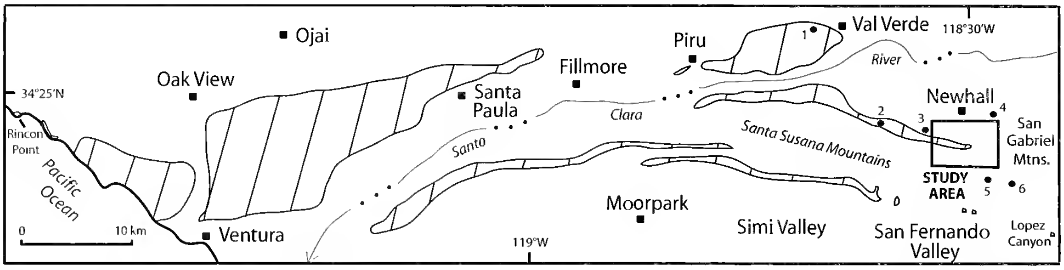


Figure 1 Index map showing outcrop-distribution map of the Pico Formation (slanted lines) in the Ventura Basin. Newhall-area outcrops (shown in box) based on this present report; remaining map area based on Dibblee (1987a, b, c; 1988; 1990a, b; 1991a, b; 1992a, b, c, d, e, f; 1993; 1996a, b). Specific locales: 1 = Holser Canyon; 2 = Pico Canyon, the type section of the Pico Formation; 3 = Valencia; 4 = Running Horse area; 5 = Los Angeles County Aqueduct (the "cascades"); and 6 = Stetson Ranch Park area.

Pico Formation, and the latter beds are now referred to as the Towsley Formation of early Pliocene age (Winterer and Durham, 1962; Kern, 1973). English (1914) and Kew (1918) used "Fernando Group" and "Fernando formation," respectively, for outcrops in the eastern Ventura Basin, but these units are vague, ambiguous, and should not be used.

Kew (1923) was the first worker to use the name "Pico" (following Clark's 1921 informal use of this name) for the lower part of the "Fernando Group." Kew (1924) formally defined the Pico Formation by designating a type section area in the vicinity of Pico Canyon, 11 km northwest of Newhall Pass (Fig. 1). Although he listed megafossils found in the Pico Formation, none of his localities are from the Newhall area. Kew (1924) incorrectly correlated beds in Elsmere Canyon to his Pico Formation. Grant and Gale (1931) over-applied Kew's (1924) name "Pico" to include all the Pliocene marine beds in the Ventura Basin. They failed to recognize that the beds, now referred to as the Towsley Formation, are lithologically different from the overlying Pico Formation. They subdivided the so-called "Pico" unit into three zones and correlated the fossiliferous beds in the Newhall area just west of Newhall Pass to their "San Diego Zone." They mistakenly referred any molluscan species found in the Newhall area to a "middle" Pliocene age. They mentioned and illustrated a few fossils from four localities just west of Newhall Pass (see "Localities" for equivalency to Natural History Museum of Los Angeles County Invertebrate Paleontology Section [LACMIP] localities).

Detailed geologic maps of all or part of the Newhall area were prepared by Rynearson (1938), Oakeshott (1958), Winterer and Durham (1958, 1962), Kern (1973), Barrows et al. (1975), Nelligan (1978), Dibblee (1991a, 1992a, 1996a), and Yerkes and Campbell (2005). No two maps are in agreement with regard to the outcrop distribution of the Pico Formation, and there are also inconsistencies as to which stratigraphic name(s) should be used.

Rynearson (1938), Winterer and Durham (1962:table 4), and Dibblee (1992a) mentioned a few fossil localities. They are in the central part of the study area and were recollected by the author (see "Localities" for equivalency to LACMIP localities). Rynearson was a student at Caltech, and his senior-thesis fossil collections became part of the LACMIP collection when Caltech donated its collections to LACMIP. Winterer and Durham (1962:table 4) provided a faunal list of some species they collected, but none of their specimens were illustrated or assigned a museum catalog number and they could not be located. Winterer and Durham (1962) also studied the benthic foraminifera fauna of Pico Formation just north of Gavin Canyon in the southwestern part of the Newhall area.

Dibblee (1991a) reported exposures of the Pico Formation just south of the study area in 1) a prominent cliff where the Los Angeles Aqueduct is aboveground at the "cascades" and 2) in another prominent cliff approximately 1.8 km to the east, in the Stetson Ranch area of Sylmar (Fig. 1). Both areas were examined by the author, and the exposures were placed in the Towsley Formation because they include greenish-gray sandstones like those of the Towsley Formation.

Oakeshott (1958:81), Ehlig (1975:14), and Powell (1993:43) reported that there are outcrops of the Pico Formation along the trend of the San Gabriel Fault just north of Placerita Canyon and approximately 1.5 km northeast of the northeastern corner of the Newhall area. Dibblee (1996b) mapped these same outcrops as the Saugus Formation. In order to resolve the issue, the area of Running Horse Road (Fig. 1), just north of the Placerita Nature Center, was examined, and these exposures possibly belong to the Sunshine Ranch Member? of the Saugus Formation.

Squires (2008) studied the geology of the Eocene Juncal Formation east of Newhall and provided a generalized geologic map that included the Pico and Saugus formations. Squires et al. (2006) studied the Pico Formation immediately west of the western border of the Newhall area. The term "Pico Formation" is used in this present report because of the historic usage of the term, thereby reducing further stratigraphic nomenclature confusion. A more appropriate term would be "marine facies of the Saugus Formation."

MATERIALS AND METHODS

Field work was begun in March 2006 but most of field time occurred during the last half of 2011. The geology was mapped at a scale of 1:12,000, and megafossils and rock samples were collected. Every available road and trail was hiked, and a considerable amount of cross-country traversing was done. The field area comprises steep terrain, and 30-m-high or higher vertical cliffs are common, as is dense vegetation that is impenetrable in many places. The shoreface deposits in the uppermost part of the formation are especially difficult to access because of these problems. There is no continuous stratigraphic section to measure the formation from its base to its top because of faults and local incisement by overlying stratigraphic units. Thicknesses were derived by means of graphical techniques: the Elsmere Ridge area was used for the fluvial part of the formation, and the Gavin Ridge area was used for the marine part of the formation (Fig. 2).

Fossils were studied from 15 localities: eight previously known and seven new localities. Some of the previously known localities have been assigned, over the years, to different but equivalent or approximately equivalent locality numbers. Approximations had to be made for some of the previous localities because their word descriptions are inexact and the localities were never precisely plotted on a map but are in close proximity to where the present collections were made. In those cases, new locality numbers based on personal mapping (e.g., LACMIP locs. 17917 and 17918) were assigned.

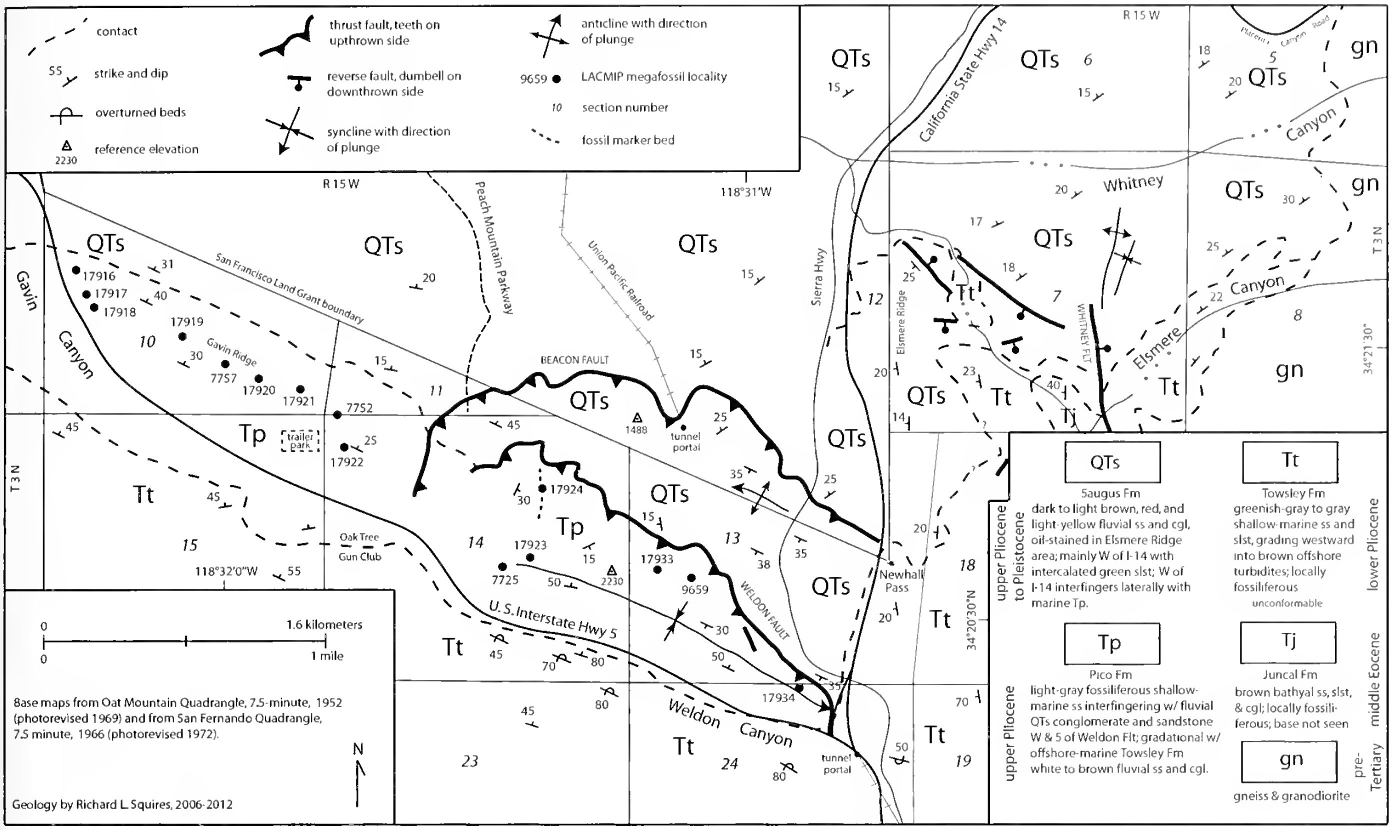


Figure 2 Geologic map of the study area south of Newhall, northern Los Angeles County, California.

A total of 2020 specimens were studied, and approximately half of these specimens were personally collected. The figured specimens, as well as all the other megafossils collected in the course of this study, were deposited in the LACMIP collection.

Matrix was removed from the fossils by the use of hammer and chisel, and, for fine cleaning, a high-speed drill. A systematic treatment for each megafaunal species is not given here because no new information was gleaned for most of the species collected during the present study. Previous synonymies, distinctive morphologic characters, and stratigraphic distributions, etc. are available for most of the species in works such as Arnold (1903), Grant and Gale (1931), Hertlein and Grant (1972), Groves (1991), Davis (1998), and Squires et al. (2006). New information is given here in the "Systematics" section for newly recognized synonyms of the pectinid *Argopecten invalidus* and for two potential new species of gastropods. Figures of the taxa listed in Table 1 are included here in order to verify this list, and the numerical order of these figures corresponds to the systematic organization used for the faunal list.

ABBREVIATIONS: Abbreviations used for locality and/or catalog numbers are CAS (California Academy of Sciences, San Francisco; includes the Stanford University [SU] collection), and LACMIP (Natural History Museum of Los Angeles County, Invertebrate Paleontology Section).

LOCALITIES

All are LACMIP localities in the Pico Formation of upper Pliocene age, and located relative to the United States Geological Survey Oat Mountain Quadrangle (7.5 minute), 1952 (photorevised 1969), Los Angeles County, southern California.

7725. 118°31′40″W, 34°20′35″N. Elevation 549 m (1800 ft.), crest of spur at base of power-line tower, 703 m (2300 ft.) north and 703 m (2300 ft.) west of southeast corner of section 14. Collectors: H.M. Rice (*circa* early 1930s) and R.L. Squires, October 1, 2011. **7752 [= 5547].** 118°31′15″W, 34°21′08″N. Elevation 427 m (1400 ft.), northeast of trailer park in north–south-trending canyon, on south section-line, 91 m (300 ft.) east of northeast corner of section 14. Locality represents float material from a bed located a short distance to the north at the head of a box canyon with inaccessible vertical cliffs. Collectors: H.M. Rice (*circa* early 1930s); L.G. Barnes and G. Campbell, April 1965; and R.L. Squires, October 9, November 13, and December 4, 2011. **7757.** 118°32′33″W, 34°21′15″N. Elevation 525 m (1725 ft.), on ridgeline, 290 m (950 ft.) north and 1036 m (3400 ft.) east of southwest corner of section 10. Collectors: H.M. Rice (*circa* early 1930s) and R.L. Squires, October 21, 2011. **9659.** 118°31′14″W, 34°20′34″N. Elevation 637 m (2090 ft.), on ridgeline, 655 m (2150 ft.) north and 381 m (1250 ft.) east of southwest corner of section 24. Collectors: G.A. Rynearson (1938) and R.L. Squires, September 4, 2011. Equivalent to loc. 212 of Grant and Gale (1931:102). **17916.** 118°32′49″W, 34°21′33″N. Elevation 434 m (1425 ft.), south side of disused road near south end of housing tract south of Calgrove Blvd., 899 m (2950 ft.) north and 168 m (550 ft.) east of southwest corner of section 10, T 3 N, R 16 W. Collector: R.L. Squires, October 21, 2011. **17917 [= 7761 and approximately 7226 and 10339].** 118°32′47.5″W, 34°21′30″N. Elevation 480 m (1575 ft.), east side of power line road east of Gavin Canyon, 747 m (2450 ft.) and 213 m (700 ft.) east of southwest corner of section 10, T 3 N, R 16 W. Collectors: H.M. Rice (*circa* early 1930s); G.M. Dorwat, March 22, 1943; C.R. Stauffer, 1949; and R.L. Squires, October 21, 2011. **17918 [= 7760].** 118°32′48″W, 34°21′28″N. Elevation 450 m (1475 ft.), north side of power line

Table 1 Megafossils of the Newhall area Pico Formation listed systematically and with relative abundance vs. localities (arranged west to east).

	LACMIP locs.														
Taxa	17916	17917	17918	17919	7757	17920	17921	7752	17922	17925	17923	17924	17933	9659	17934
Brachiopoda: Articulata															
Terebratalia occidentalis (Dall, 1871)		A*	A*	R*				C*		A*					
Mollusca: Bivalvia															
Jupiteria taphria (Dall, 1896)		R*	A*				R*	R							
Arcopsis sp.			R												
Anadara trilineata (Conrad, 1856)								R							R*
Limaria sp., cf. *L. orcutti* (Hertlein & Grant, 1972)		F													
Myrakeena veatchii (Gabb, 1866)	R	A*	F	A*	R*	R		C*						A*	F
Argopecten invalidus (Hanna, 1924)		A*	A*	A*	A*	F		A*	F*	C*	C*	F		C*	A*
Lyropecten catalinae (Arnold, 1906)	F	R	F*	R	R			F*		C*		R		F	R*
Swiftopecten parmeleei (Dall, 1898)				R											
Leopecten stearnsii (Dall, 1878)						R				F*					
Patinopecten healeyi (Arnold, 1906)		R*	R	R		R			R	C	R	R*		R*	
Pododesmus macroschisma (Deshayes, 1839)		R													
Epilucina californica (Conrad, 1837)			F					R		R					
Here excavata (Carpenter, 1857)	R	F*	A*		R	R	R	A*			R		F		R
Lucinisca nuttalli (Conrad, 1837)			R							R					
Lucinoma annulatum (Reeve, 1850)			R*								R				
Miltha xantusi (Dall, 1905)	F	F		R		R		R*	F*	R*		F*			R*
Cyclocardia occidentalis Conrad, 1855		C	A		R	A				C					R
Trachycardium (*Dallocardia*) *quadragenarium* (Conrad, 1837)		R	R*	R	R*	R		F*		C	R*		R	R	F*
Chione (*Anomalocardia*) *fernandoensis* English, 1914			A	R*			R	R*		C				R	R
Callithaca tenerrima (Carpenter, in Gould and Carpenter, 1857)	R	R*	R*	R*				F*		R					R
Compsomyax subdiaphana (Carpenter, 1864)		R*	R*		R			F							
Amiantis callosa (Conrad, 1837)	F							F							
Dosinia ponderosa (Gray, 1838)										R*					
Saxidomus nuttalli Conrad, 1837							R*	R*							
Tresus nuttallii (Conrad, 1837)	R*							F*							R*
Macoma (*Rexithaerus*) *secta* (Conrad, 1837)	R*							R*		F*		R*			
Macoma nasuta (Conrad, 1837)	R*							F							
Leporimetis obesa (Deshayes, 1855)		F*		R*	R*		R*	R*							
Tellina (*Tellinella*) *idae* Dall, 1891		R*	R*			F*							R*		R*
Gari sp.		R*		R	F					R*					
Solen (*Ensisolen*) *sicarius* Gould, 1850	R	F	C	F	A*	R	R	C	R	C	R				
Solen sp., cf. *Solen perrini* Clark, 1915			R					C			R*				
Panopea abrupta (Conrad, 1849)	R*	R*	R*		R			A*		R*	R				R*
?*Chaceia ovoidea* (Gould, 1851)					R										
Pandora (*Heteroclidus*) *punctuata* Conrad, 1837			R		R										
?*Cyathodonta pedroana* Dall, 1915				R	R			R							
Mollusca: Gastropoda															
Haliotis sp.							R								
Calliostoma sp., C. cf. *splendens* Carpenter, 1864			F					R							
Calliostoma sp.,aff. C. *grantianum* Berry, 1940			R												

Table 1 Continued.

	LACMIP locs.														
Taxa	17916	17917	17918	17919	7757	17920	17921	7752	17922	17925	17923	17924	17933	9659	17934
Chlorostoma gallina form *multifilosa* Stearns, 1892		R						F							
Homoploma paucicostatum? (Dall, 1871)			R												
Pomaulax gradata Grant and Gale, 1931		R	F					C							R
Lirobittium asperum (Gabb, 1861)			A					R							
Turritella cooperi Carpenter, 1864	A	A	A	A	A	A	F	A	F	A	A	A	C	A	A
?*Calyptraea* (*Trochita*) sp.		F	A					R		R					
Crepidula aculeata (Gmelin, 1791)	R		A					R		A					
Grandicrepidula princeps (Conrad, 1857)							R								
Zonaria (*Neobernaya*) *spadicea* (Swainson, 1823)					R			R							
Glossaulax reclusiana (Deshayes, 1839)	R	F	A	F	F	F		A	R	C	R			R	
Cryptonatica clausa (Broderip & Sowerby, 1829)								R							
Sinum scopulosum (Conrad, 1849)			R		R			R							
Asperiscala sp., cf. A. *minuticostata* (De Boury, 1912)	R				R										
Amaea (*Scalina*) sp., cf. *A.* (*S.*) *edwilsoni* DuShane, 1977		R													R
Cymatium sp., cf. C. (*Reticutriton*) *elsmerense* (English, 1914)		R													
Ocinebrina atropurpurea (Carpenter, 1865)								R							
Ocinebrina sp., aff. *O. fraseri* (Oldroyd, 1920)			R												
Calicantharus humerosus (Gabb, 1869)		A	C	R	C	R	R	A		C	C	R			C
Calicantharus fortis (Carpenter, 1864)		F	R		R	R									
Alia tuberosa (Carpenter, 1864)			F												R
Amphissa sp.			R												
Barbarofusus barbarensis (Trask, 1855)		R	C	R											R
Nassarius (*Demondia*) *californianus* (Conrad, 1856)		F	A		R		R	C		A					A
Callianax baetica (Carpenter, 1864)			R												
Californiconuscalifornicus? (Reeve, 1843a)			R		R										
Ophiodermella inermis (Reeve, 1843b)			R		R										
Cockerella conradiana (Gabb, 1866)			R												
Elaeocyma sp.			R					R							
Crassispira sp.			R												
Terebra (*Strioterebra*) *martini* English, 1914		R	A		R	R		F		R					R
Cancellaria altispira Gabb, 1869															R
Cancellaria hemphilli Dall, 1909					R										
Cancellaria tritonidea? Gabb, 1866								R							
Cancellaria hamlini Carson, 1926				R											
Turbonilla sp.			R												
Rictaxis painei grandior Grant & Gale, 1931			R					R		R				R	
Acteocina culcitella? (Gould, 1853)			R												
Mollusca: Scaphopoda															
Dentaliumneohexagonum Sharp and Pilsbry, in Pilsbry and Sharp, 1897		R		R											
Arthropoda: Crustacea: Cirripedia(barnacles)															
Balanus? sp.		R						R							

Table 1 Continued.

Taxa	LACMIP locs.														
	17916	17917	17918	17919	7757	17920	17921	7752	17922	17925	17923	17924	17933	9659	17934
Arthropoda: Decapoda															
Crab leg (partial)			R												
Echinodermata: Echinoidea (sea urchins)															
Eucidaris sp. (spine)		R	R				F	R							
Vertebrata:Chrondrichthyes															
Myliobatis sp. (ray tooth)								R							
Plantae: Pinophyta (conifers)															
Pine cone								R							

Abbreviations: A = abundant (>10 specimens); C = common (5–9 specimens); F = few (3–4 specimens); R = rare (≤2 specimens).
* Some or all valves paired.

road east of Gavin Canyon, 701 m (2300 ft.) north and 267 m (875 ft.) east of southwest corner of section 10, T 3 N, R 16 W. Collectors: G.M. Dorwat, March 22, 1943, and R.L. Squires, October 21, 2011. **17919.** 118°32′38″W, 34°21′16.5″N. Elevation 506 m (1660 ft.), on ridgeline just below "0" in "10," 480 m (1575 ft.) north and 777 m (2550 ft.) east of southwest corner of section 10, T 3 N, R 16 W. Collector: R.L. Squires, November 7, 2010, and October 21, 2011. **17920.** 118°32′30″W, 34°21′12″N. Elevation 518 m (1700 ft.), on ridgeline 259 m (850 ft.) north and 419 m (1375 ft.) west of southeast corner of section 10, T 3 N, R 16 W. Collector: R.L. Squires, December 10, 2011. **17921.** 118°32′22″W, 34°21′,10″N. Elevation 549 m (1800 ft.), on ridgeline 152 m (500 ft.) north and 129 m (425 ft.) west of southeast corner of section 10, T 3 N, R 16 W. Collector: R.L. Squires, December 10, 2011. **17922.** 118°32′14″W, 34°21′00″N. Elevation 479 m (1570 ft.), on east side of power line road just east of trailer park, 198 m (650 ft.) south and 122 m (400 ft.) east of northwest corner of section 14. Collector: R.L. Squires, October 9, 2011. **17923.** 118°31′40″W, 34°20′35.5″N. Elevation 610 m (2000 ft.), 739 m (2425 ft.) north and 533 m (1750 ft.) west of southeast corner of section 14. Collector: R.L. Squires, September 4, 2011. Equivalent to southernmost loc. of Dibblee (1992a). **17924.** 118°31′38″W, 34°20′53″N. Elevation 632 m (2075 ft.), on north–south-trending ridgeline, 1204 m (3950 ft.) north and 488 m (1600 ft.) west of southeast corner of section 14. Collector: R.L. Squires, September 25, 2011. Equivalent to loc. 213 of Grant and Gale (1931:102) and to the northernmost loc. of both Rynearson (1938) and Dibblee (1992a). **17933.** 118°31′16″W, 34°20′35″N. Elevation 582 m (1910 ft.), small outcrop north side of road along ridgeline, 671 m (2200 ft.) north and 183 m (600 ft.) east of southwest corner of section 13. Collector: R.L. Squires, September 4, 2011. **17934 [= approximately 422, 4720, and 7797].** 118°30′22″W, 34°20′15″N. Elevation 552 m (1810 ft.), on east side of power line road just north of small concrete building, 30 m (100 ft.) north and 975 m (3200 ft.) east of southwest corner of section 13. Collectors: G.P. Kanakoff (date unknown), G.A. Rynearson (1938), and R.L. Squires, September 4, 2011. In vicinity of locs. 211 and 214 of Grant and Gale (1931:102) and loc. F76 of Winterer and Durham (1962).

STRATIGRAPHY AND DEPOSITIONAL ENVIRONMENTS

In the eastern and central parts of the study area (Figs. 2, 3), the Saugus Formation consists of fluvial (braided-river) deposits that include siltstone, sandstone, conglomeratic sandstone, and interspersed lenses of conglomerate. No mudstone was found, nor were any fossils. The siltstone is green, red, or brown and crops out mainly in the eastern part of the study area. West of California State Highway 14, the green siltstones are intercalated within lighter colored and coarser deposits. The sandstone is medium to coarse grained and white on fresh surfaces. Horizontal laminated bedding and low-angle crossbedding are common. Locally, there can be higher angle, large-scale trough crossbedding. The conglomerate occurs as channel fills with erosive bases and sharp tops. Crude fining-upward sequences are common, and crude imbrication of clasts is less common. Clasts are matrix supported and poorly to moderately well sorted. Most of the pebble- to boulder-size (up to 50 cm length) clasts are commonly rounded to subrounded, but some are flat. They mostly consist of leucogranite and granite, which together make up approximately one-half of all the clasts, with the granite commonly accounting for 30% and leucogranite 20%. Other clasts, listed in decreasing abundance are gneiss, volcanic porphyry, quartzite, anorthosite, hornblende-rich diorite, schist,

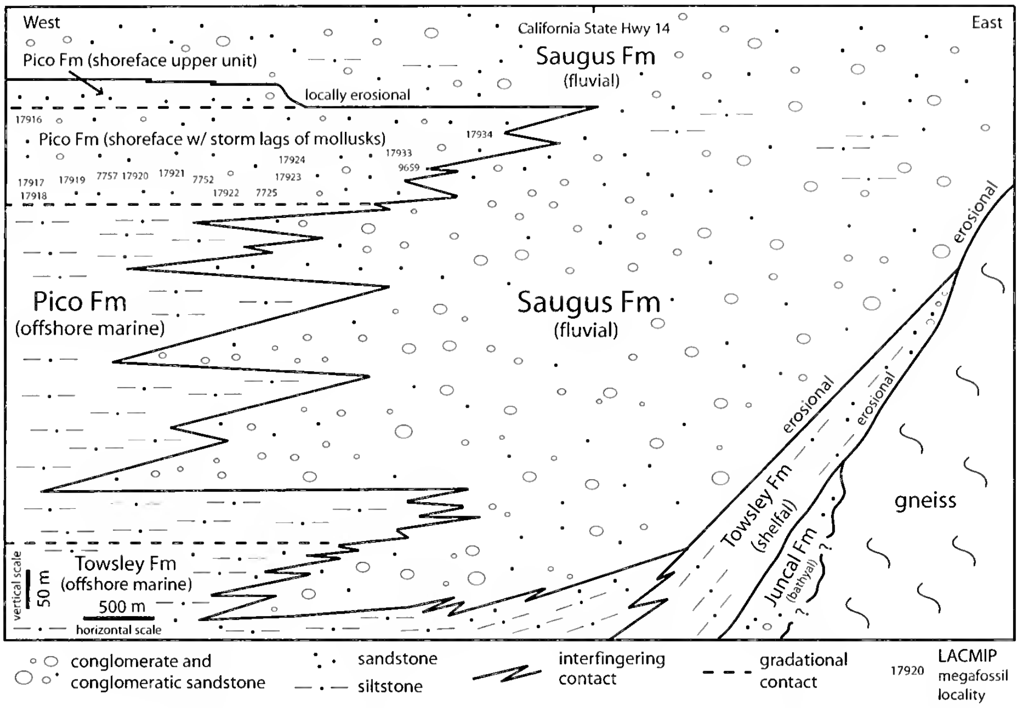


Figure 3 Schematic cross section of the study area braid delta, with folds and faults removed. Vertical exaggeration ×5.5.

and argillite. Up-section, the amount of conglomerate decreases. Beds in the Saugus Formation commonly weather brown or orange-brown, and, locally, are oil stained and weather gray, especially in lower Elsmere Canyon. The sandstone is white on fresh surfaces. Stratigraphic relationships of the Saugus Formation with the underlying and overlying rocks are shown in Figure 3. The lower part of the Saugus Formation in the study area has many dark-colored deposits (e.g., dark brown, yellow brown, green, and red) that eventually might prove to belong to Oakeshott's (1950) Sunshine Ranch stratigraphic unit, whose type section is approximately 5.5 km south of the study area.

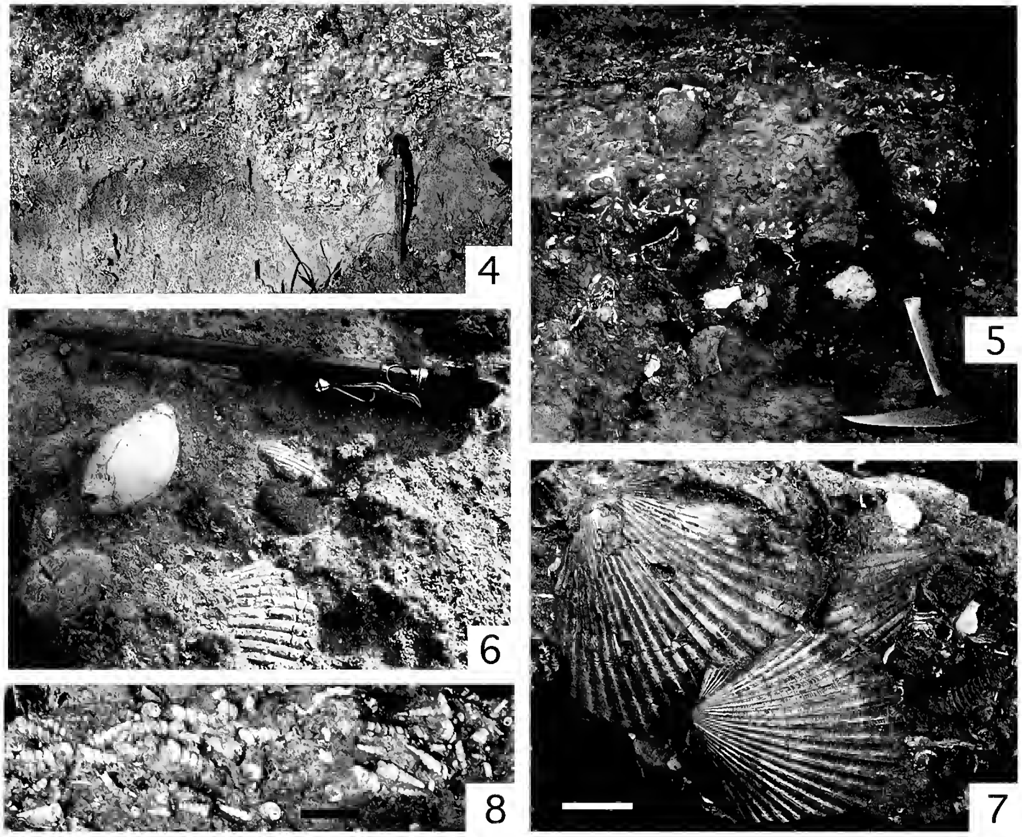
In the western part of the study area, the Saugus Formation laterally interfingers with the marine Pico Formation, and the term "braid delta," which McPherson et al. (1987) coined for a gravel-rich delta that forms where a braided river system progrades into a standing body of water, aptly applies to the study area. Initially, the fluvial deposits interfingered with offshore-marine siltstones (barren of megafossils) in the upper part of the Towsley Formation and in the lower and middle parts of the Pico Formation. The conglomerates that interfinger with these relatively quiet-water offshore siltstones are unfossiliferous. They are also thicker, more wedge-shaped, more laterally continuous; have much more distinct boundaries; and show more incisement (up to 3 m) than do the commonly fossiliferous conglomeratic storm lags that are present higher in the section in the shoreface deposits. This interfingering continues, but to a lesser degree, in the adjacent Valencia area to the west.

The offshore-marine siltstone (approximately 450 m thick) that makes up most of the western part of the Pico Formation in the study area grades up-section into the sandstones of the shoreface facies, which consists of a lower fossiliferous part and an upper unfossiliferous part. The lower part consists of grayish white, very fine to fine sandstones (approximately 130 m thick) with scattered channelized lenses and lentils filled with storm lags of mollusks and associated pebble- and cobble-sized clasts similar in size and composition to those of the fluvial facies (Figs. 4–8). Locally, there can be angular clasts in addition to the more commonly occurring rounded clasts. Locally there are coquinas, but the shells are unabraded. The shells were transported and concentrated by storm waves, and distance of transport was relatively short (see "Taphonomy" for details). These fossiliferous deposits represent a marine transgression that deposited the shoreface facies as far east as LACMIP loc. 17934, in the immediate vicinity of California State Highway 14, just north of the south portal of the Union Pacific Railroad tunnel. The lower part of the shoreface facies also contains some relatively thick intervals of unfossiliferous sandstone that locally have intervals of bidirectional crossbeds (e.g., in the vicinity of LACMIP loc. 7752), probably caused by inflow and outflow of tidal currents. The lower fossiliferous part of the shoreface facies is equivalent to the "basal unit" and "middle unit" described by Squires et al. (2006) for strata immediately west of the Newhall area.

The upper part of the shoreface facies (approximately 35 m thick) is gradational with the underlying megafossiliferous shoreface facies and consists of white, unfossiliferous, fine to medium sandstone that is parallel-laminated and amalgamated. Minor conglomeratic sandstone beds can also be present. The upper part of the shoreface facies crops out west of the Beacon Fault to beyond U.S. Interstate Highway 5 and is the same as the "upper unit" described by Squires et al. (2006) from strata immediately west of the Newhall area. The upper unit interfingers with the overlying Saugus Formation. East of this fault the upper unit has been removed by erosion.

OVERVIEW OF MEGAFOSSILS

The megafossils were collected mostly from localities in the lower part of the shoreface facies, which trends in a northwest–southeast direction between Gavin Canyon and California State Highway 14 (Fig. 2). The locations, whose geographic and



Figures 4–8 Selected outcrops of the megafossiliferous, shoreface storm-lag deposits in the upper part of the Pico Formation in the Newhall area. **4.** Channel, filled with fossils, vicinity of LACMIP locality 17913, pencil 13 cm length. **5.** Channelized lens of fossils, pebbles, and small cobbles, vicinity of LACMIP locality 7757, hammer 32.5 cm length. **6.** Top of channel fill with pectinid fragments, cobbles, and a complete *Zonaria* (*Neobernaya*) *spadicea* (Swainson, 1823) (same specimen shown in Figs. 68, 69), LACMIP loc. 7752, pencil 13 cm length. **7.** Part of a lens of *Turritella cooperi* showing bimodal-preferred orientation, LACMIP loc. 7752, scale bar 15 mm. **8.** Part of a fossiliferous lens with valves of *Argopecten invalidus* and scattered pebbles, LACMIP loc. 7757, scale bar 20 mm.

relative stratigraphic positions are shown on Figure 2, are from an interval approximately 130 m thick in the upper part of the shoreface facies west of the Beacon Fault. This interval contains scattered lenses of megafossils. The species and their relative abundance are listed in Table 1, along with information about the occurrence of paired valves of the bivalves. The listed megafauna consists of 83 species: one brachiopod, 36 bivalves, 40 gastropods, one scaphopod, one crab (partial leg), one barnacle, one sea urchin (spine), one shark (ray tooth), and one land plant (pine cone). All these taxa are illustrated here (Figs. 9–106). The ray tooth and pine cone occur together in the same hand specimen. A few epibionts were also found but are badly weathered: some small patches of an encrusting bryozoan and some minute tubes of an encrusting annelid (spirorbid) were detected on the same brachiopod specimens from LACMIP loc. 17918. These poorly preserved taxa are not illustrated here because of their very limited taxonomic information. Boreholes are scarce. Those made by sponges? or algae? are present on some oyster valves, those made by predatory gastropods occur on a few bivalves. Preservation differs greatly among the mollusks. Calcitic pectinids, oysters, and turritellas are well preserved, whereas aragonitic mollusks are commonly poorly preserved due to weathering. Some of the very weathered, small-sized mollusks are especially prone to disintegration upon touch.

The species found at the greatest number of localities and in the greatest numbers, are the following: *Turritella cooperi* Carpenter, 1864, *Argopecten invalidus*, *Calicantharus humerosus* (Gabb, 1869), *Glossaulax reclusiana* (Deshayes, 1839), *Myrakeena veatchii* (Gabb, 1866), and *Here excavata* (Carpenter, 1857). Paired valves are common, especially for *Argopecten invalidus*, *Myrakeena veatchii*, *Trachycardium* (*Dallocardia*) *quadragenarium* (Conrad, 1837), *Callithaca tenerrima* (Carpenter, in Gould and Carpenter, 1857), *Saxidomus nuttalli* Conrad, 1837, *Tresus nuttallii* (Conrad, 1837), and *Panopea abrupta* (Conrad, 1849).

SYSTEMATICS

Phylum Mollusca Linnaeus, 1758
Class Bivalvia Linnaeus, 1758
Family Pectinidae Rafinesque, 1815
Genus *Argopecten* Monterosato, 1889
Argopecten Monterosato, 1889:20
Plagioctenium Dall, 1898:696

TYPE SPECIES. *Pecten solidulus* Reeve, 1853, by subsequent designation (Monterosato, 1899:193) = *Pecten ventricosus* G.B. Sowerby II, 1842, not *Pecten circularis* G.B. Sowerby I, 1835 (*fide* Waller, 1995); Holocene, southern California and Gulf of California to Peru (Coan et al., 2000:235).

Argopecten invalidus (Hanna, 1924)
Figures 16–19

Pecten (*Plagioctenium*) *cooperi* Arnold, 1906:124, pl. 49, figs. 2–4. Not *Pecten cooperi* Smith, 1903.

Pecten invalidus Hanna, 1924:177, new name for *P. cooperi* Arnold, 1906.

Pecten (*Plagioctenium*) *subdolus* Hertlein, 1925:20, pl. 5, figs. 2, 4, 7.

Pecten (*Plagioctenium*) *callidus* Hertlein, 1925:22, pl. 5, figs. 1, 3, 5, 6.

Pecten (*Plagioctenium*) *invalidus* Hanna. Jordan and Hertlein, 1926:441; Minch et al., 1976:table 15.

Pecten (*Aequipecten*) *purpuratus* Lamarck variety *subdolus* Hertlein. Grant and Gale, 1931:211, pl. 5, fig. 1 (west of San Fernando Pass).

Pecten (*Aequipecten*) *purpuratus* Lamarck variety *callidus* Hertlein. Grant and Gale, 1931:211, pl. 5, fig. 4.

Pecten (*Aequipecten*) *deserti* Conrad variety *invalidus* Hanna. Grant and Gale, 1931:213–214, pl. 5, figs. 5a–c, 6a–c.

Aequipecten callidus (Hertlein). Wilson, 1955:tables 7, 8.

Aequipecten subdolus (Hertlein). Wilson, 1955:table 8.

Argopecten invalidus (Hanna). Vedder, 1960: table 151.1; Moore, 1984:B37, pl. 10, fig. 5; Squires et al., 2006:11–12, figs. 15, 16.

Pecten (*Argopecten*) *subdolus* Hertlein. Moore, 1968:50, pl. 23, figs. a, b.

Chlamys (*Argopecten*) *callida* Hertlein. Hertlein and Grant, 1972:198–199, pl. 32, figs. 9, 11.

Chlamys (*Argopecten*) *invalida* Hanna. Hertlein and Grant, 1972:200–201, pl. 33, figs. 1, 3, 8.

Chlamys (*Argopecten*) *subdola* Hertlein. Hertlein and Grant, 1972:201–202, pl. 30, figs. 7, 8; pl. 35, figs. 2, 5, 9.

Argopecten subdolus (Hertlein). Moore, 1984:B37–B38, pl. 10, figs. 3, 4.

Argopecten callidus (Hertlein). Moore, 1984:B38–B39, pl. 10, figs. 7, 9.

EMENDED DESCRIPTION. Shell medium size, up to height 117 mm; specimens commonly approximately height 45–55 mm. Valves slightly longer than high on most specimens; smaller specimens tend to be slightly longer than high, larger specimens tend to be slightly higher than long. Left valve more convex than right valve on most specimens; valves nearly equally convex on few specimens. Hinge line approximately half of disk length. Umbonal (apical angle) 100°–105°. Ribs 20–22 in number on both valves, with lamellae in interspaces. Ribs become obsolete on anteriormost and posteriormost parts of valves and tend to flatten out and become more convex in the later stages of growth. Auricles with prominent radial riblets on both valves; riblets stronger on anterior auricles of both valves. **Left valve:** ribs narrower than on right valve; interspaces wider than ribs and wider than those on right valve; anterior auricle with very small notch; posterior auricle slightly truncated; anterior and posterior auricles, both auricles with seven to nine riblets. **Right valve:** ribs wider than on left valve; interspaces narrower than ribs and narrower than those on left valve; anterior auricle with small notch; five to seven flattish riblets, strongest one coincident with notch area and variable in width and elevation; posterior auricle slightly truncate; six to seven (rarely more) radial riblets.

COMPARISON. *Argopecten invalidus*, *A. callidus*, and *A. subdolus* are conspecific based on a comparative study of actual specimens of each "species" that shows they lack consistent, reliable morphologic differences separating them from one another. Their reported differences (see Hertlein, 1925; Hertlein and Grant, 1972) were based on whether or not the ribs are flat-topped, rounded, and on the depth of the interspaces. These differences, however, are attributable to how much weathering the specimens have experienced. In the study area, for example, specimens of *A. invalidus* at any one locality show variation in the shape and depth of the ribs, with the variation clearly attributable to the degree of weathering.

In addition to *A. invalidus*, *A. callidus*, and *A. subdolus*, Grant and Gale (1931:see pages 210, 211, 212, 214) reported three other argopectinid species in the study area beds: *A. percarus* (Hertlein, 1925), *A. mendenhalli* (Arnold, 1906), and *A. imposter* (Hanna, 1924). *Argopecten percarus* differs from *A. invalidus* by having 24–25 ribs on the left valve and an umbonal angle of 118°. *Argopecten mendenhalli* differs from *A. invalidus* by having a much longer hinge line, weak sculpture on the right-valve anterior auricle, obsolete sculpture on the left-valve anterior auricle. *Argopecten imposter* differs from *A. invalidus* by having weak grooves along the sides of the major ribs and a left valve with narrower interspaces.

Argopecten invalidus is similar to *A. deserti* (Conrad, 1855) and the extant *A. ventricosus* (G.B. Sowerby II, 1842). *Argopecten invalidus* differs from *A. deserti* by having larger size, right-valve interspaces narrower than the ribs, left-valve ribs narrower than those on the right valve, left-valve interspaces wider than the ribs, more ribs on the right-valve anterior auricle, and a shorter hinge line. *Argopecten invalidus* differs from *A. ventricosus* by having a larger maximum height (95 mm), less-inflated right valve, as well as narrower and generally more ribs on the right-valve anterior auricle.

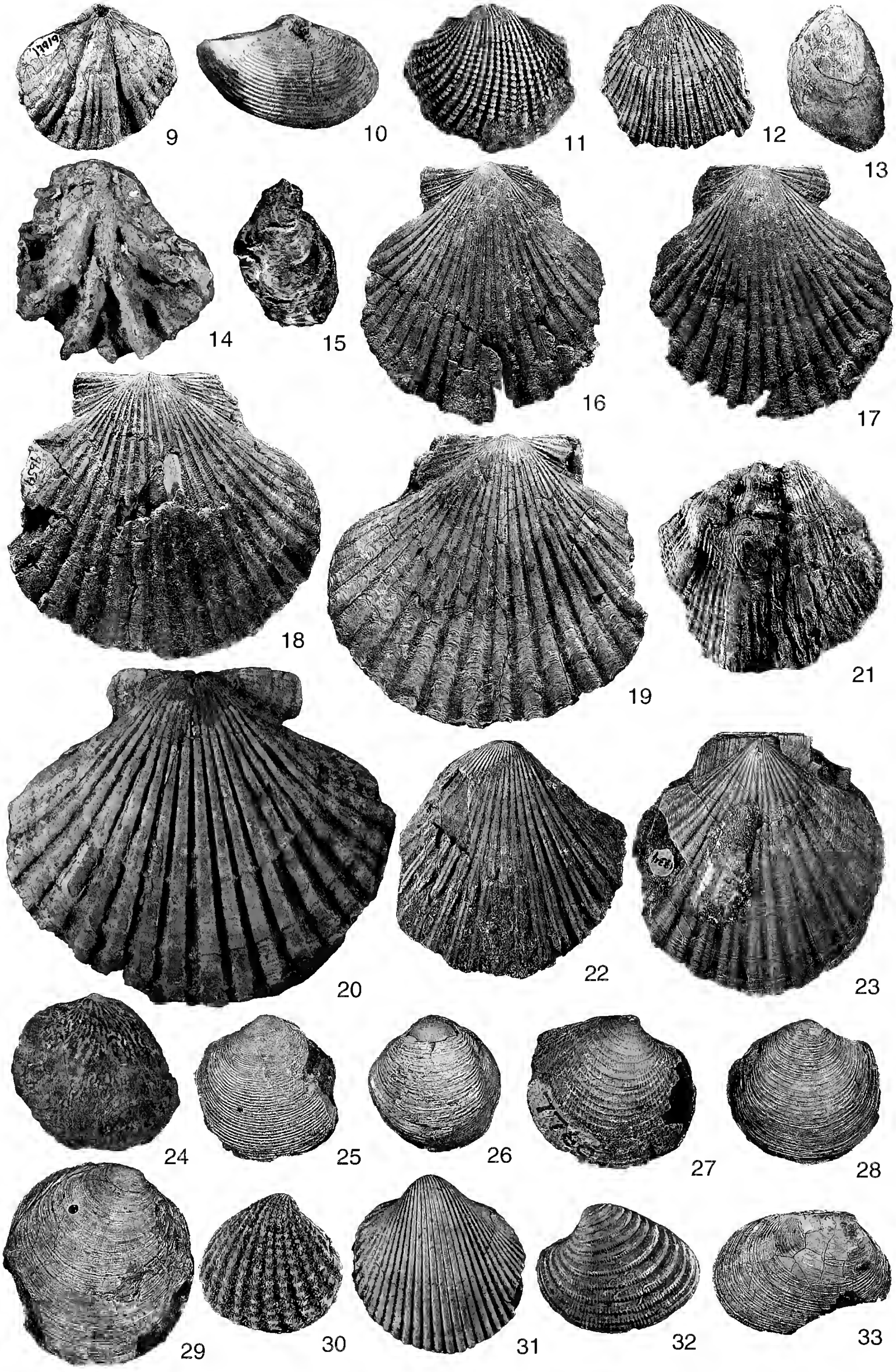
In the comparision of the above-mentioned argopectinids, only the ribs that extend continuously from the beak to the venter were counted. Specimens with one or two weak, noncontinuous ribs that are present on both the anteriormost and posteriormost sides of the specimens were not included. The largest specimen of *A. invalidus* in the study area is 70 mm in height.

TYPE MATERIAL. Holotype of *Pecten* (*Plagioctenium*) *cooperi* Arnold, 1906: CAS 61855.01 [*ex* CAS/SU 8]; holotype of *Pecten* (*Plagioctenium*) *subdolus* Hertlein, 1925: CAS 61881.01 [*ex* CAS/SU 51]; holotype of *Pecten* (*Plagioctenium*) *callidus* Hertlein, 1925: CAS 61882.01 [*ex* CAS/SU 53].

TYPE LOCALITY. Of *Pecten* (*Plagioctenium*) *cooperi*: Pacific Beach, San Diego, San Diego County, California; San Diego Formation, Pliocene. Of *Pecten* (*Plagioctenium*) *subdolus*: CAS loc. 61881 [*ex* SU loc. 115], San Diego County, California; San Diego Formation, Pliocene. Of *Pecten* (*Plagioctenium*) *callidus*, CAS loc. 61882 [*ex* SU loc. 116], Cedros Island, Baja California, Mexico, Almejas Formation, Pliocene.

GEOLOGIC AGE. Early to late Pliocene.

STRATIGRAPHIC DISTRIBUTION. LOWER PLIOCENE: Almejas Formation, eastern Cedros Island and Tortugas Bay, Baja California Sur, Mexico (Hertlein, 1925; Jordan and Hertlein, 1926; Minch et al., 1976); Tirabuzon Formation [formerly Gloria Formation], Baja California Sur, Mexico (Wilson, 1955). UPPER PLIOCENE: Pico Formation, Holser Canyon area, Los Angeles County, (Grant and Gale, 1931); Pico Formation, northern Simi Valley (especially Las Llajas Canyon), Ventura and Los Angeles counties, California (new information); and Valencia and Newhall areas, northern Los Angeles County, California (Grant and Gale, 1931; Squires et al., 2006; present report); Niguel Formation, San Juan Capistrano, Orange County, California (Vedder, 1960); San Diego Formation, lower member, San Diego County, California (Hertlein and Grant, 1972;



Figures 9–33 Brachiopod (first figure) and bivalves from upper Pliocene Pico Formation in the Newhall area. All specimens coated with ammonium chloride. 9. *Terebratalia occidentalis* (Dall, 1871), hypotype LACMIP 14335, LACMIP loc. 17919, brachial valve, height 32.6 mm, ×0.7. 10. *Jupiteria taphria* (Dall, 1896), hypotype LACMIP 14336, LACMIP loc. 17917, right valve, height 5.7 mm, ×3. 11. *Arcopsis* sp., hypotype LACMIP 14337, LACMIP loc. 17917, partial left valve, height 6.8 mm, ×3. 12. *Anadara trilineata* (Conrad, 1856), hypotype LACMIP 14338, LACMIP loc. 7752, partial

Deméré, 1983); and Infierno Formation (Wilson, 1955), Baja Californa Sur, Mexico.

REMARKS. *Argopecten invalidus* is one of the most common megafossils in the study area, and its preservation is excellent. Specimens range from 3 mm to 67.6 mm in height. Although they can be weathered, they are unabraded, many have their fragile auricles intact, and many specimens are paired valves (i.e., Table 1).

Class Gastropoda Cuvier, 1797
Family Calliostomatidae Thiele, 1924
Genus *Calliostoma* Swainson, 1840

TYPE SPECIES. *Trochus conulus* Linnaeus, 1758, designated by Herrmannsen, 1846; Holocene, Mediterranean Sea.

Calliostoma sp., aff. *C. grantianum* Berry, 1940
Figures 53–54

REMARKS. This gastropod is represented by three specimens from LACMIP loc. 17918. Preservation is very good, but two of the specimens are incomplete. The illustrated specimen, which is the most complete one, consists of approximately 3.25 teleoconch whorls and is 5 mm in height. This gastropod is similar to *Calliostoma grantianum* Berry (1940:12–13, pl. 2, figs. 4, 5) from middle Pleistocene strata in San Pedro, Los Angeles County, California. The Pico Formation specimens differ by having smaller size, fewer whorls, wider pleural angle, more closely spaced spiral ribs on the sides of the teleoconch whorls, beads on the spiral rib adjacent to the suture on the last half turn of the last whorl, obsolete spiral ribs on the medial part of the flattish base, and three rather than five ribs in the umbilical region. The immaturity of the Pico Formation specimens could explain the difference in size and fewer whorls. Mature *C. grantianum* have up to 6.5 whorls and are 15.4 mm in height. There is a possibility that the Pico Formation specimens represent a new species, but specimens that are more mature are needed for confirmation.

The Pico Formation gastropod resembles *C. canaliculatum* (Lightfoot, 1786), whose chronologic range is late Pliocene to Holocene (Grant and Gale, 1931:833). This gastropod's species name stems from Martyn (1784:table 1, pl. 32), but his work was rejected for nomenclatural purposes by the International Commission on Zoological Nomenclature (1957:Opinion 456). As noted by Rehder (1967:19), Lightfoot (1786:101, no. 2220) is regarded by modern workers as the author of this species. See McLean (1978:19, fig. 7.2) for a description and illustration of it. The Pico Formation specimens differ by having a much smaller size, 10° wider pleural angle, lower spire, fewer and more widely spaced spiral ribs on last whorl, some beading, and fewer and less well-developed ribs on the base.

According to McLean (1978:19), *C. dolarium* (Holten, 1802) is a synonym of *C. canaliculatum*. Moore (1968:56, pl. 27, fig. b) illustrated a specimen that she identified as *C. doliarium* [sic] from Pliocene strata in San Diego, and this particular specimen looks very similar to the Pico Formation gastropod in terms of the spacing of the spiral ribs on the last whorl. The Pico Formation gastropod differs by having fewer, more widely spaced, and less well-developed ribs on the base, as well as by having some beading on the spiral rib next to the suture on the last whorl.

Family Muricidae Rafinesque, 1815
Genus *Ocinebrina* Jousseaume, 1880

TYPE SPECIES. *Murex corallinus* Scacchi, 1836, by original designation; Holocene, North Atlantic and Mediterranean.

Ocinebrina sp., aff. *O. fraseri* (Oldroyd, 1920)
Figures 77–79

REMARKS. This gastropod is represented by a single specimen from LACMIP loc. 17918. Preservation is good, but the tip of its spire is missing, as well as some of the shell on the dorsal surface of the last whorl. The specimen, which is 19.3 mm in height, is similar to the extant *Ocinebrina fraseri* (Oldroyd, 1920:135, pl. 4, figs. 1–3), from the Pacific Northwest. Northeastern Pacific species formerly placed in *Ocenebra* Gray, 1847 were transferred to *Ocinebrina* by McLean (1996). The Pico Formation specimen differs from Oldroyd's species by having slightly stronger irregular varices, more and narrower spiral ribs, and reticulate sculpture on the spire whorls and posterior half of the last whorl. The Pico Formation specimen is unusual for an *Ocinebrina* because it has both an immature-stage open siphonal canal and a mature-stage outer lip (i.e., outer lip interior with at least four strong nodes). In *Ocinebrina*, the siphonal canal remains open until final maturity and the lip expands and forms labrial denticles (McLean, 1996:80). Future collecting might show that this species is new.

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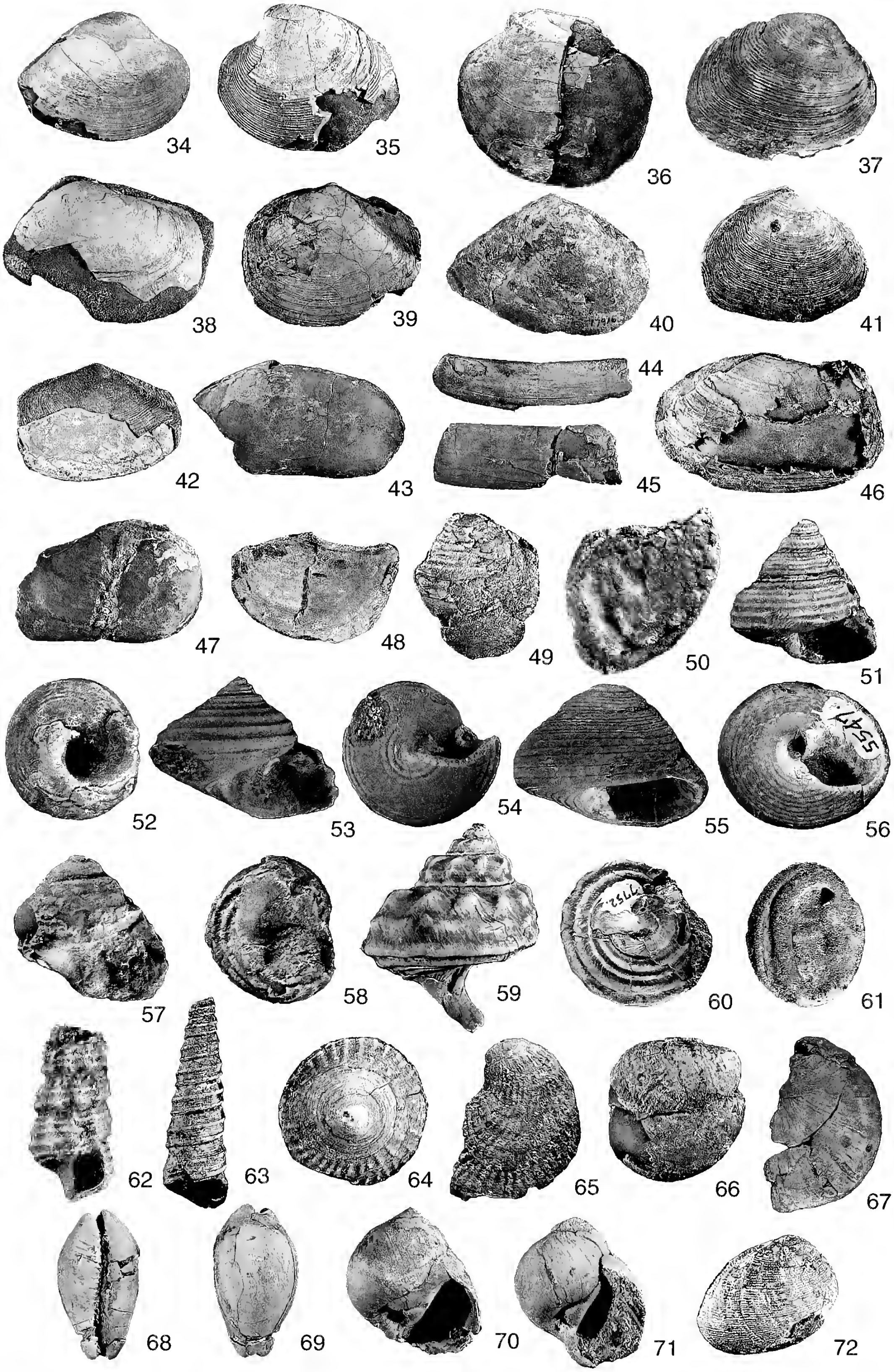
left valve, height 23.2 mm, ×1. **13.** *Limaria* sp., cf. *L. orcutii* (Hertlein and Grant, 1972), hypotype LACMIP 14339, LACMIP loc. 17917, steinkern of left? valve, height 45.7 mm, ×0.5. **14.** *Myrakeena veatchii* (Gabb, 1866), hypotype LACMIP 14340, LACMIP loc. 9659, left valve, height 68.8 mm, ×0.5. **15.** *Myrakeena veatchii* (Gabb, 1866), hypotype LACMIP 14341, LACMIP loc. 9659, right valve (juvenile), height 18.2 mm, ×1.2. **16–19.** *Argopecten invalidus* (Hanna, 1924). **16.** Hypotype LACMIP 14342, LACMIP loc. 9659, left valve (originally paired with following specimen), height 61 mm, ×0.7. **17.** Hypotype LACMIP 14343, LACMIP loc. 9659, right valve, height 60 mm, ×0.7. **18–19.** Hypotype LACMIP 14344, LACMIP loc. 9659, height 66.7 mm, ×0.7. **18.** left valve. **19.** right valve. **20.** *Lyropecten catalinae* (Arnold, 1906), LACMIP 14345, LACMIP loc. 7752, right valve, height 122 mm, ×0.4. **21.** *Swiftopecten parmeleei* (Dall, 1898), hypotype LACMIP 14346, LACMIP loc. 17917, left? valve, height 53 mm, ×0.6. **22.** *Leopecten stearnsii* (Dall, 1878), hypotype LACMIP 14347, LACMIP loc. 7752, right valve, height 57.2 mm, ×0.6. **23.** *Patinopecten healeyi* (Arnold, 1906), hypotype LACMIP 14348, LACMIP loc. 9659, right valve, height 58.6 mm, ×0.7. **24.** *Pododesmus macroschisma* (Deshayes, 1839), hypotype LACMIP 14349, LACMIP loc. 17917, left valve, height 49 mm, ×0.5. **25.** *Epilucina californica* (Conrad, 1837), hypotype LACMIP 14350, LACMIP loc. 7752, left valve, height 26.7 mm, ×0.9. **26.** *Here excavata* (Carpenter, 1857), hypotype LACMIP 14351, LACMIP loc. 17920, left valve, height 17.9 mm, ×1.2. **27.** *Lucinisca nuttalli* (Conrad, 1837), hypotype LACMIP 14352, LACMIP loc. 17918, right valve, height 14 mm, ×1.7. **28.** *Lucinoma annulatum* (Reeve, 1850), hypotype LACMIP 14353, LACMIP loc. 17917, left valve, height 56.4 mm, ×0.4. **29.** *Miltha xantusi* (Dall, 1905), hypotype LACMIP 14354, LACMIP loc. 17934, right valve, height 98.3 mm, ×0.2. **30.** *Cyclocardia occidentalis* Conrad, 1855, hypotype LACMIP 14355, LACMIP loc. 7752, right valve, height 8.2 mm, ×2.6. **31.** *Trachycardium (Dallocardia) quadragenarium* (Conrad, 1837), hypotype LACMIP 14356, LACMIP loc. 7752, left valve, height 73.3 mm, ×0.4. **32.** *Chione (Anomalocardia) fernandoensis* English, 1914, hypotype LACMIP 14357, LACMIP loc. 17918, left valve, height 11.2 mm, ×1.8. **33.** *Callithaca tenerrima* (Carpenter, in Gould and Carpenter, 1857), hypotype LACMIP 14358, LACMIP loc. 17918, right valve, height 85 mm, ×0.2.



Figures 34–72 Bivalves and gastropods from upper Pliocene Pico Formation in the Newhall area. All specimens coated with ammonium chloride. 34. *Compsomyax subdiaphana* (Carpenter, 1864), hypotype LACMIP 14359, LACMIP loc. 7757, right valve, height 30.6 mm, ×07. 35. *Amiantis callosa* (Conrad, 1837), hypotype LACMIP 14360, LACMIP loc. 7752, left valve, height 47.5 mm, ×0.5. 36. *Dosinia ponderosa* (Gray, 1838), hypotype LACMIP 14362, LACMIP loc. 7725, left valve, height 101.7 mm, ×0.3. 37. *Saxidomus nuttalli* Conrad, 1837, hypotype LACMIP 14361, LACMIP loc.

DISCUSSION

AGE

The chronologic ranges of the Newhall-area species that have the shortest ranges are depicted in Figure 107. Based on overlap of these ranges, these species indicate a late Pliocene age, which is in agreement with the age reported by Squires et al. (2006) for the Pico Formation in the Valencia area. Their age was based on mollusks and benthic foraminifera, as well as on paleomagnetic studies of the overlying Saugus Formation. Squires et al. (2006:fig. 23) provided a diagram showing the chronostratigraphic framework for the Pliocene and Pleistocene and included magnetostratigraphy and various biostratigraphic zones/stages. Their figure, however, is out of date in terms of the age of the base of the Pleistocene. In 2009, the International Commission on Stratigraphy (see Gibbard et al., 2009) reported that the Pliocene ranges from 5.33 to 2.58 Ma. The "early Pliocene" (Zanciean Stage) ranges from 5.33 to 3.6 Ma, and the "late Pliocene" (Piacenzian Stage) ranges from 3.6 to 2.58 Ma. The "middle Pliocene" is no longer recognized.

A late Pliocene age for the Pico Formation in the Newhall area contradicts a latest Miocene to earliest Pliocene age (5.5 ± 0.4 Ma) reported by Berry et al. (2009:fig. 4) based on strontium-isotope studies of fragments of oyster and pectinid shells from Gavin Canyon. Weathered shells might account for the contradictory age report.

Presence of the gastropods *Cancellaria hamlini* Carson, 1926 and *Rictaxis painei grandior* Grant and Gale (1931) in the Newhall area Pico Formation refines their poorly known geologic age. Carson (1926:51) reported *C. hamlini* only from strata of early Pliocene age in Elsmere Canyon, but Kern (1973), in his detailed study of the fauna there, did not detect this species. Grant and Gale (1931:444) reported *R. p. grandior* only from undifferentiated Pliocene strata in Holser Canyon near Val Verde, Ventura County, California. These strata are part of an almost continuous section of Pico Formation that extends from Newhall Pass to Holser Canyon (Grant and Gale, 1931:33). In conclusion, the geologic age of both of these gastropods is late Pliocene.

The taxonomic composition of the megafauna of the Pico Formation in the Newhall area and adjacent Valencia area is most similar to the upper Pliocene Niguel Formation at San Juan Capistrano, Orange County, California (see Vedder, 1960; Stadum, 1984) and to the upper Pliocene lower member of the San Diego Formation, San Diego County, California (see Deméré, 1983). There is also similarity to the megafauna of the upper Pliocene Cebada and Craciosa members of the Careaga Sandstone, Santa Maria, Santa Barbara County (see Woodring and Bramlette, 1950).

DEPTH

Table 2 provides the depth-range data for the 41 extant species found in the Newhall area; the average depth range of these species is 8 to 144 m. Using Valentine's (1961:fig. 2) diagram of the classification of marine environments, the Newhall-area megafauna lived predominantly in the inner sublittoral marine environment.

Winterer and Durham (1962) reported that based on benthic foraminifera, the marine facies on the north side of Gavin Canyon shallowed up-section. The extant *Epistominella pacifica* (Cushman, 1927) is especially common in beds referred here to the quiet-water, offshore-marine braid-delta siltstones of the Pico Formation. They reported that this species lives in waters that range in depth from 7 to 70 m. Up-section, in the lower part of the overlying shoreface sandstone, they found sparse benthic foraminifera, with the extant *Nonion scaphum* (Fichtel and Moll, 1798) as the best-represented species. They reported that this species lives in waters that range in depth from intertidal to 16 m. They found no benthic foraminifera in the stratigraphically higher deposits in the Pico Formation.

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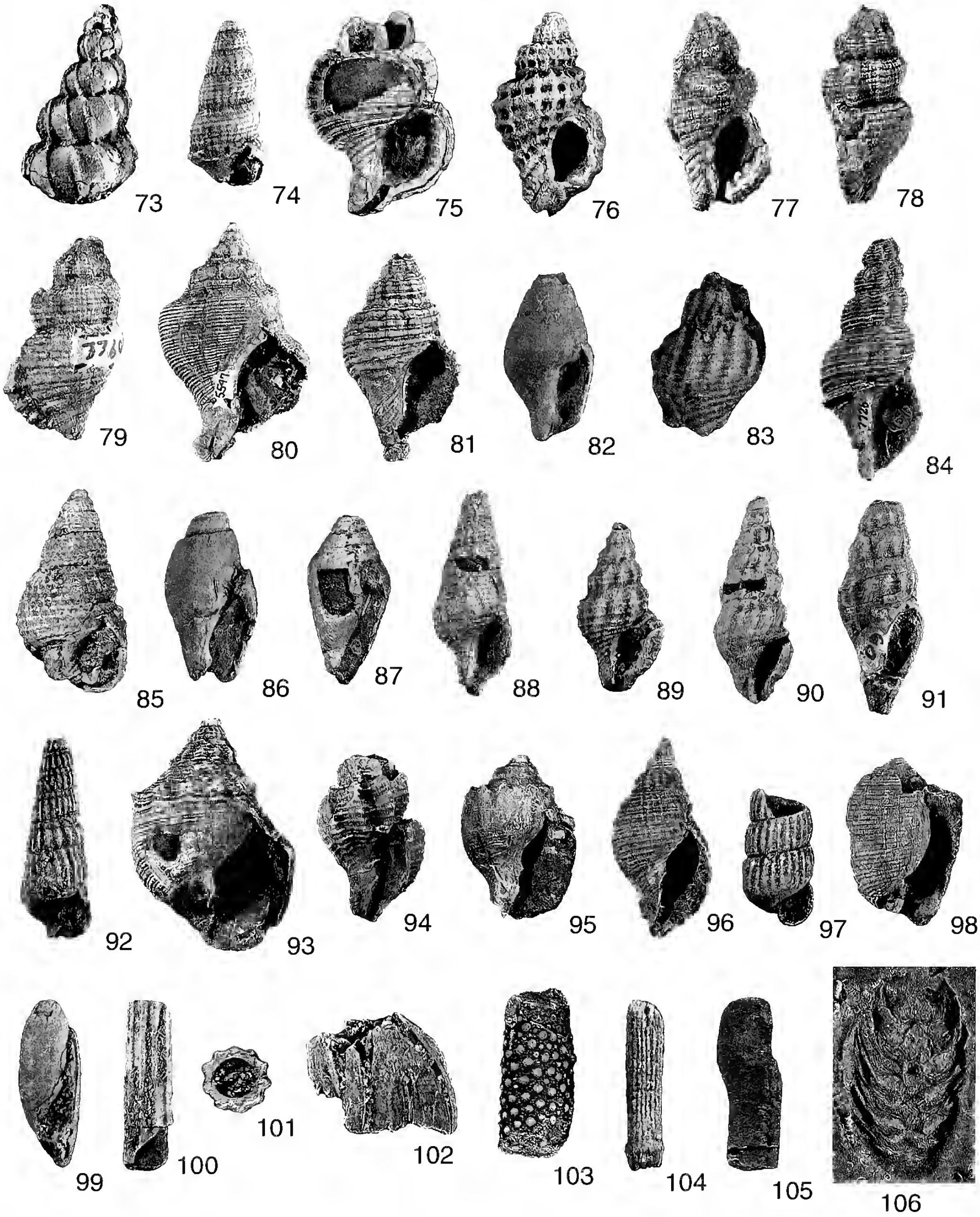
17921, right valve, height 89.7 mm, ×0.3. **38.** *Tresus nuttallii* (Conrad, 1837), hypotype LACMIP 14370, LACMIP loc. 17918, right valve, height 60 mm, ×0.4. **39.** *Macoma* (*Rexithaerus*) *secta* (Conrad, 1837), hypotype LACMIP 14364, LACMIP loc. 7752, left valve, height 54.5 mm, ×0.4. **40.** *Macoma nasuta* (Conrad, 1837), hypotype LACMIP 14365, LACMIP loc.17916, right valve, height 49.4 mm, ×0.4. 41. *Leporimetis obesa* (Deshayes, 1855), hypotype LACMIP 14366, LACMIP loc. 17921, right valve, height 33.3 mm, ×0.7. **42.** *Tellina* (*Tellinella*) *idae* Dall, 1891, hypotype LACMIP 14363, LACMIP loc. 17920, external mold of right valve, height 24.3 mm, ×0.7. 43. *Gari* sp., hypotype LACMIP 14367, LACMIP loc. 7757, internal mold of partial left valve, height 62.4 mm, ×0.3. **44.** *Solen* (*Ensisolen*) *sicarius* Gould, 1850, hypotype LACMIP 14368, LACMIP loc. 17917, left? valve, height 10.5 mm, ×0.6. 45. *Solen* sp., cf. *S. perrini* Clark, 1915, hypotype LACMIP 14369, LACMIP loc. 17917, right? valve, height 32.6 mm, ×0.3. **46.** *Panopea abrupta* (Conrad, 1849), hypotype LACMIP 14371, LACMIP loc. 17917, left valve, height 65.6 mm, ×0.3. 47. ?*Chaceia ovoidea* (Gould, 1851), hypotype LACMIP 14372, LACMIP loc. 7757, right valve, height 42.9 mm, ×0.4. **48.** *Pandora* (*Heteroclidus*) *punctuata* Conrad, 1837, hypotype LACMIP 14373, LACMIP loc. 7757, right-valve interior, height 10.1 mm, ×1.6. **49.** ?*Cyathodonta pedroana* Dall, 1915, hypotype LACMIP 14374, LACMIP loc. 7757, partial right valve, height 47.7 mm, ×0.5. 50. *Haliotis* sp., hypotype LACMIP 14375, LACMIP loc. 17921, partial specimen, longest dimension 57 mm, ×0.33. 51–52. *Calliostoma* sp., cf. *splendens* Carpenter, 1864, hypotype LACMIP 14376, LACMIP loc. 17918, height 6.7 mm, ×3.3. **51.** apertural view. 52. umbilical view. **53–54.** *Calliostoma* sp., aff. C. *grantianum* Berry, 1940, hypotype LACMIP 14377, LACMIP loc. 17918, height 5 mm, ×4.2. 53. apertural view. **54.** umbilical view. **55–56.** *Chlorostoma gallina* form *multifilosa* Stearns, 1892, hypotype LACMIP 14378, LACMIP loc. 7753, height 15.8 mm, ×1.4. 55. apertural view. 56. umbilical view. 57–58. *Homoploma paucicostatum*? (Dall, 1871), hypotype LACMIP 14379, LACMIP loc. 17918, height 5.9 mm, ×4. 57. apertural view. 58. ventral view. **59–60.** *Pomaulax gradata* Grant and Gale, 1931, hypotype LACMIP 14380, LACMIP loc. 7752, height 36.4 mm, ×0.6. **59.** apertural view. 60. umbilical view. 61. Operculum of ?*Pomaulax gradata* Grant and Gale, 1931, hypotype LACMIP 14381, LACMIP loc. 7752, interior view, longest dimension 17.5 mm, ×1.3. 62. *Lirobittium asperum* (Gabb, 1861), hypotype LACMIP 14382, LACMIP loc. 17918, apertural view of partial specimen, height 5.5 mm, ×4.8. 63. *Turritella cooperi* Carpenter, 1864, hypotype LACMIP 14383, LACMIP loc. 17917, apertural view, height 31.8, ×1. 64. ?*Calyptraea* (*Trochita*) sp., hypotype LACMIP 14384, LACMIP loc. 17918, dorsal view, diameter 7.5 mm, ×3. 65–66. *Crepidula aculeata* (Gmelin, 1791), LACMIP loc. 17918. 65. Hypotype LACMIP 14385, dorsal view, height 16.7 mm, ×1.4. 66. hypotype LACMIP 14386, two specimens vertically stacked, total height 26.9 mm, ×0.5. 67. *Grandicrepidula princeps* (Conrad, 1857), hypotype LACMIP 14387, LACMIP loc. 17921, dorsal view, height 56.4, ×0.5. 68–69. *Zonaria* (*Neobernaya*) *spadicea* (Swainson, 1823), hypotype LACMIP 14388, LACMIP loc. 7752, height 40.1 mm, ×0.6. 68. Apertural view. 69. dorsal view. 70. *Glossaulax reclusiana* (Deshayes, 1839), hypotype LACMIP 14389, LACMIP loc. 7752, apertural view, height 46.7 mm, ×0.5. 71. *Cryptonatica clausa* (Broderip and Sowerby, 1829), hypotype LACMIP 14390, LACMIP loc. 7752, apertural view, height 9.6 mm, ×2.4. 72. *Sinum scopulosum* (Conrad, 1849), hypotype LACMIP 14391, LACMIP loc. 7757, abapertural view, height 19.6 mm, ×0.8.



Figures 73–106 Gastropods and other megafauna from upper Pliocene Pico Formation in the Newhall area. All specimens coated with ammonium chloride. 73. *Asperiscala* sp., cf. *A. minuticostata* (De Boury, 1912), hypotype LACMIP 14392, LACMIP loc. 7757, apertural? view, base missing, height 8 mm, ×3.3. 74. *Amaea* (*Scalina*) sp., cf. *A.* (*S.*) *edwilsoni* DuShane, 1977, hypotype LACMIP 14393, LACMIP loc. 17917, apertural? view, base missing, height 20.2, ×1.1. 75. *Cymatium* sp., cf. *C.* (*Reticutriton*) *elsmerense* (English, 1914), hypotype LACMIP 14394, LACMIP loc. 17917, spire missing, height 27.5 mm, ×1.3. 76. *Ocinebrina atropurpurea* (Carpenter, 1865), hypotype LACMIP 14395, LACMIP loc. 7752, height 11.4 mm, ×2.4. 77–79. *Ocinebrina* sp., aff. *O. fraseri* (Oldroyd, 1920), hypotype LACMIP 14396, LACMIP loc. 17918, height 19.3 mm, ×1.3. 77. apertural view. 78. Right-lateral view. 79. Abapertural view. 80. *Calicantharus humerosus* (Gabb, 1869), hypotype LACMIP 14397, LACMIP loc. 7752, height 43.5, ×0.7. 81. *Calicantharus fortis* (Carpenter, 1864), hypotype LACMP 14398, LACMIP loc. 17917, height 33.1 mm, ×0.8. 82. *Alia tuberosa* (Carpenter, 1864), hypotype LACMIP 14399, LACMIP loc. 17918, height 5.2 mm, ×4.2. 83. *Amphissa* sp., hypotype LACMIP 14400, LACMIP loc. 17918, abapertural view, height 5.2 mm, ×4.2. 84. *Barbarofusus barbarensis* (Trask, 1855), hypotype LACMIP 14401, LACMIP loc. 17917, height 49.4 mm, ×0.7. 85. *Nassarius* (*Demondia*) *californianus* (Conrad, 1856), hypotype LACMIP 14402, LACMIP loc. 17918, height 20.7 mm, ×1.3. 86. *Callianax baetica* (Carpenter, 1864), hypotype LACMIP 14403, LACMIP loc. 7752, height 9 mm, ×2.6. 87. *Californiconus californicus*? (Reeve, 1843a), hypotype LACMIP 14404, LACMIP loc. 7757, height 16.9 mm, ×1.4. 88. *Ophiodermella inermis* (Reeve, 1843b), hypotype LACMIP 14405, LACMIP loc. 7757, height 14.3 mm, ×1.9. 89. *Cockerella conradiana* (Gabb, 1866), hypotype LACMIP 14406, LACMIP loc. 17918, height 6.4 mm, ×3.5. 90. *Elaeocyma* sp., hypotype LACMIP 14407, LACMIP loc. 7752, height 17.6 mm, ×1.6. 91. *Crassispira* sp., hypotype LACMIP 14408, LACMIP loc. 17918, height 21.7 mm, ×1.3. 92. *Terebra* (*Strioterebra*) *martini* English, 1914, hypotype LACMIP 14409, LACMIP loc. 17918, height 15.8 mm, ×1.7. 93. *Cancellaria altispira* Gabb, 1869, hypotype LACMIP 14410, LACMIP loc. 17934, height 44.3 mm, ×0.7. 94. *Cancellaria hemphilli* Dall, 1909, hypotype LACMIP 14411, LACMIP loc. 7757, spire missing, height 18.4 mm, ×1.2. 95. *Cancellaria tritonidea*? Gabb, 1866, hypotype LACMIP 14412,

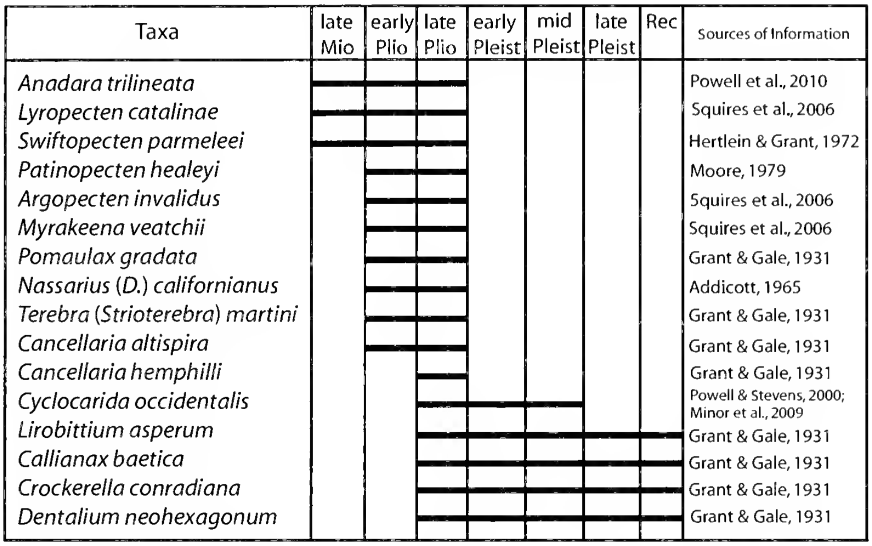


Figure 107 Chronostratigraphic distribution of the study area species with the most constrained geologic ranges indicating a late Pliocene age.

SUBSTRATE

At least three substrate types are recognized for the study area deposits: fine-grained offshore sediments, fine- to medium-grained sandy deltaic sediments, and hard surfaces. The first type was located immediately seaward of the delta and essentially fringed the delta; the second occurred on the delta complex itself; and the third occurred in association with coarse debris on the delta. The presence of fine-grained offshore substrate is indicated by the very abundant gastropod *Turritella cooperi*. Valentine and Mallory (1965) assigned this species to their Group III Pleistocene offshore fossil community, along with the bivalve *Lucinoma annulatum* (Reeve, 1850), another megafaunal element, but a rare one, of the Newhall Pico Formation assemblages. Although details are lacking about how *T. cooperi* lives, it is probably like most species of extant *Turritella*. Bandel (1976) reported that *Turritella variegata* (Linnaeus, 1758) from the Caribbean coast of Colombia lives as a suspension feeder shallowly buried in soft substrates. Large populations migrate only at the time of spawning once a year, and they crawl to more sandy bottoms or bottom covered with gravel where they can attach their spawn more firmly in coarse debris than is possible in muddy environments. Allmon et al. (1992) reported that *Turritella gonostoma* Valenciennes, 1832, from the northern Gulf of California lives in depths less than 5 m and, in the winter, migrates into shallow water to reach nutrient-rich waters and to lay its eggs. It seems very likely that the specimens of *T. cooperi* that dominate the fossil assemblages at most localities in the Newhall area preferred to live in close proximity to a river delta because the river would deliver nutrients on which it feeds. During the winter, individuals could migrate, from silty substrate to shallower water and sandy and gravelly substrates, in order to lay their eggs.

The fine- to medium-grained sandy delta substrate is indicated by paired-valved epifaunal bivalves (e.g., *Argopecten*, *Lyropecten*, *Patinopecten*), epifaunal gastropods (e.g., *Glossaulax*, *Conus*), and paired-valved infaunal bivalves (e.g., *Trachycardium*, *Saxidomus*, *Tresus*, *Panopea*). Hard-surface biotopes were very localized. The *Haliotis* specimen and the *Terebratalia occidentalis* brachiopods most likely attached to shell debris or larger rock clasts. The latter, in a few cases, provided hard substrate for encrusting bryozoan and spirorbid tubes. Some individuals of the plicate oyster *Myrakeena veatchii* lived attached to each other, based on a cluster of specimens found attached to each other at LACMIP loc. 9659, where a growth series of this oyster was also found. The occurrence of the paired-valved single specimen of the pholadid ?*Chaecia ovoidea* (Gould, 1851) is anomalous because this species normally bores into clay or shale (Coan et al., 2000). Kennedy (1974:39) reported that *C. ovoidea* has been known to bore into waterlogged wood, and this could explain its presence in the study area megafauna.

The above-mentioned three types of substrate are compatible with the findings derived from Table 2 showing that the majority of the 41 extant species of the Pico Formation megafauna live in/on sand or mud; only a few live on hard surfaces (Table 2).

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LACMIP loc. 7752, height 23.8 mm, ×0.9. 96. *Cancellaria hamlini* Carson, 1926, hypotype LACMIP 14413, LACMIP loc. 17919, height 21.5 mm, ×0.9. 97. *Turbonilla* sp., hypotype LACMIP 14414, LACMIP loc. 17918, upper spire missing, height 6 mm, ×3.1. 98. *Rictaxis painei grandior* Grant and Gale, 1931, hypotype LACMIP 14415, LACMIP loc. 7752, height 13.3 mm, ×1.7. 99. *Acteocina culcitella*? (Gould, 1853), hypotype LACMIP 14416, LACMIP loc. 7760, height 3 mm, ×7.5. 100–101. Scaphopod *Dentalium neohexagonum* Sharp and Pilsbry, in Pilsbry and Sharp, 1897, LACMIP loc. 7752. 100. Hypotype LACMIP 14417, height 9.8 mm, ×2.4. 101. Hypotype LACMIP 14418, diameter 2.3 mm, ×3.7. 102. Barnacle *Balanus*? sp., hypotype LACMIP 14419, LACMIP loc. 17917, side view, height 5.5 mm, ×2. 103. Crab leg (partial), hypotype LACMIP 14420, LACMIP loc. 17918, height 10.2 mm, ×2.2. 104. Echinoid spine *Eucidaris* sp., hypotype LACMIP 144421, LACMIP loc. 17917, height 4.2, ×5.4. 105. Ray tooth *Myliobatis* sp., hypotype LACMIP 14422, LACMIP loc. 7752, maximum dimension 25 mm, ×0.9. 106. Pine cone, hypotype LACMIP 14423, LACMIP loc. 7752, cross-section, height 50 mm, ×0.6.

Table 2 Depth ranges, substrate preferences, geographic ranges, and faunal provinces of Newhall area Pico Formation extant species.

	Meters	Substrate	Latitudinal range (°N)	Refs.
Terebratalia occidentalis	50–250	On hard surfaces	26–23	1
Jupiteria taphria	10–100	In sand and clay	39.5–28.2	2
Pododesmus macroschisma	0–90	On hard surfaces	70.6–27.9	2
Epilucina californica	0–80	Sand and gravel of exposed shorelines	41.8–25	2
Here excavata	25–125	In sand or mud	34.4–27.9	2
Lucinisca nuttalli	10 to 75	In sand or muddy sand	36.7–27.8 into Gulf of California to 22.4	2
Lucinoma annulatum	0–665	In sand of exposed shorelines	60.8–25.7	2
Miltha xantusi	20–150	In sand	22.1 into Gulf of California to Panama (8.3)	3
Trachycardium (D.) quadragenarium	0–50	In sand or mud, bays and offshore	36.6–27	2
Callithaca tenerrima	0–30	In gravelly sand	57.1–27.6	2
Compsomyax subdiaphana	2–500	In soft mud	60.8–30.4 + local pop. in Gulf of California (30.3)	2
Amiantis callosa	0–20	In sand, exposed headlands	34.4–24.8	2
Dosinia ponderosa	0–60	Soft bottoms	27.8 into Gulf of California to Peru (3.5°S)	3
Saxidomus nuttalli	0–10	In mud or sand, bays and lagoons	40.7–27.7	2
Tresus nuttallii	0–80	In mud, sheltered bays and foreshores	57–24.6	2
Macoma (Rexithaerus) secta	0–100	In silt and sand of bays	54–24.6	2
Macoma nasuta	0–50	In sand or silt, exposed or sheltered	60.2–27.7	2
Leporimetis obesa	subtidal–50	In sand	34.5–24.6	2
Tellina (Tellinella) idae	0–100	In sand	34.4–32.7	2
Solen (Ensisolen) sicarius	intertidal	In sand or mud, sheltered bays	54–30.4	2
Panopea abrupta	0–100	In sand or mud	57.6–33.6	2
?*Chaecia ovoidea*	0–subtidal	Boring into clay, shale, or wood	37.9–27.7	2, 4
Pandora (Heteroclidus) punctuata	subtidal–50	In mud	49.9–26.2	2
Cyathodonta pedroana	9–114	In mud	36.7–24.6	2
Calliostoma splendens	?	Rocky areas	35–32.5	5
Chlorostoma gallina form *multifilosa*	mid tidal	Rocky areas	34–25	6
Turritella cooperi	25–100	On sand	37–24 into W side Gulf of California to head of Gulf	7
Crepidula aculeata	intertidal	On hard surfaces	42–Chile (30°S)	8
Zonaria (Neobernaya) spadicea	sublittoral	Under overhung rock ledges	35–28	9
Glossaulax reclusiana	0–50	On sand or mud, common in bays	41.8 into Gulf of California to 21.5	10
Cryptonatica clausa	9–970	On soft bottoms	60–32.5	10
Sinum scopulosum	15–171	On sand or mud, common in bays	36.5–27.6	10
Asperiscala minuticostata	18–137	On sand and broken shells	28 into Gulf of California to Ecuador (0°)	11
Ocinebrina atropurpurea	0–sublittoral	Rocky bottoms	60–30.5	9
Alia tuberosa	sublittoral	In gravel under kelp	60–25	9
Barbarofusus barbarensis	50–350 m	Soft bottoms	36.5–23	7
Callianax baetica	0–offshore	On sandy bottoms	55–23	9
Californiconus californicus	0–30	On rock and sand	37.5–24.5	9
Ophiodermella inermis	0–70	Soft bottoms	53–24.5	7
Crockerella conradiana	24–240	Soft bottoms	34–32	7
Acteocina culcitella	0–offshore	On sand flats and mudflats in bays	55–27.5	9

References: 1 = Hochberg, 1994; 2 = Coan et al., 2000; 3 = Coan & Scott, 2012; 4 = Kennedy, 1974; 5 = Grant and Gale, 1931; 6 = McLean, personal communication; 7 = McLean, 1996; 8 = Keen, 1971; 9 = McLean, 1978;10 = Marincovich, 1977; 11 = DuShane, 1979.

TAPHONOMY

As mentioned earlier, the shoreface-facies megafauna occurs in channelized, storm-lag deposits. It is striking how the taxonomic composition of one storm-lag deposit differs so much from one that is nearby, in either a lateral or vertical stratigraphic sense. For example, at LACMIP loc. 17918, *Turritella cooperi* shells are so abundant that they constitute a coquina bed (with unworn specimens). In a storm lag a few meters up section, there are relatively few *T. cooperi*. Instead, there are concentrations of both the brachiopod *Terebratalia hemphilli* and the gastropod *Crepidula aculeata* (Gmelin, 1791) (some of which are vertically stacked). In addition, both species are represented by juvenile and adult specimens.

The storm-lag deposits in the upper Pico Formation commonly represent a mixture of species that lived in different life associations on different types of substrate. Occasional large storm waves raked all these shallow waters and thereby mixed the life associations together. Distance of postmortem transport was short based on the presence of paired valves of most of the brachiopods and many of the bivalves (e.g., *Panopea*, *Solena*, *Myrakeena*, *Argopecten*, *Lyropecten*) (see Table 1). None of

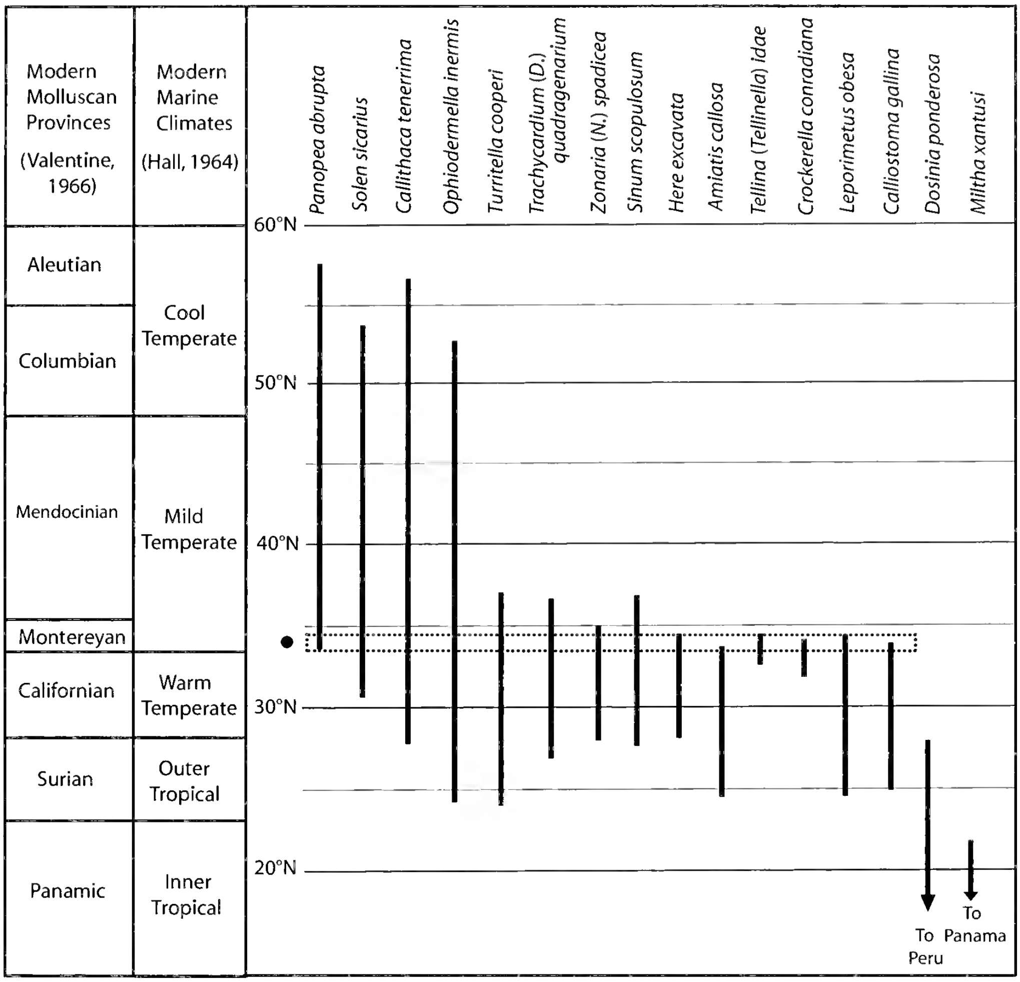

Figure 108 Latitudinal distribution of selected mollusks (see Table 2 for details) from the upper part of the Pico Formation, Newhall area vs. modern molluscan provinces and marine climates. Dashed box shows zone of maximum overlap of mollusk distributions at 31°N to 33.5°N. Solid circle = latitude of the study area (34°21′N).

these infaunal bivalves were found in their burrows. These specimens were displaced from their burrows and transported while alive. Additional evidence of short distance of transport is based a scarcity of any obvious signs of abrasion. Some examples are fragile protoconchs of some specimens of *Calliostoma* sp., aff. *C. grantianum* (Fig. 53), *Nassarius* (*Demondia*) *californianus* (Conrad, 1856) and *Cancellaria hamlini* Carson, 1926 (Fig. 96); delicate apical tips of many *Turritella cooperi*; delicate auricles of the pectinids, including those of juvenile *Argopecten invalidus*; thin varices of *Asperiscala minuticostata*? (De Boury, 1921); and four sets of two vertically stacked specimens of *Crepidula aculeata* at LACMIP loc. 17918. This is the first report of vertical stacking of this species. An additional indicator of short distance of transport is the presence, at LACMIP loc. 9659, of a growth series of the oyster *Myrakeena veatchii*. Specimens range from 18.5 to 85 mm in height. The smallest specimen is illustrated (Fig. 15) because no juvenile specimen of this species has ever been illustrated.

Some of the lentils in the upper Pico Formation storm deposits consist of dense concentrations of unworn, small-sized, mostly disarticulated specimens of bivalves. There are also a few lenses containing abundant *Turritella cooperi* that show preferred bimodal distribution (Fig. 8) in the way their shells were oriented by shallow-marine wave movements. Occasional large storm waves, which would be more common during the winter, would move and concentrate the copious *Turritella* shells, as well as other offshore shells, in storm-lag deposits on the shoaling parts of the braid delta.

ZOOGEOGRAPHIC IMPLICATIONS

Squires et al. (2006) reported that the Pico Formation megafauna in the Valencia area just west of the Newhall area is mostly indicative of warm-temperate conditions, with a few species indicative of warmer conditions. This present study corroborates these findings. Table 2 lists the latitudinal ranges of all the extant species found in the Pico Formation in the Newhall area, and Figure 108 shows that the zone of maximum overlap of representative extant species from this list is between 33.5°N and 31°N. This zone plots within the "Californian" molluscan province of Valentine (1966) and the warm-temperate, marine-climate zone of Hall (1964). There is, however, a warmer water component (tropical) based on the presence of two extant species found today considerably south of maximum overlap zone:

Miltha xantusi (Dall, 1905) and *Dosinia ponderosa* (Gray, 1838) live in the southern (tropical) part of the Gulf of California, as well as much farther south (see Table 2 for references).

Two of the extinct mollusks from the Newhall area are warm-water indicators found only in fossil deposits of Southern California and Baja California, Mexico. They are *Argopecten invalidus* and *Lyropecten catalinae* (Arnold, 1906) [= *Lyropecten gallegosi* (Jordan and Hertlein, 1926)]. Both are known (Minch et al., 1976) from as far south as the Pliocene Almejas Formation just south of Bahia Tortugas on the Vizcaino Peninsula, Baja California Sur, Mexico.

Another pectinid, *Patinopecten healeyi* (Arnold, 1906) which is present at most of the localities in the study area, is also significant in the interpretation of Neogene zoogeography. This species, like *Lyropecten catalinae*, is a giant pectinid (see Addicott, 1974), because of having a size commonly greater than 90 mm. *Patinopecten healeyi* has an early to late Pliocene chronologic range (e.g., Addicott, 1974; Moore, 1979). It reached its northernmost occurrence (Cape Mendocino in northern California), but during the late Pliocene, the species ranged farther south, with its southernmost occurrence in the Almejas Formation in Baja California Sur (Moore, 1979:fig. 1)), along with the warm-water species *Argopecten invalidus* and *L. catalinae*.

The extinct epitoniid gastropod *Amaea* (*Scalina*) *edwilsoni* DuShane, 1977, tentatively identified from the Newhall area, has been reported (DuShane, 1977) only from the Pliocene Tirabuzon Formation [formerly Gloria Formation] (Wilson, 1955) near Santa Rosalia on the Gulf of California, Baja Sur, Mexico.

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