

# POLYPLACOPHORA (MOLLUSCA) FROM THE SAN DIEGO FORMATION: A REMARKABLE ASSEMBLAGE OF FOSSIL CHITONS FROM THE PLIOCENE OF SOUTHERN CALIFORNIA<sup>1</sup>

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**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 contrast to the paucity of reported chitons from the older and warmer Miocene deposits

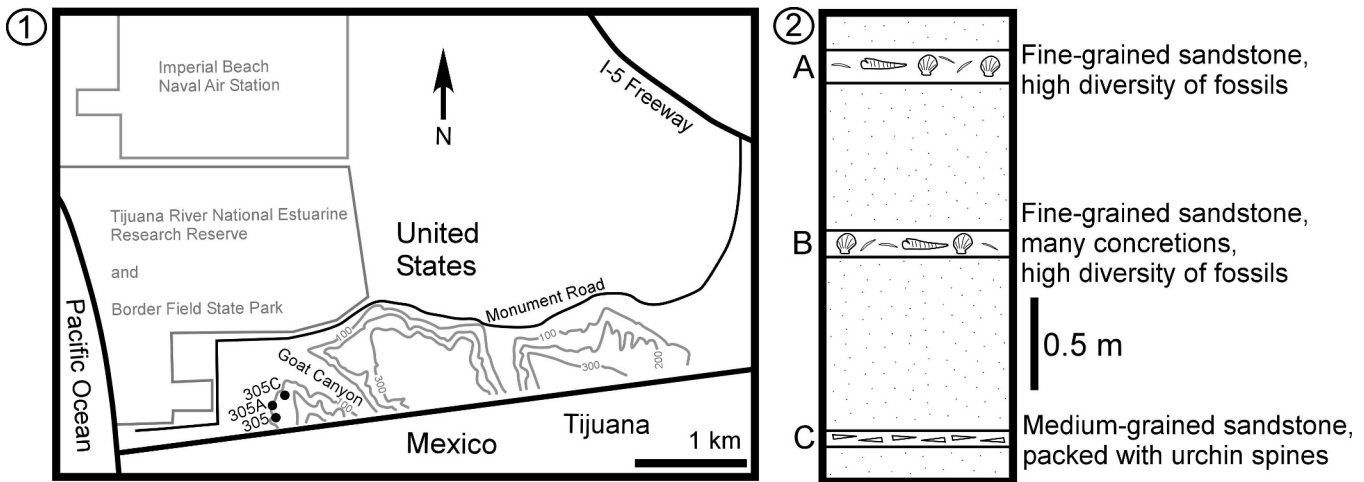
<sup>1</sup> URL: [www.nhm.org/scholarlypublications](http://www.nhm.org/scholarlypublications)

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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.

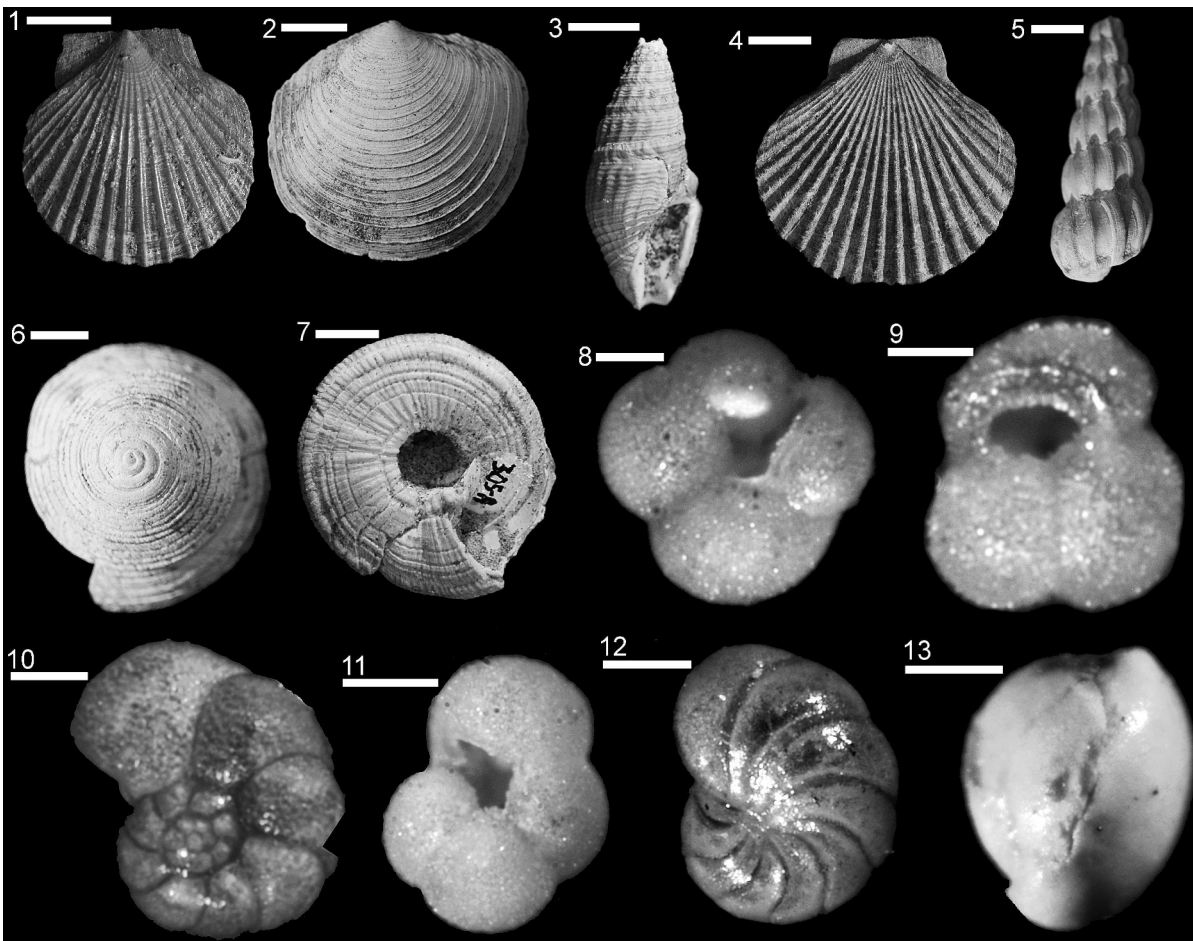
The fossils of the San Diego Formation were first listed by Dall (1874, 1898), who assigned the name “San Diego beds” to fossiliferous rocks extracted in the process of digging a well in Cabrillo Canyon near San Diego, California (now Balboa Park). Arnold (1903) later referred to the sediments as the “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



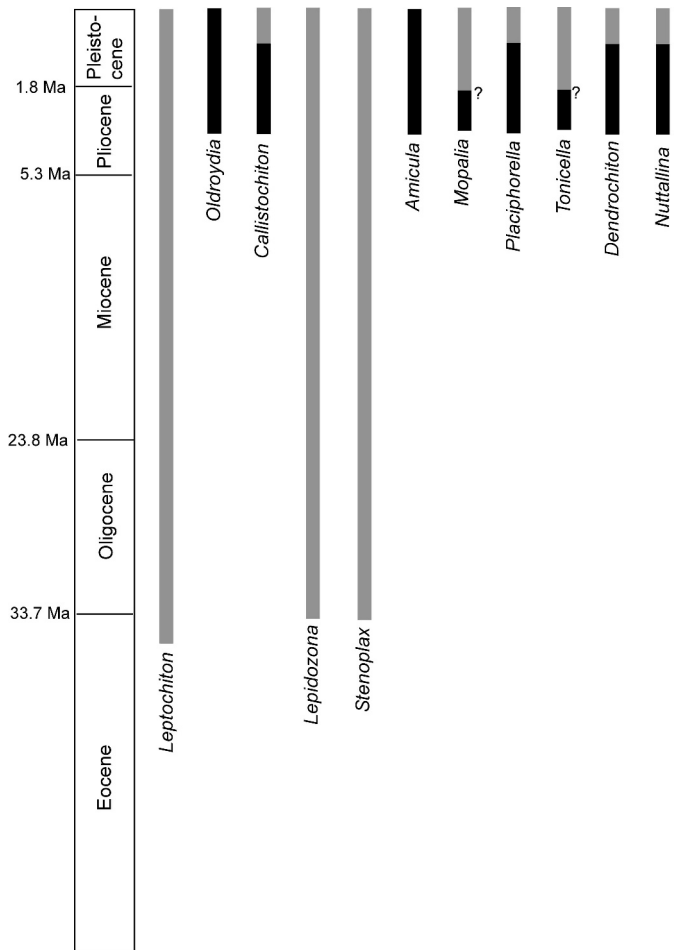
**Figure 2** Fossils of biostratigraphic and paleoenvironmental significance from LACMIP locality 305. 1, *Patinopecten bealeyi* (Arnold, 1906) (scale bar=1 cm); 2, *Lucinoma annulatum* (Reeve, 1850) (scale bar=1 cm); 3, *Strictispira* (*Crassispira*) *zizyphus* (Berry, 1940) (scale bar=0.5 cm); 4, *Euwola 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  $\mu$ m); 9, *Globigerinoides ruber* (d'Orbigny, 1839) (scale bar=250  $\mu$ m); 10, *Globorotalia tumida* (Brady, 1877) (scale bar=100  $\mu$ m); 11, *Globigerina bulloides* (d'Orbigny, 1826) (scale bar=250  $\mu$ m); 12, *Hanzawaia nitidula* (Bandy, 1953) (scale bar=250  $\mu$ m); 13, *Quinqueloculina lamarckiana* d'Orbigny, 1839 (scale bar=250  $\mu$ m).

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 elli* Hertlein and Grant, 1972, *C. jordani* (Arnold, 1903), *Euwola 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, *Calyptrea filosa* Gabb, 1866, *C. inornata* (Gabb, 1866), *Cancellaria fergusonii* 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.

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

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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.

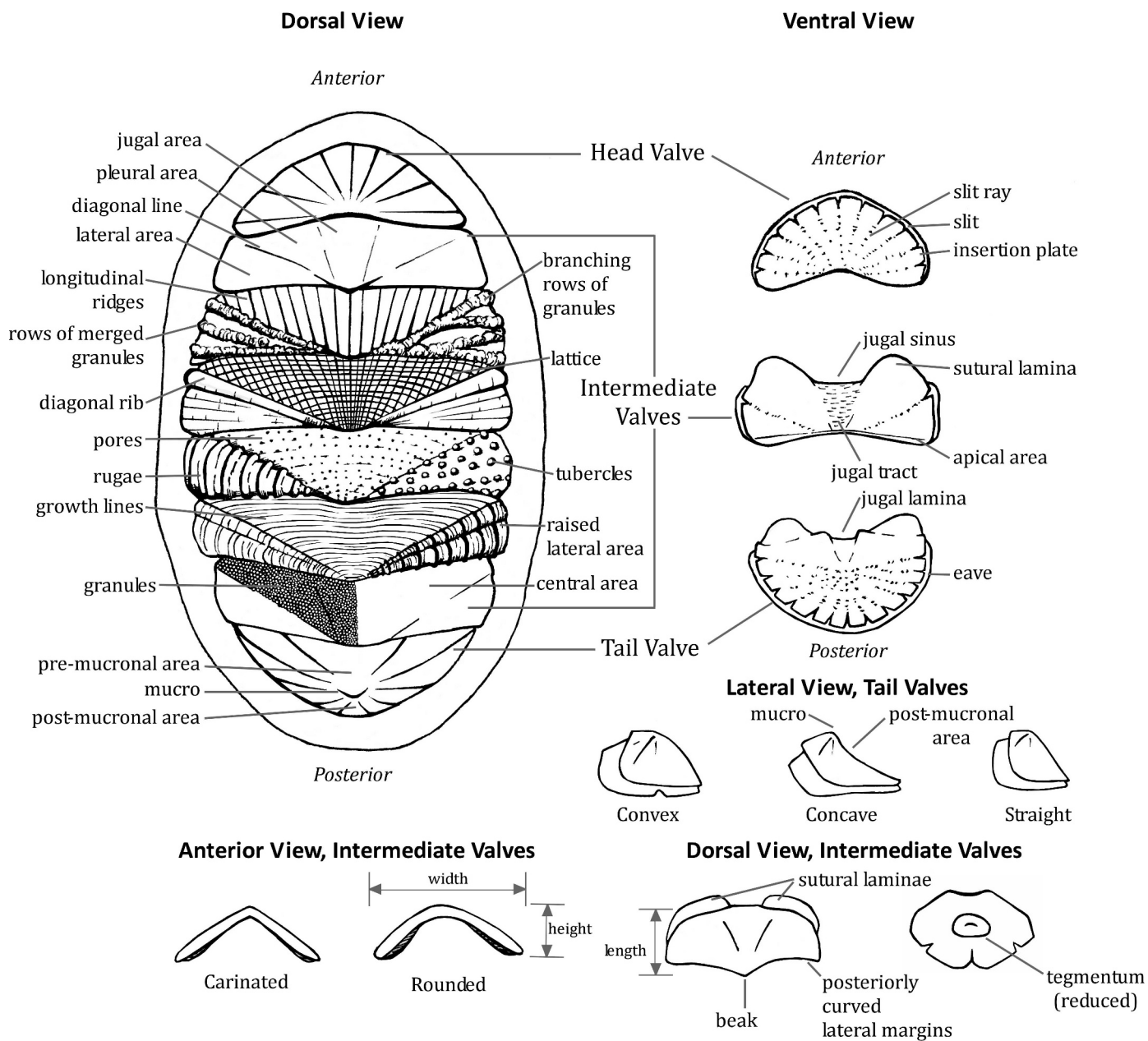
Hertlein and Grant’s original unpublished manuscript contained a list of 15 chiton species from LACMIP locality 305 that were identified by Spencer Thorpe. This list differs from ours in a number of ways, but the overall classification is similar. We could find no indication of which sets of specimens 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

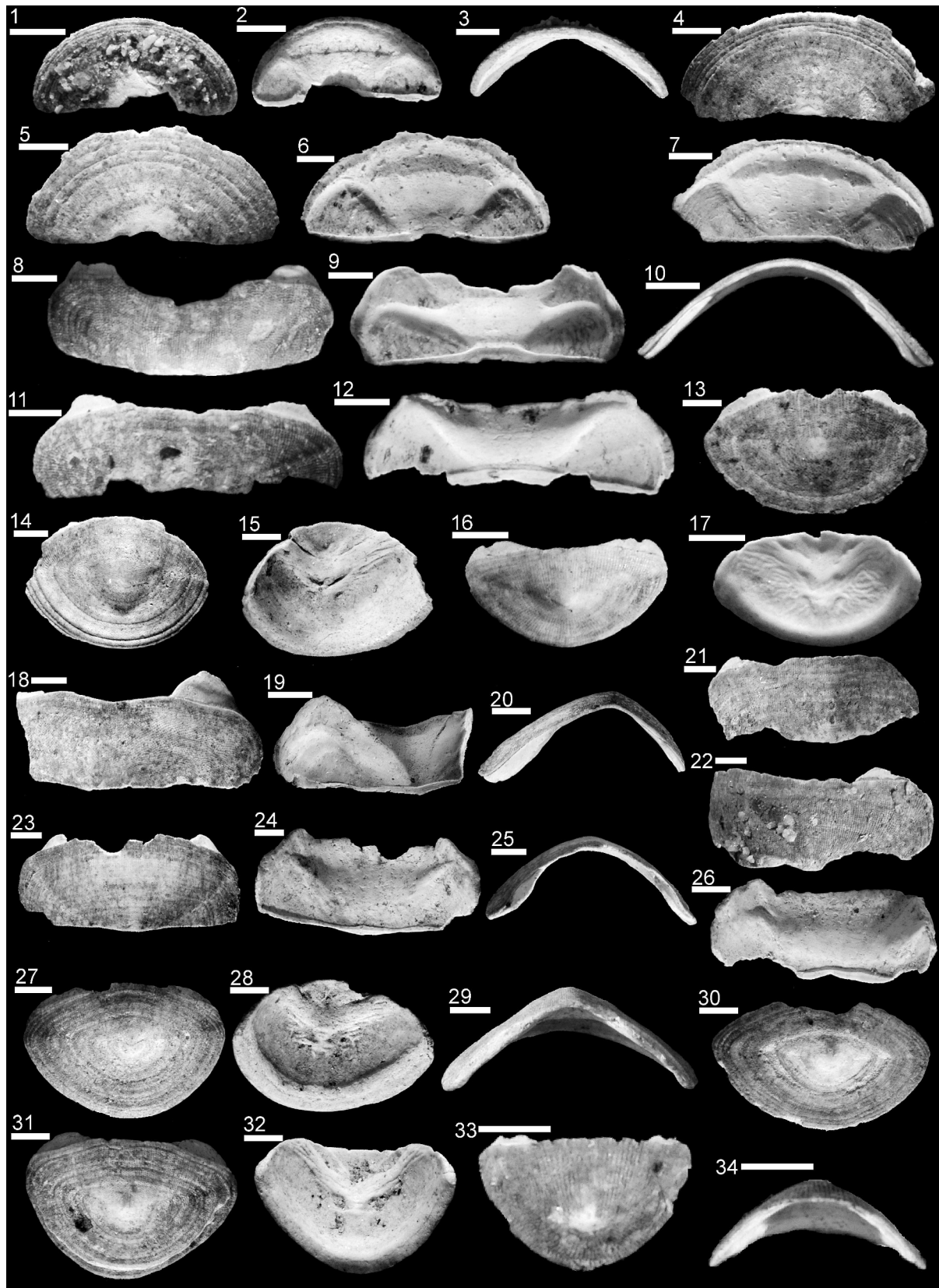


Figure 5 *Leptochiton* spp. 1–34, from LACMIP locality 305. 1–17, *Leptochiton rugatus* Pilsbry, 1892: head (1–7), intermediate (8–13), and tail (14–17) valves. 1–3, LACMIP 13730; 4, 7, LACMIP 13731; 5–6, LACMIP 13732; 8–10, LACMIP 13733; 11–12, LACMIP 13734; 13, LACMIP 13736; 14–15, LACMIP 13737; 16–17,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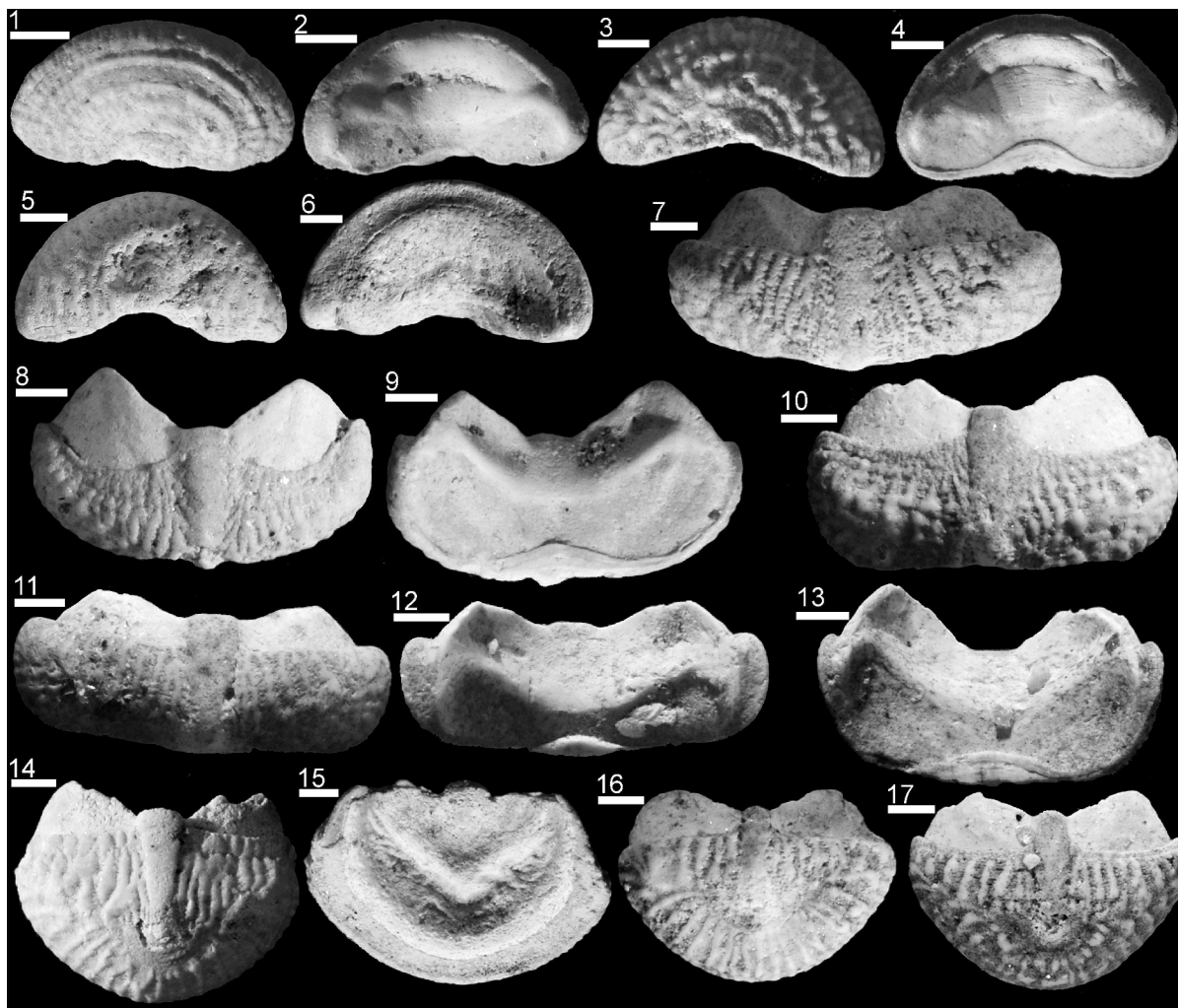


Figure 6 *Oldroydia percrassa* (Dall, 1894a): head (1–6), intermediate (7–13), and tail (14–17) valves. 1–9, 16–17, from LACMIP locality 305; 10–15, from LACMIP locality 16817 (305C). 1–2, LACMIP 13747; 3–4, LACMIP 13748; 5–6, LACMIP 13749; 7, LACMIP 13750; 8–9, LACMIP 13751; 10, 13, LACMIP 13752; 11–12,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

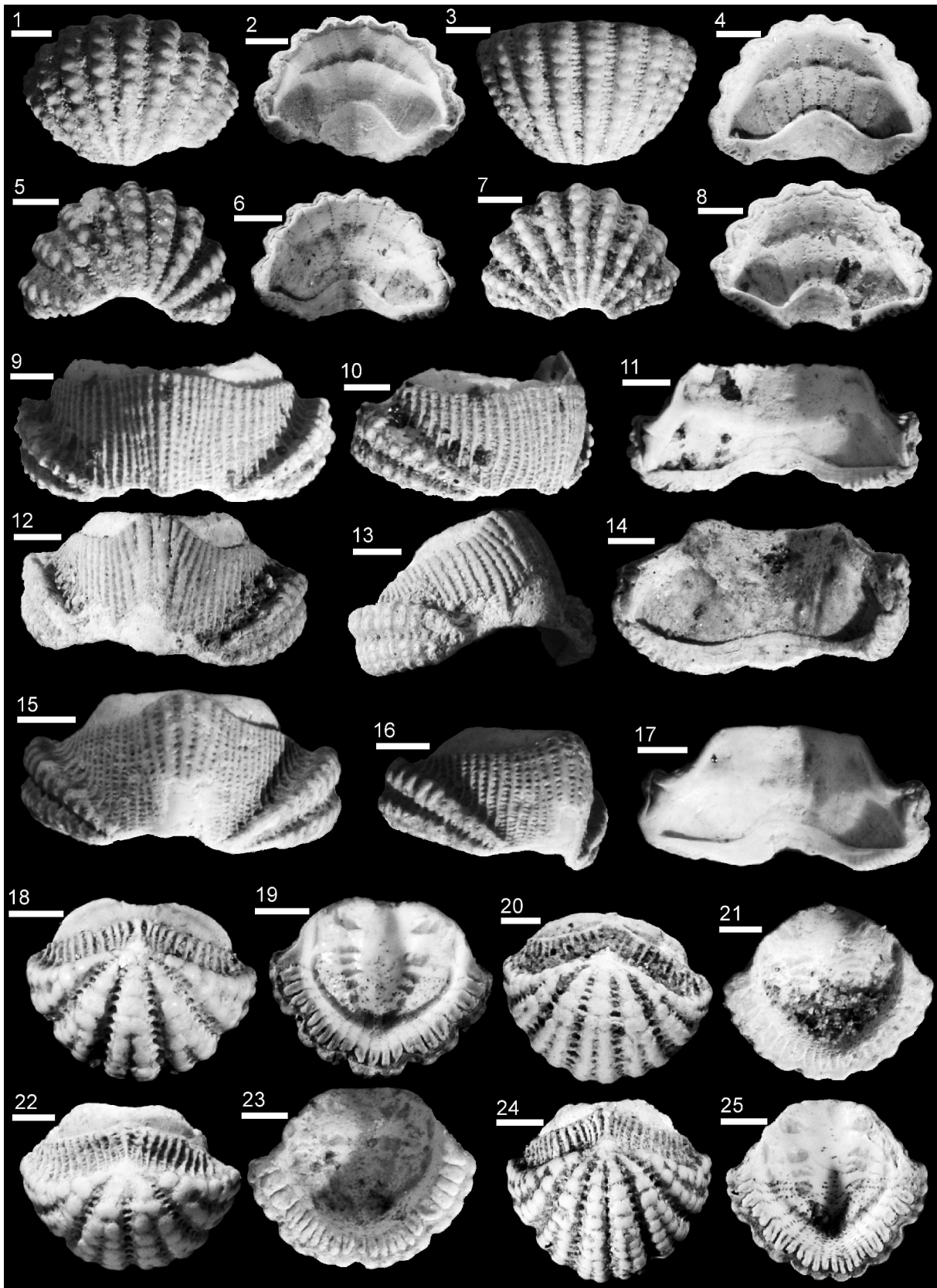
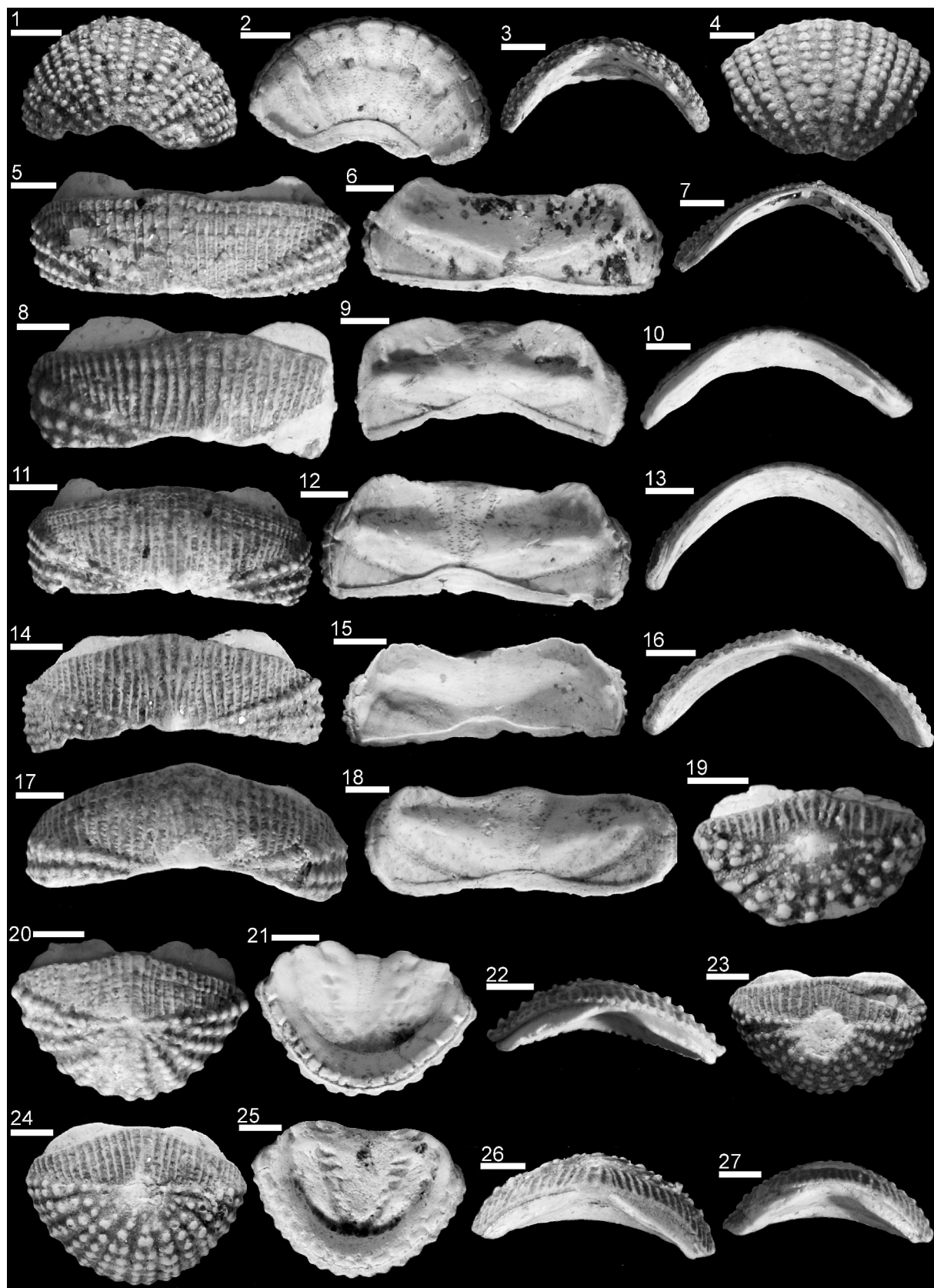


Figure 7 *Callistochiton palmulatus* Dall, 1879: head (1–8), intermediate (9–17), and tail (18–25) valves. 3–4, 20–25, from LACMIP locality 305; 1–2, 5–19, from LACMIP locality 16817 (305C). 1–2, LACMIP 13756; 3–4, LACMIP 13757; 5–6, LACMIP 13758; 7–8, LACMIP 13759; 9–11, LACMIP 13760; 12–14, LACMIP 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.



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. crassicosatus*. However, the San Diego Formation fossils differ from *C. crassicosatus* 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 articulation 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.

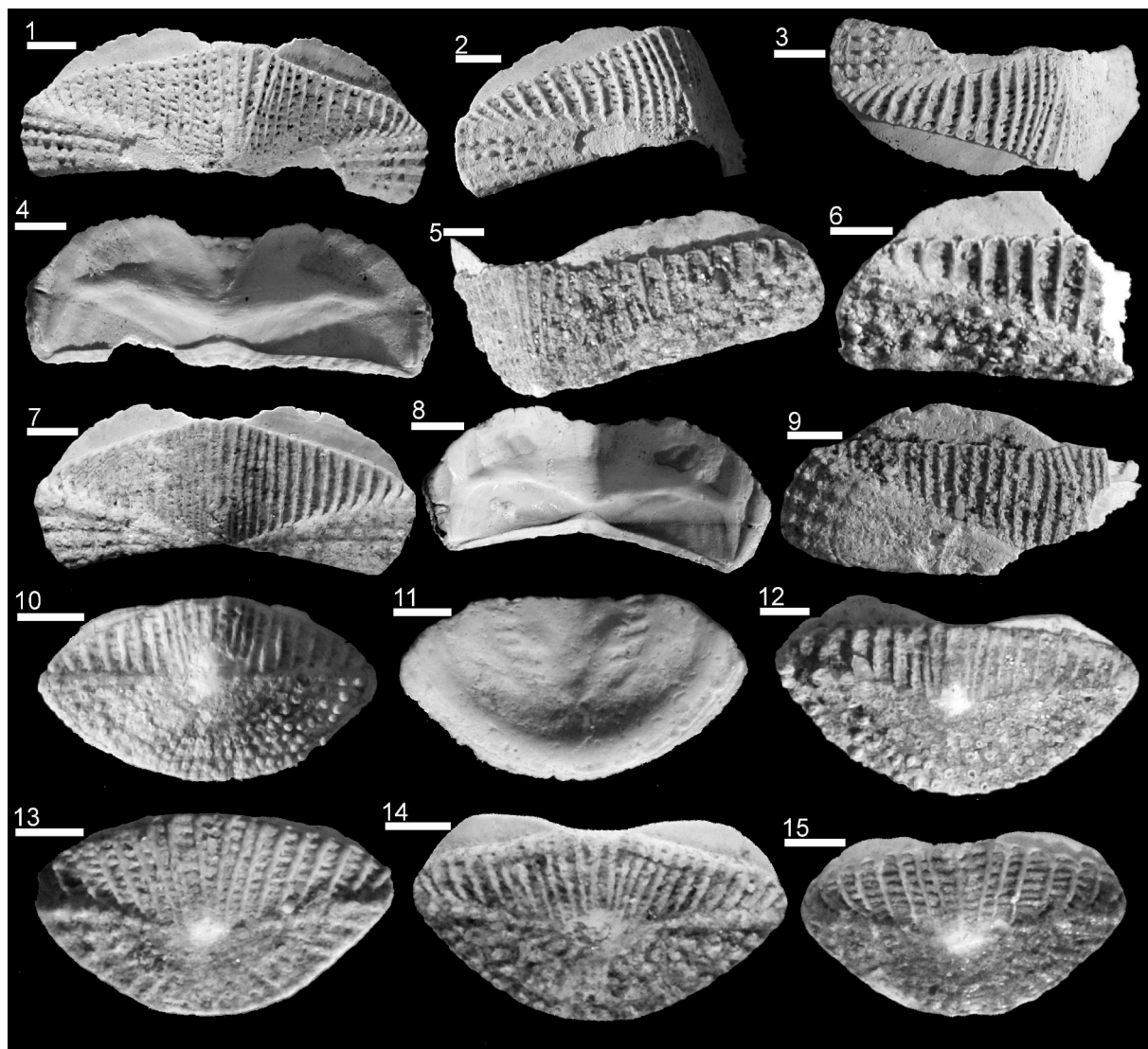
**DESCRIPTION.** Head valves half-moon-shaped in dorsal profile; 12 slits; about 22 branching rows of large, distinct granules; apical area prominent; slit rays distinct; anterior profile rounded (not carinate). Intermediate valves with relatively low aspect ratio; lateral areas with branching rows of 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. crassicosatus* 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

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**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** *Lepidozonia 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 *Lepidozonia* 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 *Lepidozonia* 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 *Lepidozonia* 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 *Lepidozonia* 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 *Callistoichiton* and *Ischnochiton*, and in fact some more weakly sculptured species of *Lepidozonia* were previously included in *Ischnochiton*. *Lepidozonia*

can be separated from *Callistochiton* based mainly on features of the articulamentum (e.g., in *Callistochiton* but not *Lepidozonia* the slits in the head valve generally correspond in number and position to the radial ribs of the tegmentum), and *Lepidozonia* 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 *Lepidozonia* 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 *Lepidozonia*, and these are closely aligned with *Tripoplax* Berry, 1919b (*sensu* Clark, 2008). *Lepidozonia simudentata* (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 *Lepidozonia*, 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 *Lepidozonia* are often quite subtle, and many modern specimens share a mixture of characters used to characterize different species. In addition, for many species of *Lepidozonia* 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 *Lepidozonia* and have set aside a number of specimens at LACMIP as indeterminate *Lepidozonia*.

*Lepidozonia 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 (Lepidozonia) mertensii*: Berry, 1917:26.

*Lepidozonia 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 *Lepidozonia* (as *Chiton mertensii*).

**REMARKS.** Ferreira (1978) differentiated *Lepidozonia 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 *Lepidozonia* 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 *Lepidozonia* from 30+ m depth off of San Diego. The fossils here differ slightly from their *Lepidozonia* sp. A in having relatively larger tubercles; from their *Lepidozonia* sp. B in having more distinct sculpture overall, in particular more protruding longitudinal ridges and tubercles; and from their *Lepidozonia* sp. C in having larger tubercles.

*Lepidozonia 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), *Lepidozonia retiporosa*, and *Callistochiton palmulatus*. However, *L. mertensii* is generally rare south of Point Conception, Santa Barbara County, California.

*Lepidozonia pectinulata* (Carpenter in Pilsbry, 1893)

Figure 10

*Ischnochiton* (*Lepidopleurus*) *pectinatus* Carpenter, 1864:612 (*nomen nudum*).*Ischnoplax pectinatus*: Keep, 1887:112.*Ischnochiton pectinulatus*: Berry, 1922:412, 414, 421, table 1 (fossil).*Ischnochiton clathratus*: Pilsbry, 1892:128.*Lepidozonia 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* (*Lepidozonia*) *californiensis* Berry, 1931:255, pl. 29, figs. 1–2.*Lepidozonia 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.** Ferreira (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 *Lepidozonia pectinulata* and its taxonomic authority is described in detail by Ferreira (1978).

Valves of *Lepidozonia 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 *Lepidozonia*, whose tail valves have up to 14 slits (Ferreira, 1978). Some Panamic species of *Lepidozonia* 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 *Lepidozonia* spp. A and C of Stebbins and Eernisse (2009) in having more closely spaced tubercles and longitudinal ridges; and from *Lepidozonia* 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.

*Lepidozonia 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).

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

Figure 11 (1–5)

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

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

*Lepidozonia* 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.*Lepidozonia 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).



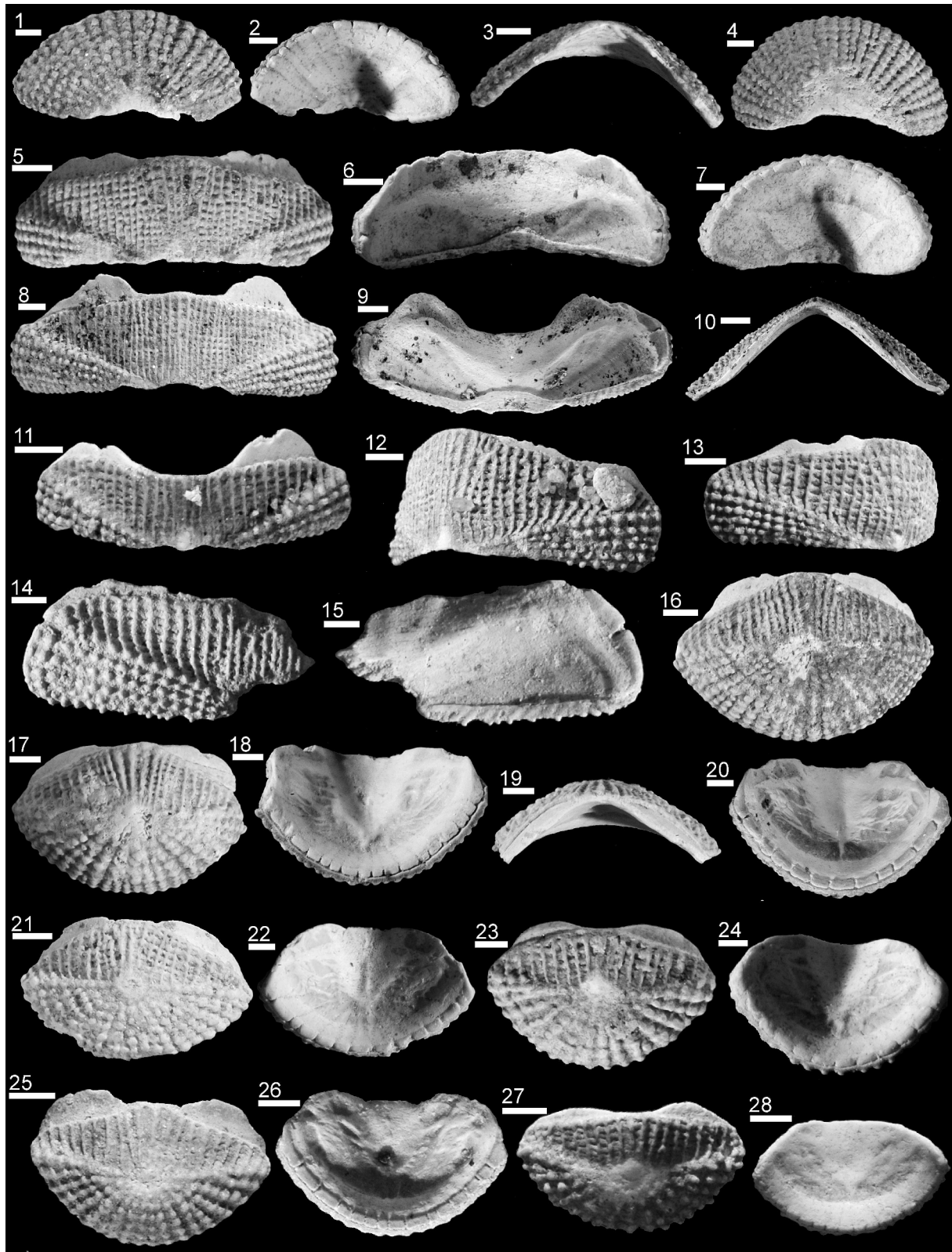


Figure 10 *Lepidozona pectinulata* (Carpenter in Pilsbry, 1893): head (1–4, 7), intermediate (5–6, 8–15), and tail (16–28) valves. 1–12, 14–24, from LACMIP locality 305; 13, 25–28 from LACMIP locality 16817 (305C). 1–3, LACMIP 13787; 4, 7, LACMIP 13788; 5–6, LACMIP 13789; 8–10, LACMIP 13790; 11, LACMIP 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.

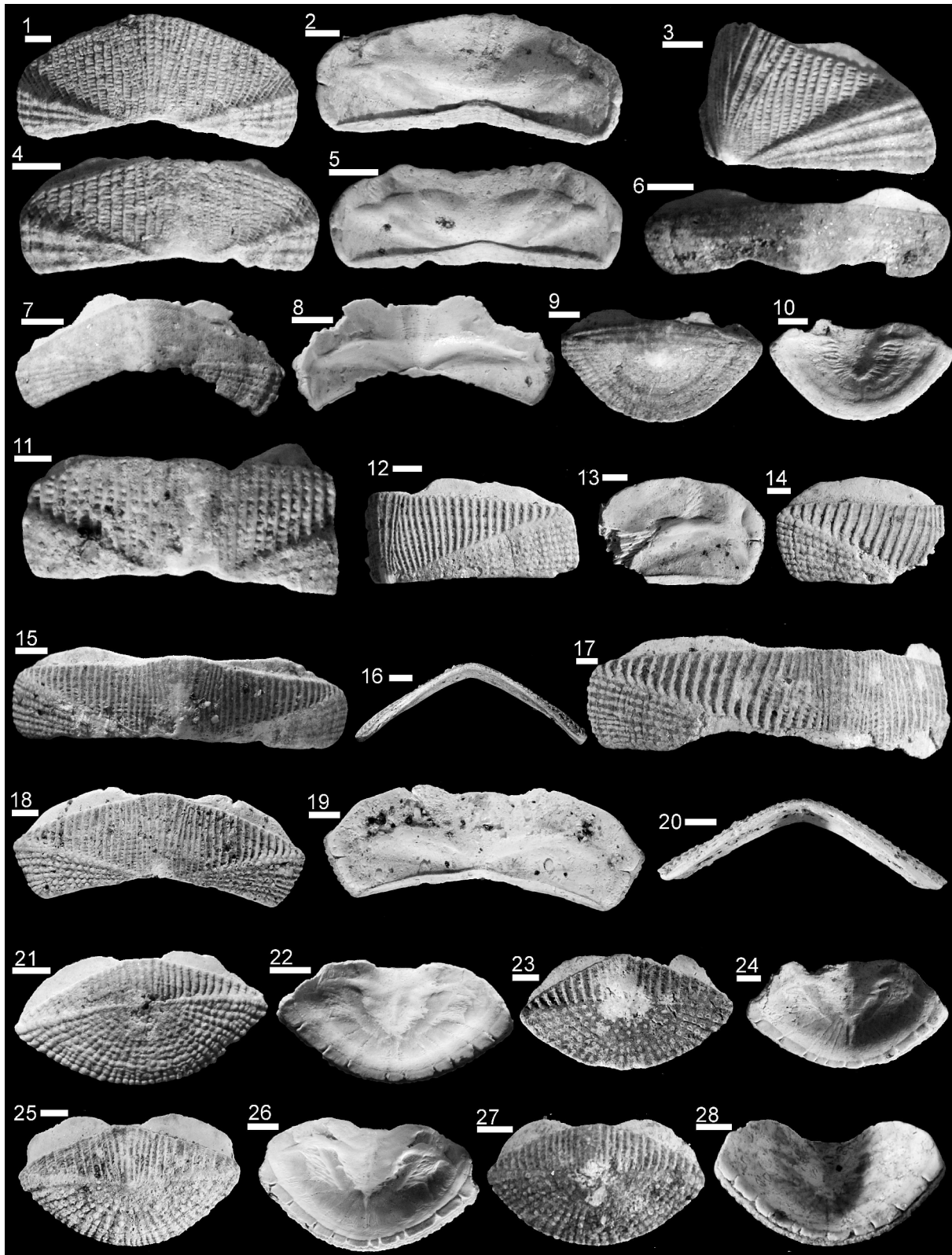


Figure 11 *Lepidozonia* spp. 1–20, 23–28, from LACMIP locality 305; 21–22, from LACMIP locality 16817 (305C). 1–5, *Lepidozonia* sp. cf. *L. rothi* Ferreira, 1983: intermediate valves. 1–2, LACMIP 13801; 3, LACMIP 13802; 4–5, LACMIP 13803; 6–10, *Lepidozonia* sp. cf. *L. radians*: intermediate (6–8) and tail (9–10) valves. 6, LACMIP 13804; 7–8, LACMIP 13805; 9–10, LACMIP 13806; 11–28, *Lepidozonia 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 *Lepidozonia 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 *Lepidozonia interstincta* (Gould, 1846). Eernisse et al. (2007; see also Kelly and Eernisse, 2007; Stebbins and Eernisse, 2009) revised *Lepidozonia 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 *Lepidozonia* spp. A–C (Stebbins and Eernisse, 2009) in lacking distinct tubercles in lateral areas of intermediate valves.

*Lepidozonia 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.

*Lepidozonia 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 *Lepidozonia* species in tegmental sculpture and shape of the projections of the articulamentum. However, they differ from all known members of *Lepidozonia* 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 *Lepidozonia* in having a large jugal angle and more prominent longitudinal ridges. In addition, this species is larger than most species of *Lepidozonia* 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; Bielokrysz, 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

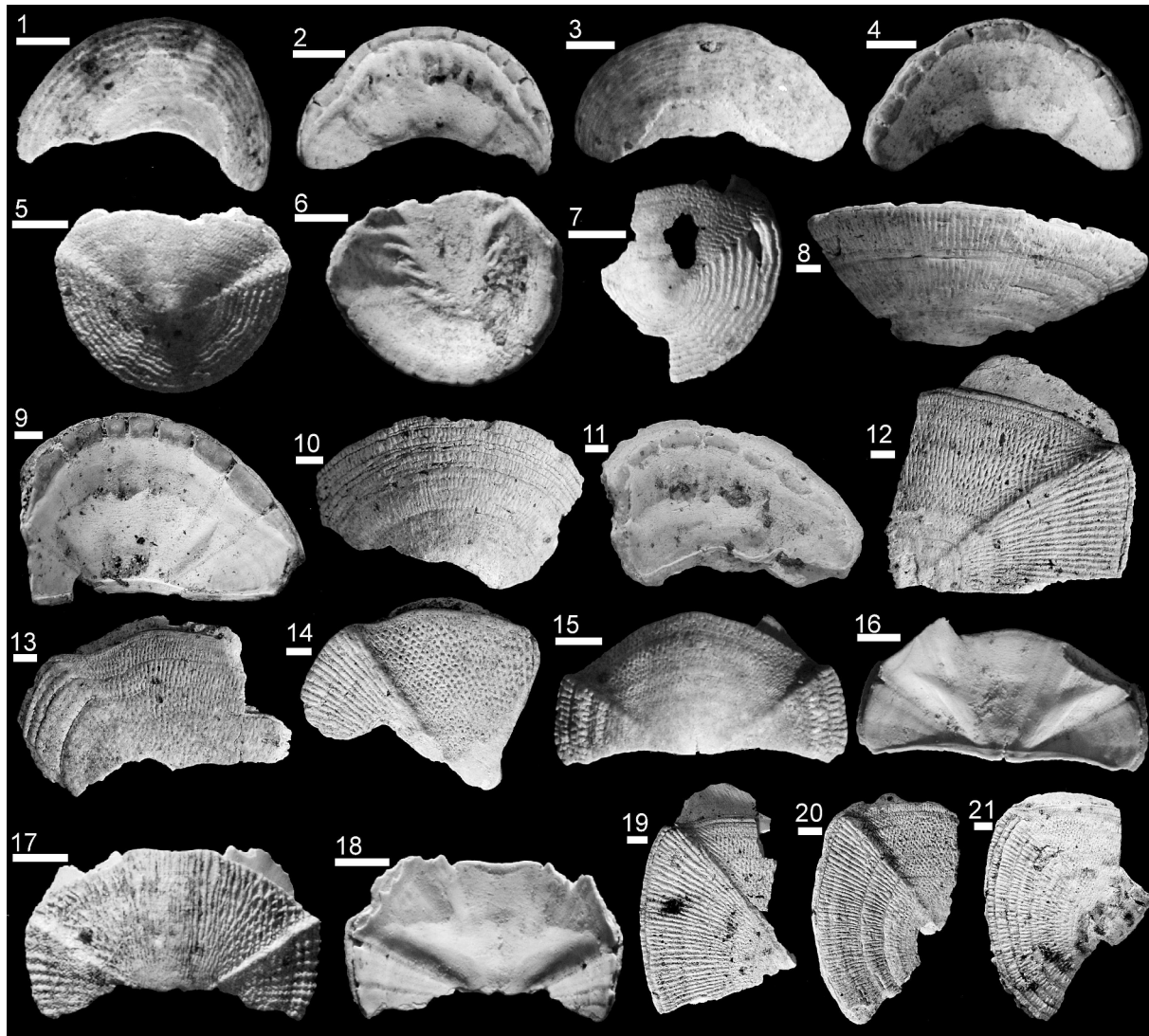


Figure 12 *Stenoplax* spp. 1–4, 8–14, 17–21, from LACMIP locality 305; 5–7, 15–16, from LACMIP locality 16817 (305C). 1–7, *Stenoplax circumsenta* Berry, 1956: head (1–4) and tail (5–7) valves. 1–2, LACMIP 13817; 3–4, LACMIP 13818; 5–6, LACMIP 13819; 7, LACMIP 13820; 8–21, *Stenoplax fallax* (Carpenter 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. magdalenensis*, and *S. heathiana*), as well as smaller and less well known species, can each have distinctive girdele 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 circumscinta*.

**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 circumscinta*. Although *S. circumscinta* was previously synonymized 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. circumscinta*, 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. circumscinta*. We maintain the separation of *S. circumscinta* 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. circumscinta* 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. circumscinta* (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. circumscinta*.

Kaas and Van Belle (1987:294, map 48) show an occurrence of *S. circumscinta* 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 circumscinta* 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. circumscinta*, *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

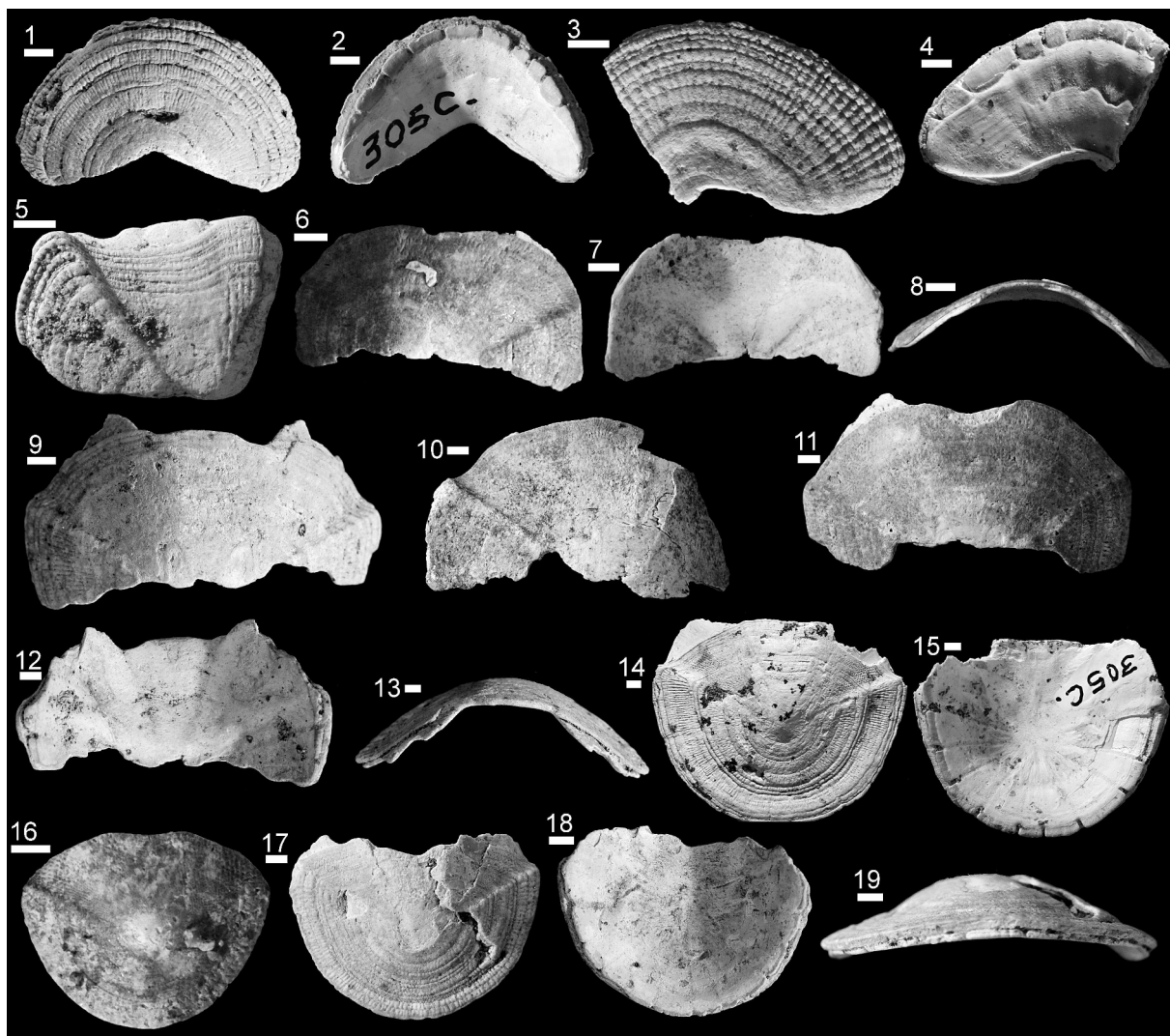


Figure 13 *Stenoplax* sp. cf. *S. heathiana* Berry, 1946: head (1–4), intermediate (5–13), and tail (14–19) valves. 1–13, 16–19, from LACMIP locality 305; 14–15 from LACMIP locality 16817 (305C). 1–2, LACMIP 13832; 3–4, LACMIP 13833; 5, LACMIP 13834; 6–8, LACMIP 13835; 9, 12–13, LACMIP 13836; 10, LACMIP 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. circumscissa*, *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*.

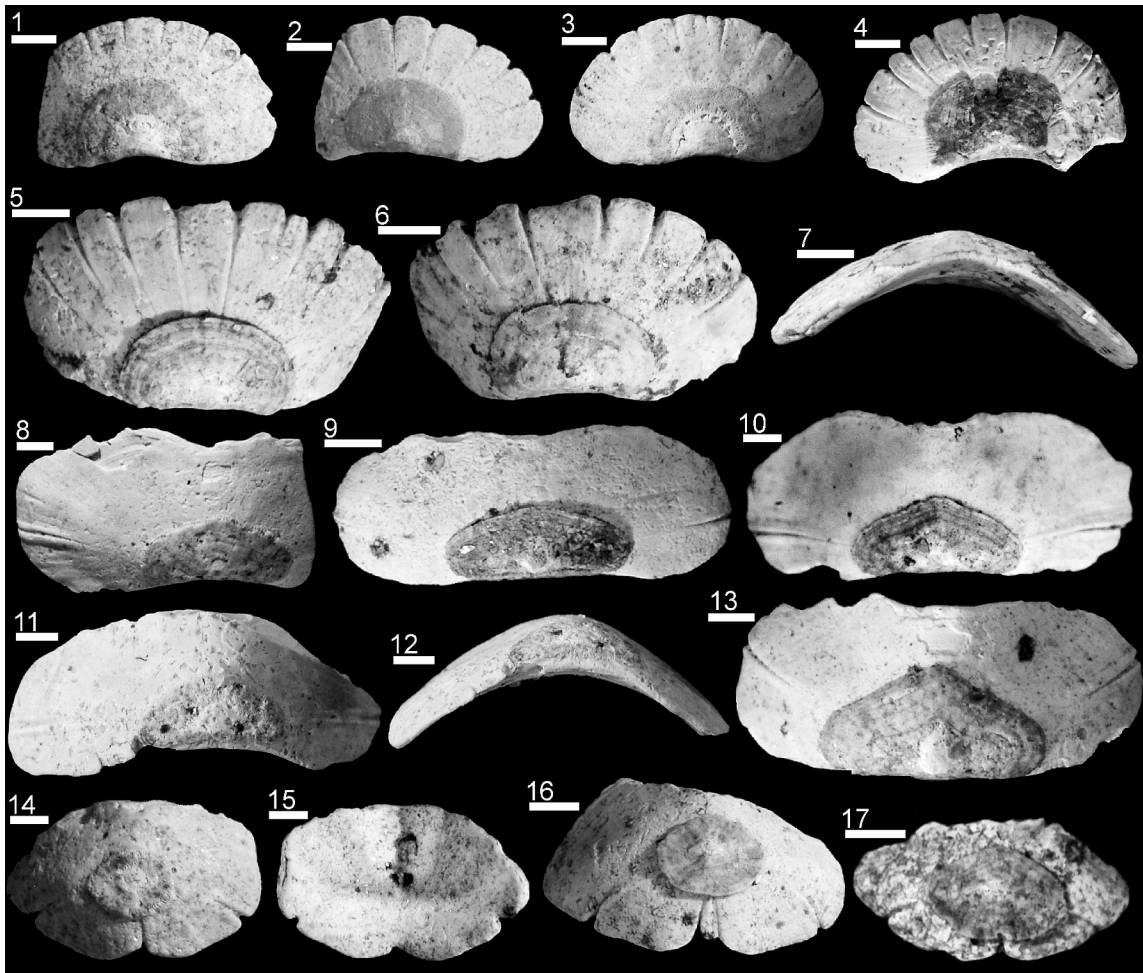
However, species of *Stenoplax* vary with respect to their tegmentum sculpture (Kaas and Van Belle, 1987; MJV, personal observation) and many species of *Stenoplax* can have 10 slits in the tail valve, as observed in the fossil tail valve, so we only provisionally assign these valves to *S. heathiana*. Some of the

fossils may belong to *S. conspicua*, *S. magdalenensis*, or *S. sonarana*, 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, and 1 unfigured, LACMIP 14321, and 16862 (305A); 1 head, 1 intermediate, and 1 tail valve, all in unfigured lot, LACMIP 14322); 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 mopalid 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 synonyms *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  $\sim 0.36$ ;

tegumentum 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; tegumentum 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 tegumentum, 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 tegumentum, 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 tegumentum; a typically suboval, less heart-shaped tegumentum; 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 Arctic (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  $8/1/\text{sinus}+2$  (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.

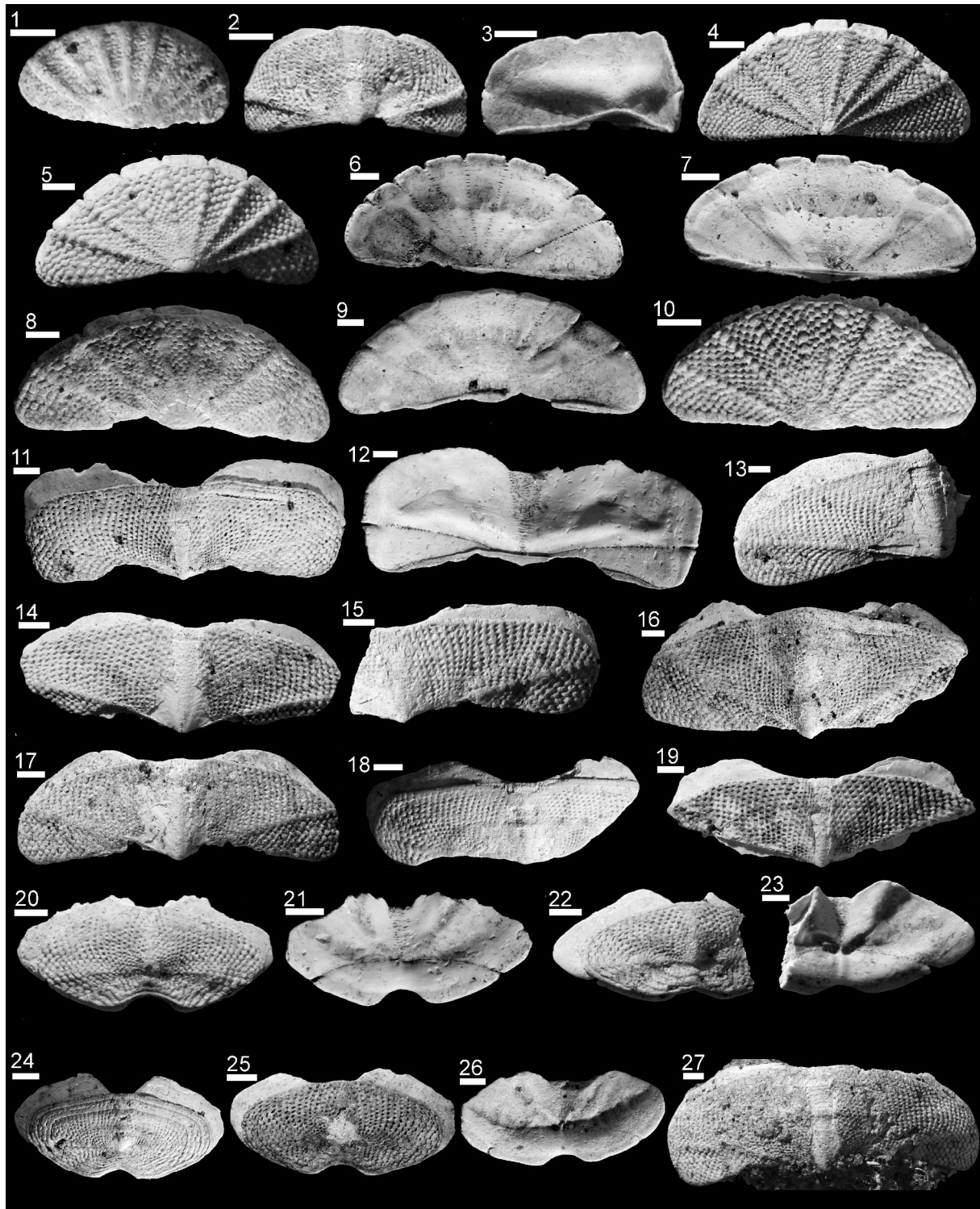
**MATERIAL EXAMINED.** Numerous specimens from at or near the type locality at SBMNH and LACM.

**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 north-eastern 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 (Bielokrysz, 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

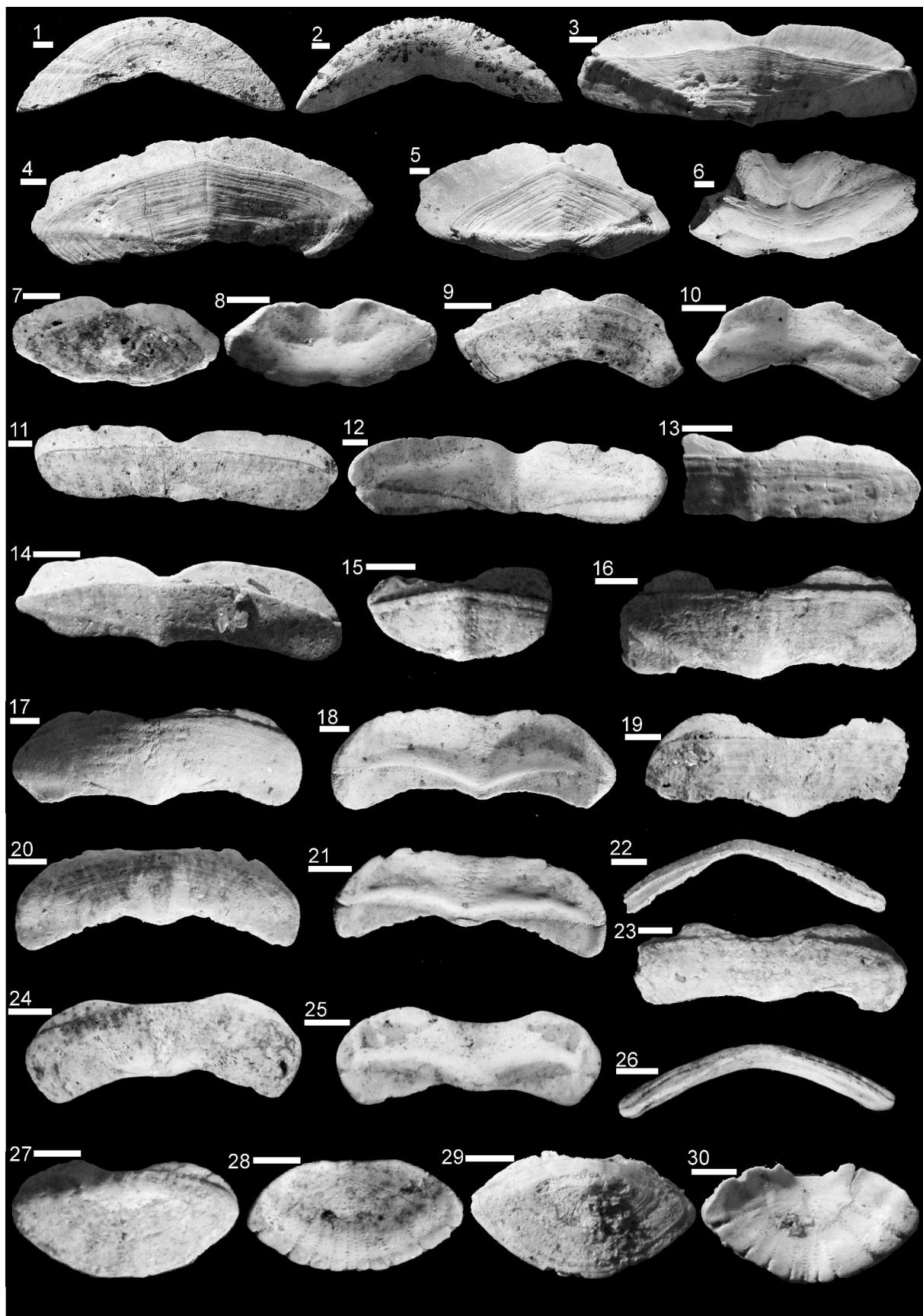
Figure 16 (16–30)

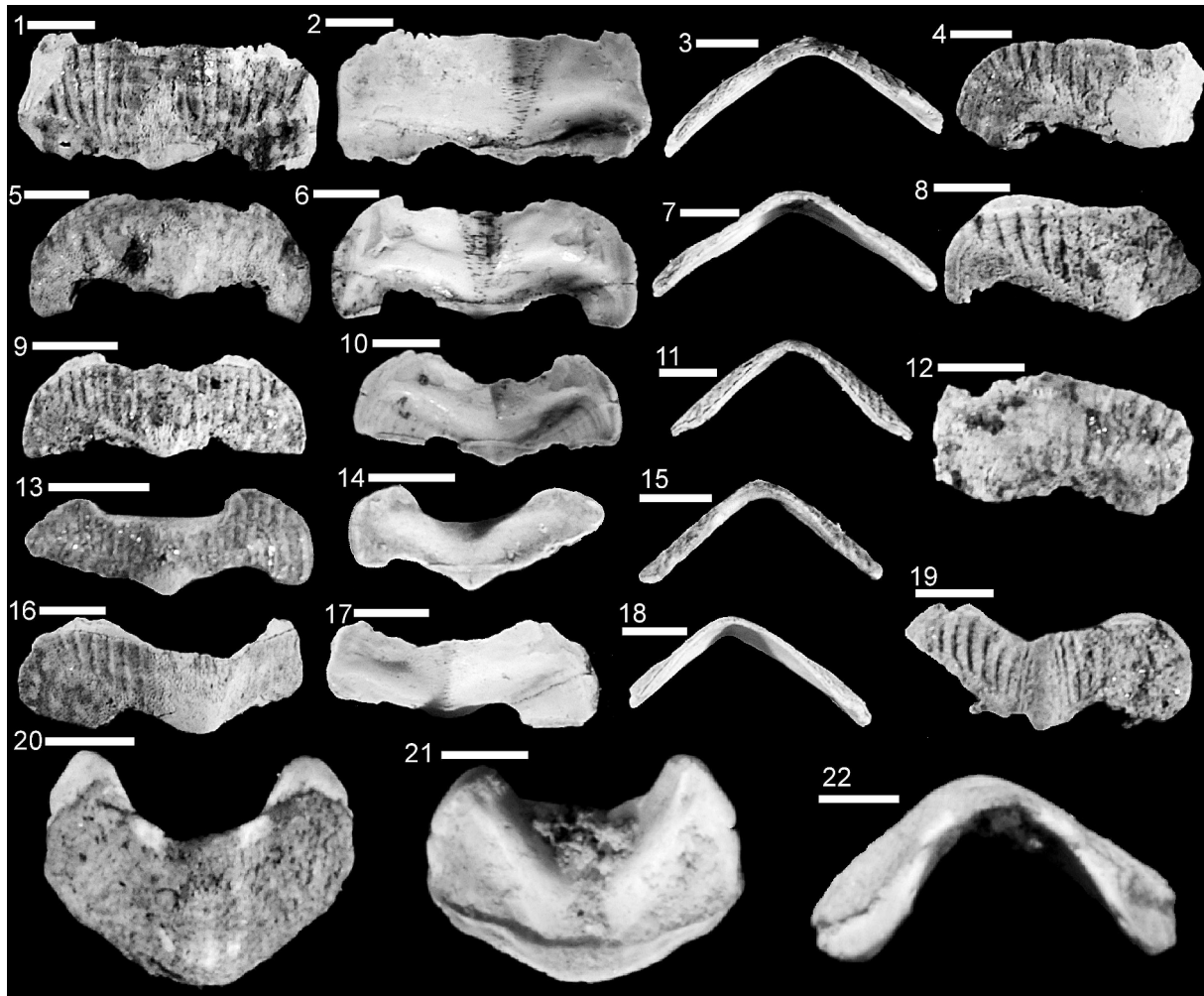
[*Tonicella venusta* Clark, 1999:41, figs. 25–32, 34 (contains more complete synonymies).]

**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





**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

←

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

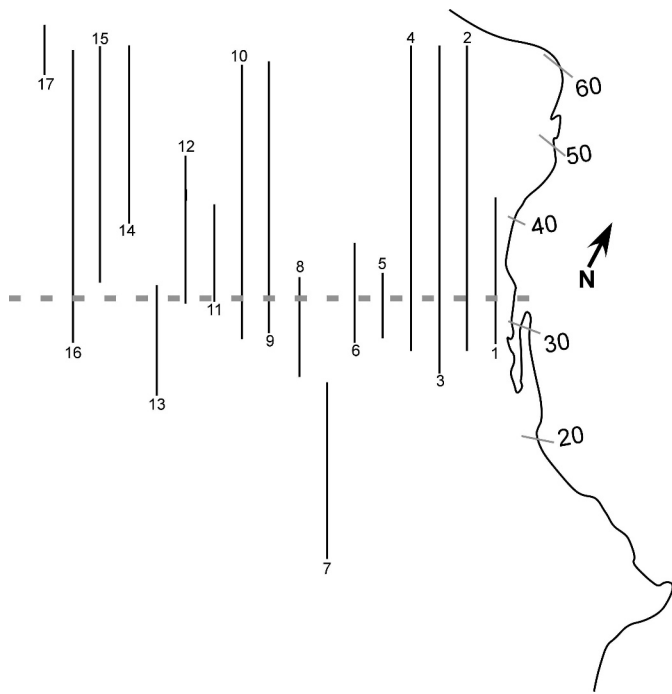
Another genus that likely diversified relatively recently in the North Pacific is *Lepidozonia*, which is mostly restricted to that region. The greatest diversity of *Lepidozonia* is in the northeastern Pacific (Stebbins and Eernisse, 2009), with the oldest fossils apparently being from the Miocene of Japan (Itoigawa and Nishimoto, 1975) and one valve from the latest Eocene or earliest Oligocene of Washington (Dell’Angelo et al., 2011). *Lepidozonia* 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*, *Lepidozonia*, *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, *Lepidozonia rothi* (as *Lepidozonia* sp. cf. *L. rothi*); 8, *L. pectinulata*; 9, *L. mertensii*; 10, *L. radians* (as *Lepidozonia* sp. cf. *L. radians*); 11, *Stenoplax heathiana* (as *Stenoplax* sp. cf. *S. heathiana*); 12, *S. fallax*; 13, *S. circumscissa*; 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*, *Kanebaria*, 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 northeastern 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).

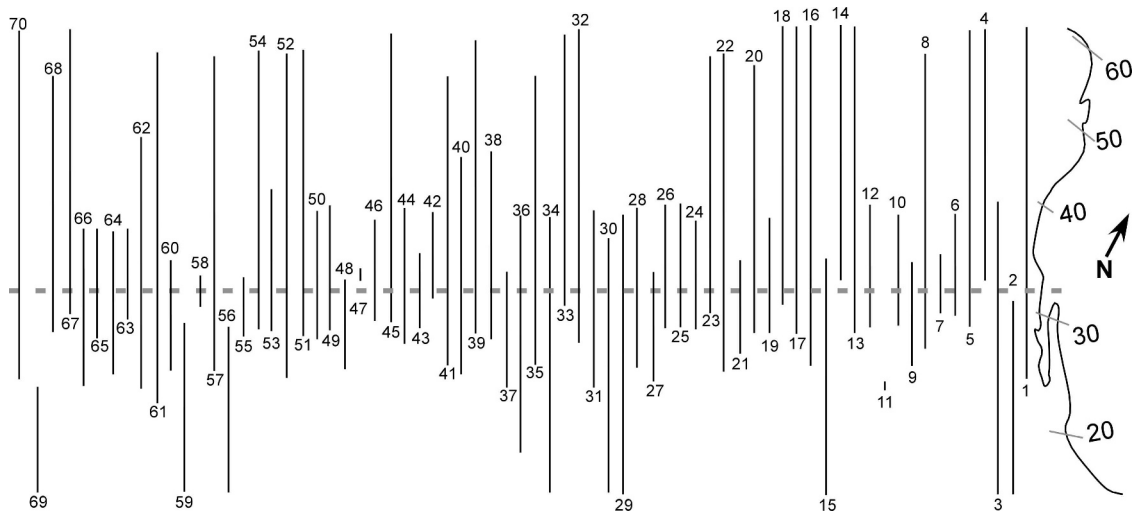
The very high diversity of chitons endemic to the North Pacific indicates diversification in the region. A large proportion of species of many chiton genera occur in the northeastern Pacific and some chiton genera have a slightly earlier fossil record in the western Pacific than in the eastern Pacific. 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, *Luciniscia 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, *Comus californicus*; 29, *Crepidula aculeata*; 30, *C. onyx*; 31, *Crossata californica*; 32, *Cylichnia attonsa*; 33, *Diadora arnoldi*; 34, *Epitonium minutocostata*; 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, *Pseudomelatomia 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 thoursii*; 70, *Cancer productus*.

1842), *Clinocardium nuttalli* (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. imporata*. 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 *Lepidozonia rothi* (as *Lepidozonia* 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  $\sim 17^{\circ}\text{C}$  to  $29^{\circ}\text{C}$  but occurs at highest abundances at  $\sim 27^{\circ}\text{C}$  (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  $23^{\circ}\text{C}$  and  $27^{\circ}\text{C}$  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  $23^{\circ}\text{C}$  and  $27^{\circ}\text{C}$ . 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  $10^{\circ}\text{C}$  and  $30^{\circ}\text{C}$ . 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  $13^{\circ}\text{C}$  and  $20^{\circ}\text{C}$  (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  $13^{\circ}\text{C}$  to  $20^{\circ}\text{C}$ . The one slightly anomalous record, *Ambolastreacon* sp. O, has an inferred temperature tolerance of  $13^{\circ}\text{C}$  to  $18^{\circ}\text{C}$ . 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 ( $\sim 3.15$  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.

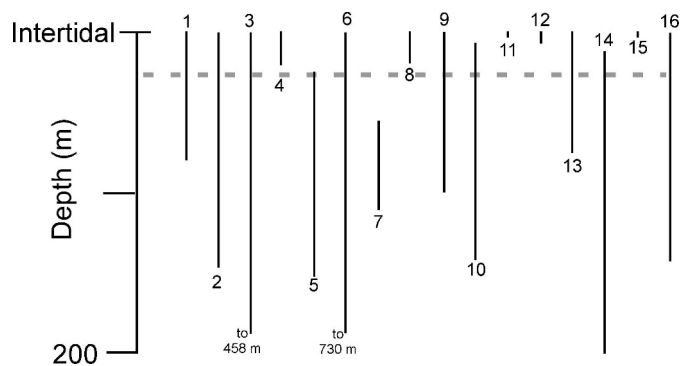


Figure 20 Known depth ranges for modern chiton species with representatives in the San Diego Formation. Dashed line indicates inferred depth of deposition (25 m, based on analysis of the total fauna). Key as in Figure 18.

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).

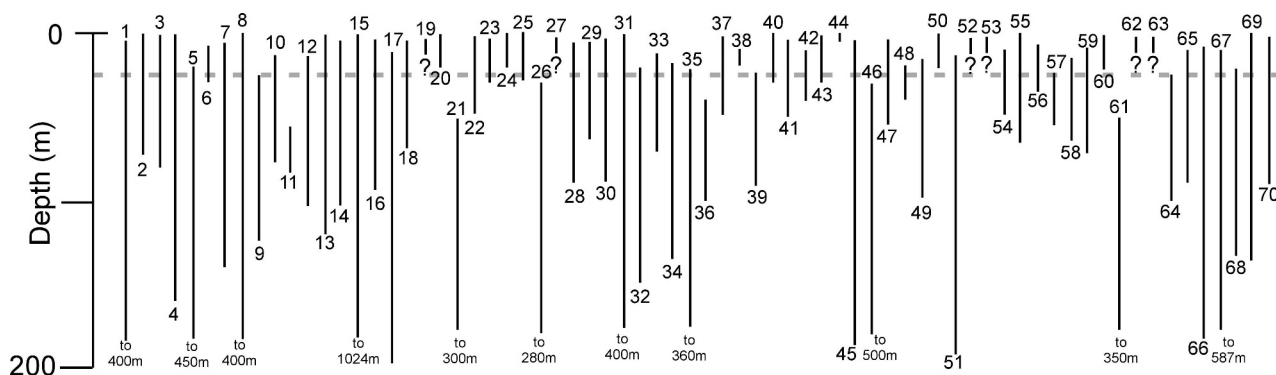


Figure 21 Known depth ranges for other molluscan (nonchiton) species with representatives in the San Diego Formation. Dashed line indicates inferred depth of deposition (25 m). Key as in Figure 19.

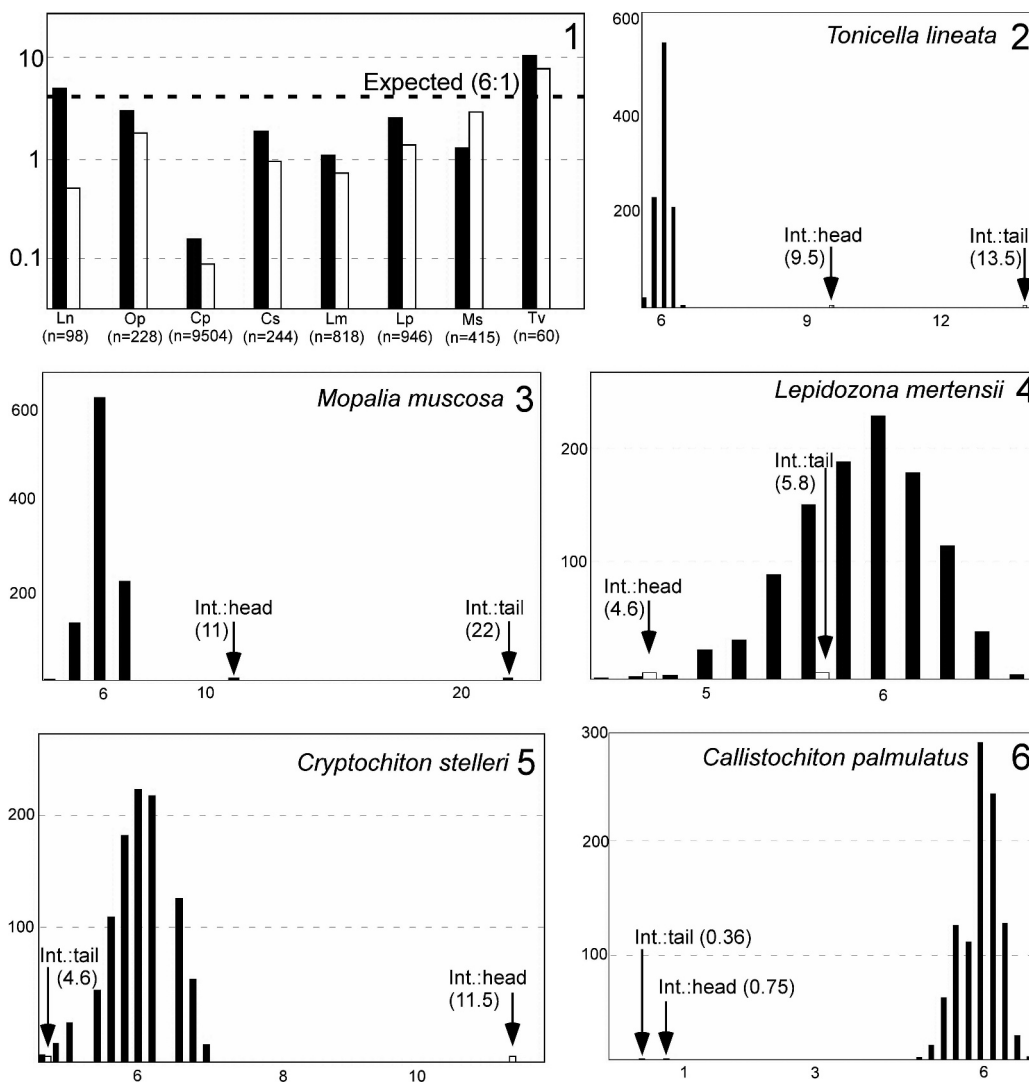
The assemblages of chiton valves from the Border localities are quite similar to those seen in modern sediments dredged from ~15 to 30 m off the California coast (based on examination of samples at LACM; Vendrasco, 1999). For example, LACM station 65–35, from ~27 m off San Pedro, California, contains valves of *Callistochiton palmulatus*, *Leptochiton nexus*, *Oldroydia percrassa*, and *Lepidozonia* 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*, *Lepidozonia pectinulata*, *Stenoplax fallax*, *Nuttallina* sp., and species questionably identified here such as *S. beathiana*, 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 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=*Lepidozonia mertensii*; Lp=*Lepidozonia 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, *Lepidozonia mertensii*, n=32; 5, *Cryptochiton stelleri*, n=30; 6, *Callistochiton palmulatus*, n=61.

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*, *Lepidozonia 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 gully east of 305; 686 m east and 347 m south of the northwest corner of Section 8, T 19 S, R 2 W, San Bernardino 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
<b>Mollusca</b>				
<b>Bivalvia</b>				
<i>Acila castrensis</i> (Hinds, 1843)	a; 305	5–400	Bering Sea, AK, to Sea of Cortez, MX	2b, C
<i>Aligena diegoana</i> Hertlein & Grant, 1972 <sup>1</sup>	c; 305, A, C	N/A		2b
<i>Anadara trilineata</i> (Conrad, 1856b) <sup>1</sup>	a; 305, A	N/A		2b
<i>Anomia peruviana</i> d'Orbigny, 1846	r; 305, A, C	IT to 120	Monterey, CA, to Sechura, Peru	2b, C
<i>Arca sisquocensis</i> Reinhardt, 1937 <sup>1</sup>	c; 305, A	N/A		2b
<i>Argopecten callida</i> (Hertlein, 1925) <sup>1</sup> [fide Moore, 1984]	?; 305	N/A		2b
<i>Argopecten ventricosus</i> Sowerby, 1842 [as <i>Chlamys</i> ( <i>Argopecten</i> ) <i>circularis</i> ]	r; 305, A	1–55	Santa Barbara, CA, to Bayovar, Peru	2b, C
<i>Axinopsida serricata</i> (Carpenter, 1864)	vr; 305, A	low IT to 275	Point Barrow, AK, to Punta San Pablo, BC	2b, C
<i>Barbatia illota</i> (Sowerby, 1833) <sup>2</sup>	a; 305, A	IT to 73	Punta Peñasco, MX, to Lobitos, Peru	2b, K
<i>Basterotia hertleini</i> Durham, 1950 <sup>1</sup>	vr; C	N/A		
<i>Brachidontes adamsianus</i> (Dunker, 1857) (as <i>Aeidimytillus adamsianus</i> )	vr; C	IT	Anacapa Island, CA, to Islas Galapagos	2b, C
<i>Cardiomya pectinata</i> (Carpenter, 1864) [as <i>Cuspidaria pectinata</i> ]	vr; A	5–1,000	Prince William Sound, AK, to Isla la Plata, Ecuador	2b, C
<i>Chama arcana</i> Bernard, 1976 [as <i>C. pellucida</i> ]	a; 305, A	IT to 80	Santa Cruz County, CA, to Costa Rica	2b, C
<i>Chlamys hastata</i> (Sowerby, 1842) <sup>3</sup>	a; 305, A, C	IT to 160	Afognak Island, AK, to San Diego, CA	2b, C
<i>Chlamys hastata ellisi</i> Hertlein & Grant, 1972 <sup>1</sup>	vr; 305	N/A		
<i>Chlamys jordani</i> (Arnold, 1903) <sup>1</sup>	?; 305	N/A		2b
<i>Chione</i> sp. cf. <i>C. undatella</i> (Sowerby, 1835)	?; 305	IT to 40	Goleta, CA, to Paita, Peru	2b, C
<i>Clinocardium nuttalli</i> (Conrad, 1837) <sup>3</sup>	?; 305	IT to 180	Punuk Islands, AK, to San Diego, CA	2b, C
<i>Compsomyax subdiaphana</i> (Carpenter, 1864)	r; 305, A	2–500	Prince William Sound, AK, to Bahía San Quintin, BC	2b, C
<i>Crassidoma gigantea</i> (Gray, 1825) [as <i>Hinnites giganteus</i> ]	vr; 305	IT to 80	Prince William Sound, AK, to Bahía Magdalena, BC	2b, C
<i>Crassinella pacifica</i> (Adams, 1852) [as <i>Crassinella branneri</i> ]	r; 305, C	IT to 160	Santa Cruz Island, CA, to Zorritos, Peru	2b, C
<i>Crenella decussata</i> (Montagu, 1808) [as <i>C. inflata</i> ]	vr; 305, A, C	IT to 200	Beaufort Sea, AK, to Peru	2b, C
<i>Cryptomya californica</i> (Conrad, 1837) [also as <i>C. californica magna</i> ]	c; 305, A	IT to 80	Montague Island, AK, to Bayovar, Peru	2b, C
<i>Cuningia</i> sp. cf. <i>C. californica</i> Conrad, 1837	r; 305, C	IT to 65	Crescent City, CA, to Bahía San Juanico, BC	2b, C
<i>Cyathodonta</i> sp.	vr; 305	N/A		
<i>Cyclocardia occidentalis</i> (Conrad, 1855) <sup>1</sup>	vr?; A	N/A		
<i>Cyclocardia ventricosa</i> (Gould, 1850)	a; 305, A, C	20–450	Prince William Sound, AK, to Punta Rompiente, BC	2b, C
<i>Cyclopecten pernominus</i> (Hertlein, 1935) <sup>2</sup>	r; A, C	2–1,720	Isla Cedros, BC, to La Libertad, Ecuador	2b, K
<i>Dendostrea? vesperina</i> (Conrad, 1854) <sup>1</sup> [= <i>Myrakeena veatchii</i> ]	?; 305, A	N/A		2b, S
<i>Dermatomya tenuiconcha</i> (Dall, 1913) <sup>3</sup>	vr; 305	293–2,200	Aleutian Islands, AK, to La Jolla, CA	2b, C
<i>Diplodonta orbella</i> (Gould, 1851)	vr; 305	IT to 46	Monterey, CA, to Isla Espíritu Santo, BC	2b, C
<i>Diplodonta sericata</i> (Reeve, 1850) <sup>2</sup> [as <i>D. cornea</i> ]	r; 305, C	IT to 75	Santa Cruz, Island, CA, to Laguna San Ignacio, BC	2b, C
<i>Dosinia ponderosa diegoana</i> Hertlein and Grant, 1972 <sup>1</sup>	r; 305, A	N/A		
<i>Ensis myrae</i> Berry, 1953a	a; 305, A, C	5–25	Monterey Bay, CA, to Punta San Pablo, BC	2b, C
<i>Epilucina californica</i> (Conrad, 1837) [as <i>Lucina</i> ( <i>Epilucina</i> ) <i>californica</i> ]	c; 305, A, C	IT to 80	Crescent City, CA, to Rocas Alijos, BC	2b, C
<i>Euvoila stearnsii</i> (Dall, 1874) <sup>1</sup> [as <i>Pecten</i> ( <i>Flabellipecten</i> ) <i>stearnii</i> ]	a; 305, A, C	N/A		
<i>Gari fucata</i> (Hinds, 1845) [as <i>Gobreaeus edentulus</i> ]	a; 305, A, C	5 to 137	Santa Cruz Island, CA, to Isla Cedros, BC	2b, C
<i>Glans carpenteri</i> (Lamy, 1922) [as <i>G. subquadrata</i> ]	r?; 305, A	IT to 100	Frederick Island, CAN, to Punta Rompiente, BC	2b, C
<i>Glycymeris septentrionalis</i> (von Middendorff, 1849) [as <i>G. profunda</i> and <i>G. greuingki</i> ]	a; 305, A	IT to 400	Cook Inlet, AK, to Rocas Alijos, BC	2b, C
<i>Gregariella chenui</i> (Récluz, 1842)	vr; C	IT to 100	Monterey, CA, to Callao, Peru	2b, C
<i>Here excavata</i> (Carpenter, 1857) [as <i>Lucina</i> ( <i>Here</i> ) <i>excavata</i> ]	a; 305, A, C	2.5–12.5	Santa Barbara, CA, to Bahía Santa Maria, BC	2b, C
<i>Hiattella arctica</i> (Linnaeus, 1767)	r; 305, C	IT to 1,190	Point Barrow, AK, to Chile	2b, C
<i>Juliacorbula luteola</i> (Carpenter, 1864) [as <i>Corbula luteola</i> ]	c; 305, A	low IT to 60	Monterey Bay, CA, to Cabo San Lucas, BC	2b, C
<i>Kellia suborbicularis</i> (Montagu, 1803) [as <i>K. laperosii</i> ]	r; 305, A, C	IT to 20	Prince William Sound, AK, to Zorritos, Peru	2b, C
<i>Leporimetis obesa</i> (Deshayes, 1855) [as <i>Florimetis biangulata</i> ]	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
<i>Leukoma staminea</i> (Conrad, 1837) [as <i>Protothaca staminea</i> ]	vr; 305	IT to 10	Attu Island, AK, to Bahía Santa María, BC	2b, C
<i>Limaria orcutti</i> (Hertlein & Grant, 1972) <sup>1</sup> [as <i>Lima (Limaria) orcutti</i> ]	vr; 305, C	N/A		
<i>Luciniscia nuttalli</i> (Conrad, 1837) [as <i>Lucina (Lucinoma) nuttalli</i> ]	a; 305, A, C	10 to 75	Monterey Bay, CA, to Laguna Ojo de Libre, BC	2b, C
<i>Lucinoma annulatum</i> (Reeve, 1850) [as <i>Lucina (Lucinoma) annulata</i> ]	c; 305, A, C	IT to 665	Kodiak Island, AK, to Guaymas, MX	C
<i>Lyropecten cerrosensis</i> (Gabb, 1866) <sup>1</sup>	vr; C	N/A		
<i>Macoma indentata</i> Carpenter, 1864	r; 305, A, C	IT to 100	Humboldt Co., CA, to Isla Santa Margarita, BC	2b, C
<i>Macoma medioamericana</i> Olsson, 1942 <sup>2</sup>	vr; ?; A	IT to 80	Sea of Cortez, MX (31° N) to Caleta la Cruz, Peru	2b, B, K
<i>Macromeris catilliformis</i> (Conrad, 1867) [as <i>Spisula (Macromeris) catilliformis</i> ]	vr; ?; 305, A	5 to 20	Duxbury Point, CA, to Laguna Ojo de Libre, BC	2b, C
<i>Macromeris hemphilli</i> (Dall, 1894b) [as <i>Spisula (Macromeris) hemphilli</i> ]	c; 305, A, C	IT to 50	Cayucos, CA, to Punta Pequeña, BC	2b, C
<i>Milneria minima</i> (Dall, 1871)	vr; 305	IT to 30	Vancouver Island, CAN, to Rocas Alijos, BC	2b, C
<i>Miltha xantusi</i> (Dall, 1905) <sup>2</sup>	a; 305, A, C	55–80	Mostly off Cabo San Lucas, BC, southern Sea of Cortez, MX	2b, K, B
<i>Miodontiscus prolongatus</i> (Carpenter, 1864) <sup>3</sup>	vr; 305	5–210	Prince William Sound, AK, to Point Loma, CA	2b, C
<i>Modiolus rectus</i> (Conrad, 1837)	?; 305, A	IT to 15	Queen Charlotte Islands, CAN, to Paíta, Peru	2b, C
<i>Modiolus sacculifer</i> (Berry, 1953b)	c; 305, A	IT to 100	Moss Beach, CA, to Punta Banda, BC	2b, C
<i>Myrakeena veatchii</i> (Gabb, 1866) <sup>1</sup> [as <i>Ostrea vespertina</i> and <i>O. veatchii</i> ]	?; 305, A	N/A		2b
<i>Mysella pedroana</i> Dall, 1899	c; 305, A	IT to 30	San Francisco, CA, to Playa Rosarito, BC	C
<i>Nemocardium centifolium</i> (Carpenter, 1864)	vr; A	30–150	Portlock Bank, AK, to Punta Rompiente, BC	2b, C
<i>Nucularia taphria</i> (Dall, 1896)	a; 305, A, C	10–100	Fort Bragg, CA, to Isla Cedros, BC	2b, C
<i>Nutricola ovalis</i> (Dall, 1902) [as <i>Psephidia ovalis</i> ]	r; C	20–150	Fort Bragg, CA, to Punta Rompiente, BC	C
<i>Nutricola tanilla</i> (Gould, 1853) [as <i>Tranzenella tanilla</i> ]	a; 305, A, C	IT to 120	Prince William Sound, AK, to Isla Cedros, BC	2b, C
<i>Pandora bilirata</i> Conrad, 1855	vr; 305	ST to 250	Prince William Sound, AK, to Sea of Cortez, MX	2b, C
<i>Pandora punctata</i> Conrad, 1837	vr; C	IT to 50	Vancouver Island, CAN, to Punta Pequeña, BC	2b, C
<i>Panopea</i> sp. cf. <i>P. priapus</i> (Tilesius, 1822) [as <i>P. sp. cf. P. beringiana</i> ] <sup>3</sup>	vr; 305	10–50	Point Barrow, AK, to Cook Inlet, AK	2b, C
<i>Panopea abrupta</i> (Conrad, 1849) [as <i>Panopea generosa</i> ] <sup>3</sup>	a; 305, A, C	low IT to 100	Kodiak Island, AK, to Newport Bay, CA	2b, C
<i>Parvilucina approximata</i> (Dall, 1901) [as <i>Lucina tenuisculpta intensa</i> ]	a; 305, A, C	IT to 1,024	Santa Barbara, CA, to Panama	2b, C
<i>Patinopecten bealeyi</i> (Arnold, 1906) <sup>1</sup>	a; 305, A, C	N/A		
<i>Pecten bellus</i> (Conrad, 1856b) <sup>1</sup>	vr; 305, C	IT to 20	Vancouver Island, CAN, to Bahía San Bartolome, BC	2b, C
<i>Penitella comadi</i> Valenciennes, 1846	vr; 305	IT to 10	Prince William Sound, AK, to Punta Pequeña, BC	C
<i>Penitella penita</i> (Conrad, 1837)	vr; A	N/A		
<i>Periploma stenopa</i> Woodring, 1938 <sup>1</sup>	vr; 305	IT to 46	Sitka, AK, to Punta Pequeña, BC	2b, C
<i>Petricola carditoides</i> (Conrad, 1837)	a; 305, A, C	IT to 90	Bering Sea, AK, to Bahía Magdalena, BC	2b, C
<i>Pododesmus macrochisma</i> (Deshayes, 1839)	r; 305, A, C	IT to 2	Monterey, CA, to Mazatlan, MX	2b, C
<i>Pristes oblongus</i> Carpenter, 1864	c; 305, A, C	IT to 30	Banarof Island, AK, to Bahía Thurloe, BC	2b, C
<i>Protothaca tenerrima</i> (Carpenter, 1857)	vr; C	N/A		
<i>Protothaca tenerrima alia</i> (Waterfall, 1929) <sup>1</sup>	vr; C	N/A		
<i>Rhanphidonta frankiana</i> (Hertlein & Grant, 1972) <sup>1</sup> [as <i>Bornia (Temblornia) frankiana</i> ]	vr; C	N/A		
<i>Rochefortia tumida</i> (Carpenter, 1864) [as <i>Mysella tumida</i> ]	?; 305, A	IT to 973	Beaufort Sea, AK, to Sea of Cortez, MX	2b, C
<i>Saxidomus nuttalli</i> Conrad, 1837 [as <i>Saxidomus nuttalli latus</i> Stewart in Woodring, Stewart, and Richards, 1940 [1941]]	vr; A	IT to 10	Humboldt Bay, CA, to Punta Rompiente, BC	2b, C
<i>Securella kanakoffi</i> (Hertlein & Grant, 1972) <sup>1</sup> [as <i>Chione (Securella) kanakoffi</i> ]	a; 305, A, C	N/A		
<i>Semele rubropicta</i> (Dall, 1871) [also as <i>S. ashleyi</i> ]	r; 305, C	IT to 100	Seldovia Bay, AK, to Sea of Cortez, MX	2b, C
<i>Septifer bifurcatus</i> (Conrad, 1837)	vr; C	IT to 50	Monterey, CA, to Cabo San Lucas, BC	2b, C
<i>Siliqua lucida</i> (Conrad, 1837)	r; 305, A, C	low IT to 50	Bodega Harbor, CA, to Boca de Soledad, BC	2b, C
<i>Solen sicarius</i> Gould, 1850	c; 305, A	IT	Queen Charlotte Islands, CAN, to Bahía San Quintin, BC	2b, C
<i>Sphenia</i> cf. <i>fragilis</i> (Adams & Adams, 1854) [as <i>S. cf. laticola</i> ]	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
<i>Swiftopecten parmeleei</i> (Dall, 1898b) <sup>1</sup> [as <i>Chlamys (Swiftopecten) parmeleei</i> ]	a; 305, A, C	N/A		
<i>Taqelus californianus</i> (Conrad, 1837)	vr; A	IT	Humboldt Bay, CA, to Costa Rica	2b, C
<i>Tellina bodogensis</i> Hinds, 1845	r; 305, A, C	IT to 100	Sitka, AK, to Bahía Magdalena, BC	2b, C
<i>Tellina carpenteri</i> Dall, 1900	c; 305, A, C	IT to 823	Sitka, AK, to Panama	2b, C
<i>Tellina idae</i> Dall, 1891 <sup>3</sup>	c; 305, A, C	IT to 100	Santa Barbara, CA, to San Diego, CA	2b, C
<i>Tellina nuculoides</i> (Reeve, 1854) [as <i>T. salmonea</i> ]	c; 305, A, C	IT to 75	Pribilof Islands, AK, to Islas Coronado, BC	2b, C
<i>Thracia trapezoides</i> Conrad, 1849 [as <i>Thracia kanakoffi</i> ]	a; 305, A, C	11–200	Wide Bay, AK, to Isla Cedros, BC	2b, C
<i>Thyasira flexuosa</i> (Montagu, 1803) [as <i>Thyasira gouldii</i> ] <sup>3</sup>	vr; 305, A	20–3,000	Beaufort Sea, AK, to Point Loma, CA	2b, C
<i>Tivela stultorum</i> (Mawe, 1823)	vr; 305, C	IT to 30	Stinson Beach, CA, to Bahía Magdalena, BC	2b, C
<i>Trachycardium quadragenarium</i> (Conrad, 1837) [as <i>Cardium (Dallocardia) quadragenarium</i> ]	vr; 305, A	IT to 50	Monterey, CA, to Punta Rompiente, BC	2b, C
<i>Tresus nuttallii</i> (Conrad, 1837)	r; 305, A	IT to 80	Kodiak Island, AK, to Bahía Magdalena, BC	2b, C
<i>Trigomulina pacifica</i> Jung, 1996 [as <i>Verticordia ornata</i> ]	r; 305	15–170	Pacific Grove, CA, to Callao, Peru	2b, C
<i>Zirfaea pilsbryi</i> Lowe, 1931	vr; 305	low IT to 125	Point Lay, AK, to Bahía Magdalena, BC	2b, C
<b>Gastropoda</b>				
<i>Acanthina emersoni</i> Hertlein and Allison, 1959 <sup>1</sup>	a; 305, A, C	N/A		K, Sk
<i>Acirsa cernaloensis</i> DuShane, 1970 <sup>2</sup>	vr; 305	7–38	Isla Angel de la Guarda to Cabo San Lucas, BC	MS, M
<i>Acmaea mitra</i> Rathke, 1833	a; 305, A, C	IT to 64	Aleutian Islands, AK, to Isla San Martín, northern BC	A, M
<i>Alvania oldroydae</i> Bartsch, 1911	a; 305, A, C	ST	Monterey Bay, CA, to Isla Asunción, BC	A, M, M3
<i>Amphissa versicolor</i> Dall, 1871	a; 305, A, C	IT to 20; chiefly IT	Graham Island, CAN, to Punta San Pablo, BC	MS, M3
<i>Angulobittium</i> sp. cf. <i>A. asperum</i> (Gabb, 1861) <sup>3</sup> [as <i>Bititium asperum</i> ]	vr; 305	27–91	Santa Rosa Island, CA, to San Diego, CA	K, Sk
<i>Architectonica nobilis</i> Röding, 1798 <sup>2</sup>	c; 305, A, C	ST to 250	Bahía Magdalena, BC to Peru	MG
<i>Balcis</i> sp. cf. <i>B. micans</i> (Carpenter, 1864)	vr; C	30–100	Kodiak Island, AK, to Punta Abreojos, BC	MG
<i>Balcis oldroydae</i> (Bartsch, 1917)	a; 305, A, C	20–90	Kachemak Bay, AK, to Isla Cedros, BC	MG, M3
<i>Barbarofusus barbarensis</i> (Trask, 1855)	a; 305, A, C	50–300	Santa Barbara, CA, to central BC	A, M, M3
<i>Barleeia</i> sp. cf. <i>B. californica</i> Bartsch, 1920a	r; 305, A, C	low IT to ST	Santa Cruz Island, CA, to Isla Cedros, BC	A, M
<i>Barleeia</i> sp. cf. <i>B. subtenius</i> Carpenter, 1864	c; 305, A, C	low IT to ST	Afognak Island, AK, to San Ignacio Lagoon, BC	M, M3
<i>Brochina occidentalis</i> (Bartsch, 1920b)	r; 305, A	?	Kachemak Bay, AK, to Bahía Magdalena, BC	M
<i>Caecum californicum</i> Dall, 1885	c; 305, C	low IT to ST	Monterey Bay, CA, to Bahía Magdalena, BC	M, M3
<i>Caecum dalli</i> Bartsch, 1920b	r; 305	ST	Farallon Islands, CA, to Isla Asunción, BC	A, M, M3
<i>Callianax buplicata</i> (Sowerby, 1825) [as <i>Olivella buplicata</i> ]	a; 305, A, C	low IT to 48	Gulf of AK to Bahía Magdalena, BC	M
<i>Calliostoma annulatum</i> (Lightfoot, 1786)	a; 305, A, C	ST in so. CA	Forrester Island, AK, to Isla San Geronimo, BC	M
<i>Calliostoma coalingense</i> catoteron Woodring and Bramlette, 1950 <sup>1</sup>	N/A			
<i>Calliostoma gemmulatum</i> Carpenter, 1864	a; C	IT to 20	Cayucos, CA, to Isla de Navidad, BC	M, M3
<i>Calliostoma supragranosum</i> Carpenter, 1864	a; 305, A, C	IT to 30	Monterey Bay, CA, to Isla Asunción, BC	M, M3
<i>Calyptraea filosa</i> Gabb, 1866 <sup>1</sup>	N/A			
<i>Calyptraea inornata</i> (Gabb, 1866) <sup>1</sup>	N/A			
<i>Calyptraea</i> sp.	a; 305, A, C	N/A		
<i>Cancellaria annoldi</i> Dall, 1909 <sup>1</sup>	a; 305, A, C	N/A		
<i>Cancellaria cooperi</i> Gabb, 1865	a; 305, A, C	30–280	Monterey Bay, CA, to Punta San Pablo, BC	MG
<i>Cancellaria fergusonii</i> Carson, 1926 <sup>1</sup>	r; C	N/A		
<i>Cancellaria lipara</i> Woodring in Woodring and Bramlette, 1950 <sup>1</sup>	vr; 305, A	N/A		
<i>Cancellaria rapa</i> Nomland, 1917 <sup>1</sup>	vr; C	N/A		
<i>Cancellaria sanctaemariae</i> Carson, 1926 <sup>1</sup>	c; 305, A, C	N/A		
<i>Cantharus</i> sp.	c; A, C			
<i>Cerithiopsis pedroana</i> Bartsch, 1907	a; 305, A, C	ST	San Pedro, CA, to Estero Todos Santos, BC	M, M3
<i>Cidarina cidaris</i> (Carpenter, 1864)	r; 305	35–300	Prince William Sound, AK, to Isla Cedros, BC	MS, MG, M3
<i>Conus californicus</i> Reeve, 1844	a; 305, A, C	low IT to 90	Farallon Islands, CA, to Bahía Magdalena, BC	A, M, M3
<i>Cranopsis cucullata</i> (Gould, 1846) [as <i>Puncturella cucullata</i> ]	c; 305, A, C	>100 in southern CA	Kodiak Island, AK, to Cabo San Quintin, BC	MS, MG
<i>Craufordiana fugleri</i> (Arnold, 1907) <sup>1</sup>	vr; A	N/A		

## Appendix 1 [Continued]

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

Appendix 1 [Continued]

Species	Frequency and locality	Depth range (m)	Geographic range in Eastern Pacific	Sources
<i>Limularia optabilis</i> (Carpenter, 1864) <sup>3</sup>	a; 305, A	5–55	Santa Rosa Island, CA, to Laguna Beach, CA	A, M3
<i>Littorina</i> sp. cf. <i>L. scutulata</i> Gould, 1849	vf; C	IT	Kodiak Island, AK, to Bahía San Bartolome, BC	M
<i>Macrarenne diegensis</i> McLean, 1964 <sup>1</sup>	c; A, C	N/A		
<i>Mangetia</i> sp.	a; 305, A, C	N/A		
<i>Maxwellia eldridgei</i> (Arnold, 1907) <sup>1</sup>	a; 305, A, C	N/A		
<i>Mediargo medicris</i> (Dall, 1909) <sup>1</sup>	vf; 305, A, C	N/A		
<i>Megalomphalus</i> sp.	f; 305, C			
<i>Megastrea turbanica</i> (Dall, 1910) <sup>2</sup> [as <i>Astraea turbanica</i> ]	a; 305, A, C	20–40	Islas Coronado, BC, to Isla Santa Margarita, BC	A, K, M3
<i>Megastrea</i> sp. cf. <i>M. carpenteriana</i> (Gabb, 1865)	a; 305, A, C	16–100	Bodega Bay, CA, to Isla Cedros, BC	M
<i>Megathura crenulata</i> (Sowerby, 1825)	a; 305, A, C	IT to 20	Monterey, CA, to Punta Pequeña, BC	A, M, Re, M3
<i>Metaxia convexa</i> (Carpenter, 1857)	f; 305, A, C	low IT to ST	Monterey Bay, CA, to Mazatlan, MX	M, M3
<i>Micranellium crebricinctum</i> (Carpenter, 1864)	a; 305, A, C	10–200	Kachemak Bay, AK, to Punta Abreojos, BC	MG
<i>Microglyphis</i> sp.	c; C			
<i>Mitra idae</i> Melvill, 1893	c; 305, C	0–100	Crescent City, CA, to Isla Cedros, central BC	M, M3
<i>Mitrella tuberosa</i> (Carpenter, 1864)	a; 305, A, C	ST	Forrester Island, AK, to southern BC	M
<i>Nassarius (Caesia)</i> sp. cf. <i>N. grammatus</i> (Dall, 1917) <sup>1</sup>	vf; 305	N/A		
<i>Nassarius perpinguis</i> (Hinds, 1844)	a; 305, A, C	low IT to ST	Point Reyes, CA, to Isla Cedros, central BC	M
Naticidae indeterminate [as <i>Polinices</i> spp.]				
<i>Neosimnia</i> sp.	vf; 305			
<i>Niveolectura funiculata</i> (Carpenter, 1864)	c; 305, A, C	20–70	Shumagin Island, AK, to Bahía Magdalena, BC	MS, MG
<i>Nodiscala spongiosa</i> (Carpenter, 1864)	c; 305, A, C	18–72	Monterey, CA, to Islas Galapagos	MG
<i>Nucella</i> sp.	vf; 305, A, C			
<i>Ocenebra</i> sp.	a; 305, A, C			
<i>Odotomia</i> sp.	a; 305, A, C	ST (to 46+)	Forrester Island, AK, to Bahía Magdalena, BC	A, M
<i>Opalia montereyensis</i> (Dall, 1907)	c; 305, A	N/A	Bristol Bay, AK, to San Luis Obispo County, CA	A, M3
<i>Opalia varicosata</i> Stearns, 1875 <sup>1</sup> [syn. <i>O. varicosata anomala</i> ]	a; 305, A, C	IT		
<i>Opalia</i> sp. cf. <i>O. borealis</i> Keep, 1881 <sup>3</sup>	a; 305, A, C	N/A		
<i>Ophiodermella graciosa</i> (Arnold, 1907) <sup>1</sup>	a; 305, A, C	IT to 65	Santa Rosa Island, CA, to Isla Asuncion, BC	M, M3
<i>Ophiodermella inermis</i> (Reeve, 1843)	c; 305, A	ST to 30	Monterey Bay, CA, to Sea of Cortez, MX	MS, M, M3
<i>Parviturbo acuticostatus</i> (Carpenter, 1864)	a; 305, A, C	3–30	Asuncion Island, BC to Port Urria, Columbia	MS, A, K
<i>Parviturbo</i> sp. cf. <i>P. stearnsi</i> <sup>2</sup> (Dall, 1918) [as <i>P. acuticostatus quoylei</i> ]	a; 305, A, C	20–50 in southern CA	Dall Island, AK, to Isla Santa Margarita, BC	A, K, M, Sk, M3
<i>Pomaulax gibberosa</i> (Dillwyn, 1817)	a; 305, A, C	15–65	San Pedro, CA, to Isla San Martin, northern BC	M, M3
<i>Pseudomelatomia grippi</i> (Dall, 1919)	a; 305, A, C	ST to 76	Crescent City, CA, to Islas Revillagigedos, MX	A, M, M3
<i>Pusula californiana</i> (Gray, 1827)	c; 305, A, C	9–72	Isla Cedros, BC to Costa Rica	A, K, KC
<i>Scalina brunneopicta</i> (Dall, 1908) <sup>2</sup>	a; 305, A, C	>20–110	Forrester Island, AK, to Cabo San Martin, BC	MS, MG
<i>Scelidontoma bella</i> (Gabb, 1865)	f; 305, A	ST	Monterey Bay, CA, to Islas Coronado, BC	M, M3
<i>Schwartziella</i> sp. cf. <i>S. bakeri</i> (Bartsch, 1902)	a; 305, A, C	low IT to 67	Monterey Bay, CA, to Punta Abreojos, BC	A, M
<i>Seila montereyensis</i> Bartsch, 1907	a; 305, A, C	0–20	Santa Barbara, CA, to Bahía Magdalena, BC	M, M3
<i>Shakysus festinus</i> (Hinds, 1844)	a; 305, A, C	IT to 30	Farallon Islands, CA, to Iquique, Chile	K, M
<i>Sinezona rimuloides</i> (Carpenter, 1865) [as <i>Coronadoa simonsae</i> ]	vf; C	15–150	Monterey Bay, CA, to Todos Santos, BC	M, M3
<i>Sinum scopulosum</i> (Conrad, 1849)	f; 305, A			MS
<i>Skenea</i> sp.	vf; 305			MG
<i>Solaniella perambilis</i> Carpenter, 1864	a; 305, A, C	50–350	Forrester Island, AK, to Isla Clarion, MX	M3
<i>Strictispira zizyphus</i> (Berry, 1940) <sup>1</sup>	a; 305, C	N/A		
<i>Tegula aureotincta</i> (Forbes, 1852)	f; 305	IT to ST	Ventura County, CA, to Bahía Magdalena, BC	MS, M
<i>Tegula gallina multiflora</i> (Stearns, 1892)	c; 305, A, C	IT	San Francisco, CA, to Sea of Cortez, MX	MS, A
<i>Tegula hemphilli</i> Oldroyd, 1921 <sup>1</sup>	vf; A, C	N/A		MS
<i>Tegula regina</i> (Stearns, 1892)	vf; 305	ST, mostly ~10	Catalina Island, CA, to Isla Asuncion, BC	M
<i>Tenostoma supravallatum</i> (Carpenter, 1864)	c; 305	ST	Los Angeles County, CA, to Isla San Geronimo, BC	M
<i>Terebra martini</i> (English, 1914) <sup>1</sup>	a; 305, A, C	N/A		
<i>Tricolia</i> sp. cf. <i>T. pulloides</i> (Carpenter, 1865)	a; A, C	low IT to ST	Puget Sound, WA, to Cabo San Lucas, BC	M
<i>Triphora pedroana</i> 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
<i>Trophon</i> sp.	c; 305, A, C			
<i>Turbonilla</i> sp.	a; 305, A, C			
<i>Turcica brevis</i> Stewart in Woodring et al. 1940[1941] <sup>1</sup>	a; 305, C	N/A		MS
<i>Turritella cooperi</i> Carpenter, 1864	a; 305, A, C	25–100	Point Piños, CA, to Bahía Magdalena, BC	MG, M3
<i>Vitrinella oldroydi</i> Bartsch, 1907	a; 305, A, C	0–20	British Columbia, CAN, to Bahía Magdalena, BC	Sur A, M, M3
<i>Zonaria</i> ( <i>Neoberraya</i> ) <i>spadicea</i> (Swainson, 1823)	f; 305	low IT to 48	Monterey, CA, to Isla Cedros, BC (rare north of Point A, M Conception, CA)	M
<b>Polyplacophora: See Table 2</b>				
<b>Scaphopoda</b>				
<i>Cadulus fusiformis</i> Pilsbry and Sharp, 1898	a; 305, A, C	10–90	Monterey, CA, to BC	O
<i>Dentalium neohexagonum</i> Sharp and Pilsbry in Pilsbry and Sharp, 1897	a; 305, A, C	9–182	Monterey, CA, to Sea of Cortez, MX	MS, K, M
<i>Dentalium</i> sp. cf. <i>D. semipolatum</i> Broderip and Sowerby, 1829	c; C	IT to 18	Monterey, CA, to Costa Rica	A
<i>Siphodontium quadrifissatum</i> (Pilsbry and Sharp, 1898)	vi; A, C	4–365	Monterey, CA, to BC	A
<b>Nonmollusks</b>				
<b>Porifera</b>				
<i>Cliona celata</i> Grant, 1825	f; 305		AK to British Columbia, CAN	G
<b>Cnidaria</b>				
<i>Astrangia</i> sp. cf. <i>A. insignifica</i> Nomland, 1916	f; 305	0–53	San Luis Obispo, CA, to Isla Santa Margarita, BC	2a
<i>Balanophyllia elegans</i> Verrill, 1864	a; 305, A, C	0–587 (>10 in southern CA)	Snipe Bay, AK, to Sacramento Reef, north BC	2a
<i>Dendrophyllia</i> sp. cf. <i>D. oldroydi</i> Faustino, 1931	vi; 305	183–366	San Pedro, CA, to San Diego, CA	2a
<i>Paraclyathus stearnsii</i> Verrill, 1869	a; 305, A, C	20–134	Queen Charlotte Islands, CAN, to Bahía Asuncion, BC	2a
<b>Bryozoa</b>				
<i>Reptadeonella violacea</i> (Johnston, 1847) <sup>2</sup>	vi; 305	9–110	Sea of Cortez, MX	2a, CB
<i>Callopora corniculifera</i> (Hincks, 1882) <sup>3</sup>	?; 305	IT to 96–126	British Columbia, CAN, to Channel islands, CA	2a, So
<i>Cellaria diffusa</i> Robertson, 1905	?; 305	IT to 216	Puget Sound WA, to Islas Galapagos	2a, So
<i>Cellaria mandibulata</i> Hincks, 1882	?; 305	IT to >140	British Columbia to Point San Eugenio	2a, So
<i>Chattereria patula</i> (Hincks, 1881)	f; 305	ST to 90	Frequently found in British Columbia, CAN, but ranges 2a, So to BC	2a, So
<i>Coleopora gigantea</i> (Canu and Bassler, 1923)	vi; 305	ST to >200	Monterey Bay, CA, to BC	2a, So2
<i>Conopeum commensale</i> Kirkpatrick and Metzelaar, 1922	?; 305			2a
<i>Diaperoforma californica</i> (d'Orbigny, 1852) [as <i>Diaperoecia californica</i> ]	?; 305	ST to 200	British Columbia, CAN, to Islas Coronados, MX	2a, So
<i>Disporella californica</i> (d'Orbigny, 1853)	?; 305	IT to 237	Nootka Island, AK, to Tenacatita, MX (perhaps an area of cool water upwelling)	2a
<i>Eurystomella bilabiata</i> (Hincks, 1884)	vi; 305			2a, So
<i>Heteropora pacifica</i> Borg, 1933	?; 305	low IT to 27	AK to central CA	2a
<i>Hippopodiniella adpressa</i> (Busk, 1854)	?; 305			2a
<i>Hippoporella gorgonensis</i> Hastings, 1930	?; 305			2a
<i>Hippothoa</i> ( <i>Celleporella</i> ) <i>hyalina</i> (Linnaeus, 1767)	f; 305	IT to 130.5	AK to CA (possibly Galapagos)	2a, So
<i>Lagenipora</i> ( <i>Lagenicella</i> ?) <i>punctulata</i> (Cabb and Horn, 1862)	?; 305	ST to 200	Northern CA to BC and Sea of Cortez, MX	2a, So
<i>Microporella californica</i> (Busk, 1856) <sup>3</sup>	vi; 305	IT to 150	AK to southern CA	2a, So
<i>Microporella cribrosa</i> Osburn, 1952	vi; 305	ST to 126	Mussel Point, central CA, to Sea of Cortez, MX	So
<i>Microporella umbonata</i> (Hincks, 1884)	?; 305			2a
<i>Microporellotoides</i> sp. [as <i>Microporella ciliata</i> (Pallas, 1766)]	vi; 305			2a
<i>Mucronella major</i> (Hincks, 1884)	f; 305			2a
<i>Parasmittina trispinosa</i> (Johnston, 1838)	f; 305			2a
<i>Porella porifera</i> (Hincks, 1884) <sup>3</sup>	?; 305	ST to 250	British Columbia, CAN, to Channel Islands CA	2a, So
<i>Puellina californensis</i> Soule, and Chaney, 1995 [as <i>Colletostia radiata</i> ]	?; 305	ST to 180	Channel Islands, CA, possibly to Sea of Cortez, MX	2a, So
<i>Reginella mucronata</i> (Canu and Bassler, 1923)	c; 305			2a

Appendix 1 [Continued]

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

## Footnotes.

<sup>1</sup> extinct taxa,<sup>2</sup> southern extralimital taxa,<sup>3</sup> 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: 2a=species included in Hertlein and Grant, 1960; 2b=species included in Hertlein and Grant, 1972; MS=species described in Hertlein 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	<i>Leptochiton rugatus</i>		305	Head	5.1–5.3
13731	<i>Leptochiton rugatus</i>		305	Head	5.4, 5.7
13732	<i>Leptochiton rugatus</i>		305	Head	5.5–5.6
13733	<i>Leptochiton rugatus</i>		305	Intermediate	5.8–5.10
13734	<i>Leptochiton rugatus</i>		305	Intermediate	5.11–5.12
13736	<i>Leptochiton rugatus</i>		305	Intermediate	5.13
13737	<i>Leptochiton rugatus</i>		305	Tail	5.14–5.15
13738	<i>Leptochiton rugatus</i>		305	Tail	5.16–5.17
13739	<i>Leptochiton nexus</i>		305	Intermediate	5.18–5.20
13740	<i>Leptochiton nexus</i>		305	Intermediate	5.21
13741	<i>Leptochiton nexus</i>		305	Intermediate	5.22, 5.26
13742	<i>Leptochiton nexus</i>		305	Intermediate	5.23–5.25
13743	<i>Leptochiton nexus</i>		305	Tail	5.27–5.29
13744	<i>Leptochiton nexus</i>		305	Tail	5.30
13745	<i>Leptochiton nexus</i>		305	Tail	5.31–5.32
13746	<i>Leptochiton nexus</i>		305	Tail	5.33–5.34
14294	<i>Leptochiton nexus</i>		305	3 head, 25 intermediate, and 60 tail valves	
14295	<i>Leptochiton nexus</i>		16817 (305C)	Tail	
14296	<i>Leptochiton nexus</i>		16862 (305A)	Tail	
13747	<i>Oldroydia percrassa</i>		305	Head	6.1–6.2
13748	<i>Oldroydia percrassa</i>		305	Head	6.3–6.4
13749	<i>Oldroydia percrassa</i>		305	Head	6.5–6.6
13750	<i>Oldroydia percrassa</i>		305	Intermediate	6.7
13751	<i>Oldroydia percrassa</i>		305	Intermediate	6.8–6.9
13752	<i>Oldroydia percrassa</i>		16817 (305C)	Intermediate	6.10, 6.13
13753	<i>Oldroydia percrassa</i>		16817 (305C)	Intermediate	6.11–6.12
13754	<i>Oldroydia percrassa</i>		16817 (305C)	Tail	6.14–6.15
13755	<i>Oldroydia percrassa</i>		305	Tail	6.16
13735	<i>Oldroydia percrassa</i>		305	Tail	6.17
14297	<i>Oldroydia percrassa</i>		305	23 head, 130 intermediate, and 50 tail valves	
14298	<i>Oldroydia percrassa</i>		16817 (305C)	2 head, 7 intermediate, and 4 tail valves	
14299	<i>Oldroydia percrassa</i>		16862 (305A)	1 head and 1 tail valve	
13756	<i>Callistochiton palmulatus</i>		16817 (305C)	Head	7.1–7.2
13757	<i>Callistochiton palmulatus</i>		305	Head	7.3–7.4
13758	<i>Callistochiton palmulatus</i>		16817 (305C)	Head	7.5–7.6
13759	<i>Callistochiton palmulatus</i>		16817 (305C)	Head	7.7–7.8
13760	<i>Callistochiton palmulatus</i>		16817 (305C)	Intermediate	7.9–7.11
13761	<i>Callistochiton palmulatus</i>		16817 (305C)	Intermediate	7.12–7.14
13762	<i>Callistochiton palmulatus</i>		16817 (305C)	Intermediate	7.15–7.17
13763	<i>Callistochiton palmulatus</i>		16817 (305C)	Tail	7.18–7.19
13764	<i>Callistochiton palmulatus</i>		305	Tail	7.20–7.21
13765	<i>Callistochiton palmulatus</i>		305	Tail	7.22–7.23
13766	<i>Callistochiton palmulatus</i>		305	Tail	7.24–7.25
1300	<i>Callistochiton palmulatus</i>		305	~2,500 head, 193 intermediate, and ~6,100 tail	
14301	<i>Callistochiton palmulatus</i>		16817 (305C)	122 head, 12 intermediate, and 448 tail valves	
14302	<i>Callistochiton palmulatus</i>		16862 (305A)	23 head, 31 intermediate, and 65 tail valves	
13767	<i>Callistochiton sphaerae</i> n. sp.	Paratype	305	Head	8.1–8.2
13768	<i>Callistochiton sphaerae</i> n. sp.	Paratype	305	Head	8.3–8.4
13769	<i>Callistochiton sphaerae</i> n. sp.	Holotype	305	Intermediate	8.5–8.7
13770	<i>Callistochiton sphaerae</i> n. sp.	Paratype	305	Intermediate	8.8–8.10
13771	<i>Callistochiton sphaerae</i> n. sp.	Paratype	305	Intermediate	8.11–8.13
13772	<i>Callistochiton sphaerae</i> n. sp.	Paratype	305	Intermediate	8.14–8.16
13773	<i>Callistochiton sphaerae</i> n. sp.	Paratype	305	Intermediate	8.17–8.18
13854	<i>Callistochiton sphaerae</i> n. sp.		16817 (305C)	Tail	8.19
13774	<i>Callistochiton sphaerae</i> n. sp.	Paratype	305	Tail	8.20–8.22
13775	<i>Callistochiton sphaerae</i> n. sp.	Paratype	305	Tail	8.23, 8.27
13776	<i>Callistochiton sphaerae</i> n. sp.	Paratype	305	Tail	8.24–8.26
14303	<i>Callistochiton sphaerae</i> n. sp.	Unfigured toptype 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	<i>Callistochiton sphaerae</i> n. sp.		16817 (305C)	3 head, 9 intermediate, and 10 tail valves	
14305	<i>Callistochiton sphaerae</i> n. sp.		16862 (305A)	2 head and 6 tail valves	
13777	<i>Lepidozonia mertensii</i>		16817 (305C)	Intermediate	9.1–9.4
13778	<i>Lepidozonia mertensii</i>		16817 (305C)	Intermediate	9.5
13779	<i>Lepidozonia mertensii</i>		16817 (305C)	Intermediate	9.6
13780	<i>Lepidozonia mertensii</i>		305	Intermediate	9.7–9.8
13781	<i>Lepidozonia mertensii</i>		305	Intermediate	9.9
13782	<i>Lepidozonia mertensii</i>		16817 (305C)	Tail	9.10–9.11
13783	<i>Lepidozonia mertensii</i>		16817 (305C)	Tail	9.12
13784	<i>Lepidozonia mertensii</i>		16817 (305C)	Tail	9.13
13785	<i>Lepidozonia mertensii</i>		305	Tail	9.14
13786	<i>Lepidozonia mertensii</i>		305	Tail	9.15
14306	<i>Lepidozonia mertensii</i>		305	200 head, 178 intermediate, and 333 tail valves	
14307	<i>Lepidozonia mertensii</i>		16817 (305C)	9 head, 48 intermediate, and 11 tail valves	
14308	<i>Lepidozonia mertensii</i>		16862 (305A)	2 head, 19 intermediate, and 8 tail valves	
13787	<i>Lepidozonia pectinulata</i>		305	Head	10.1–10.3
13788	<i>Lepidozonia pectinulata</i>		305	Head	10.4, 10.7
13789	<i>Lepidozonia pectinulata</i>		305	Intermediate	10.5–10.6
13790	<i>Lepidozonia pectinulata</i>		305	Intermediate	10.8–10.10
13791	<i>Lepidozonia pectinulata</i>		305	Intermediate	10.11
13792	<i>Lepidozonia pectinulata</i>		305	Intermediate	10.12
13793	<i>Lepidozonia pectinulata</i>		16817 (305C)	Intermediate	10.13
13794	<i>Lepidozonia pectinulata</i>		305	Tail	10.14–10.15
13795	<i>Lepidozonia pectinulata</i>		305	Tail	10.16, 10.20
13796	<i>Lepidozonia pectinulata</i>		305	Tail	10.17–10.19
13797	<i>Lepidozonia pectinulata</i>		305	Tail	10.21–10.22
13798	<i>Lepidozonia pectinulata</i>		305	Tail	10.23–10.24
13799	<i>Lepidozonia pectinulata</i>		16817 (305C)	Tail	10.25–10.26
13800	<i>Lepidozonia pectinulata</i>		16817 (305C)	Tail	10.27–10.28
14309	<i>Lepidozonia pectinulata</i>		305	131 head, 498 intermediate, and 293 tail valves	
14310	<i>Lepidozonia pectinulata</i>		16817 (305C)	1 head and 9 intermediate valves	
13801	<i>Lepidozonasp.</i> cf. <i>L. rothi</i>		305	Intermediate	11.1–11.2
13802	<i>Lepidozonasp.</i> cf. <i>L. rothi</i>		305	Intermediate	11.3
13803	<i>Lepidozonasp.</i> cf. <i>L. rothi</i>		305	Intermediate	11.4–11.5
13804	<i>Lepidozonia</i> sp. cf. <i>L. radians</i>		305	Intermediate	11.6
13805	<i>Lepidozonia</i> sp. cf. <i>L. radians</i>		305	Intermediate	11.7–11.8
13806	<i>Lepidozonia</i> sp. cf. <i>L. radians</i>		305	Tail	11.9–11.10
14311	<i>Lepidozonia</i> sp. cf. <i>L. radians</i>		305	1 head, 23 intermediate, and 9 tail valves	
14312	<i>Lepidozonia</i> sp. cf. <i>L. radians</i>		16817 (305C)	5 intermediate valves	
13807	<i>Lepidozonia kanakoffi</i> n. sp.	Paratype	305	Intermediate	11.11
13808	<i>Lepidozonia kanakoffi</i> n. sp.	Paratype	305	Intermediate	11.12
13809	<i>Lepidozonia kanakoffi</i> n. sp.	Paratype	305	Intermediate	11.13–11.14
13810	<i>Lepidozonia kanakoffi</i> n. sp.	Holotype	305	Intermediate	11.15–11.16
13811	<i>Lepidozonia kanakoffi</i> n. sp.	Paratype	305	Intermediate	11.17
13812	<i>Lepidozonia kanakoffi</i> n. sp.	Paratype	305	Intermediate	11.18–11.20
13813	<i>Lepidozonia kanakoffi</i> n. sp.		16817 (305C)	Tail	11.21–11.22
13814	<i>Lepidozonia kanakoffi</i> n. sp.	Paratype	305	Tail	11.23–11.24
13815	<i>Lepidozonia kanakoffi</i> n. sp.	Paratype	305	Tail	11.25–11.26
13816	<i>Lepidozonia kanakoffi</i> n. sp.	Paratype	305	Tail	11.27–11.28
14313	<i>Lepidozonia kanakoffi</i> n. sp.	Unfigured Topotype lot	305	25 intermediate and 22 tail valves	
14314	<i>Lepidozonia kanakoffi</i> n. sp.		16817 (305C)	1 intermediate and 1 tail valve	
13817	<i>Stenoplax circumsenta</i>		305	Head	12.1–12.2
13818	<i>Stenoplax circumsenta</i>		305	Head	12.3–12.4
13819	<i>Stenoplax circumsenta</i>		16817 (305C)	Tail	12.5–12.6
13820	<i>Stenoplax circumsenta</i>		16817 (305C)	Tail	12.7
14315	<i>Stenoplax circumsenta</i>		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	<i>Stenoplax circumscnta</i>		16817 (305C)	1 head, 1 intermediate, and 1 tail valve	
13821	<i>Stenoplax fallax</i>		305	Head	12.8
13822	<i>Stenoplax fallax</i>		305	Head	12.9
13823	<i>Stenoplax fallax</i>		305	Head	12.10–12.11
13824	<i>Stenoplax fallax</i>		305	Intermediate	12.12
13825	<i>Stenoplax fallax</i>		305	Intermediate	12.13
13826	<i>Stenoplax fallax</i>		305	Intermediate	12.14
13827	<i>Stenoplax fallax</i>		16817 (305C)	Intermediate	12.15–12.16
13828	<i>Stenoplax fallax</i>		305	Intermediate	12.17–12.18
13829	<i>Stenoplax fallax</i>		305	Tail	12.19
13830	<i>Stenoplax fallax</i>		305	Tail	12.20
13831	<i>Stenoplax fallax</i>		305	Tail	12.21
14317	<i>Stenoplax fallax</i>		305	5 head, 9 intermediate, and 10 tail valves	
14318	<i>Stenoplax fallax</i>		16817 (305C)	1 tail valve	
14319	<i>Stenoplax fallax</i>		16862 (305A)	1 head and 3 intermediate valves	
13832	<i>Stenoplax</i> sp. cf. <i>S. heathiana</i>		305	Head	13.1–13.2
13833	<i>Stenoplax</i> sp. cf. <i>S. heathiana</i>		305	Head	13.3–13.4
13834	<i>Stenoplax</i> sp. cf. <i>S. heathiana</i>		305	Intermediate	13.5
13835	<i>Stenoplax</i> sp. cf. <i>S. heathiana</i>		305	Intermediate	13.6–13.8
13836	<i>Stenoplax</i> sp. cf. <i>S. heathiana</i>		305	Intermediate	13.9, 13.12–13.13
13837	<i>Stenoplax</i> sp. cf. <i>S. heathiana</i>		305	Intermediate	13.10
13838	<i>Stenoplax</i> sp. cf. <i>S. heathiana</i>		305	Intermediate	13.11
13839	<i>Stenoplax</i> sp. cf. <i>S. heathiana</i>		16817 (305C)	Tail	13.14–13.15
13840	<i>Stenoplax</i> sp. cf. <i>S. heathiana</i>		305	Tail	13.16
13841	<i>Stenoplax</i> sp. cf. <i>S. heathiana</i>		305	Tail	13.17–13.19
13842	<i>Amicula solivaga</i> n. sp.	Paratype	305	Head	14.1
13843	<i>Amicula solivaga</i> n. sp.	Paratype	305	Head	14.2
13844	<i>Amicula solivaga</i> n. sp.	Paratype	305	Head	14.3
13845	<i>Amicula solivaga</i> n. sp.	Paratype	305	Head	14.4
13846	<i>Amicula solivaga</i> n. sp.	Holotype	305	Head	14.5
13847	<i>Amicula solivaga</i> n. sp.	Paratype	305	Head	14.6–14.7
13848	<i>Amicula solivaga</i> n. sp.	Paratype	305	Intermediate	14.8
13849	<i>Amicula solivaga</i> n. sp.	Paratype	305	Intermediate	14.9
13850	<i>Amicula solivaga</i> n. sp.	Paratype	305	Intermediate	14.10
13851	<i>Amicula solivaga</i> n. sp.		16817 (305C)	Intermediate	14.11–14.12
13852	<i>Amicula solivaga</i> n. sp.	Paratype	305	Intermediate	14.13
13853	<i>Amicula solivaga</i> n. sp.	Paratype	305	Tail	14.14–14.15
13855	<i>Amicula solivaga</i> n. sp.	Paratype	305	Tail	14.16
14320	<i>Amicula solivaga</i> n. sp.	Unfigured Topotype lot	305	3 head, 25 intermediate, and 5 tail valves	
14321	<i>Amicula solivaga</i> n. sp.		16817 (305C)	1 intermediate valve	
14322	<i>Amicula solivaga</i> n. sp.		16862 (305A)	1 head, 1 intermediate, and 1 tail valve	
13894	<i>Mopalia sinuata</i>		305	Head	15.1
13895	<i>Mopalia sinuata</i>		305	Intermediate	15.2–15.3
14323	<i>Mopalia sinuata</i>		305	12 head, 42 intermediate, and 4 tail valves	
14324	<i>Mopalia sinuata</i>		16862 (305A)	2 head and 1 intermediate valve	
13857	<i>Mopalia</i> sp. cf. <i>M. swanii</i>		16817 (305C)	Head	15.4, 15.7
13858	<i>Mopalia</i> sp. cf. <i>M. swanii</i>		305	Head	15.5–15.6
13859	<i>Mopalia</i> sp. cf. <i>M. swanii</i>		305	Head	15.8–15.9
13860	<i>Mopalia</i> sp. cf. <i>M. swanii</i>		305	Head	15.10
13861	<i>Mopalia</i> sp. cf. <i>M. swanii</i>		305	Intermediate	15.11–15.12
13862	<i>Mopalia</i> sp. cf. <i>M. swanii</i>		305	Intermediate	15.13
13863	<i>Mopalia</i> sp. cf. <i>M. swanii</i>		305	Intermediate	15.14
13864	<i>Mopalia</i> sp. cf. <i>M. swanii</i>		305	Intermediate	15.15
13865	<i>Mopalia</i> sp. cf. <i>M. swanii</i>		305	Intermediate	15.16
13866	<i>Mopalia</i> sp. cf. <i>M. swanii</i>		305	Intermediate	15.17
13867	<i>Mopalia</i> sp. cf. <i>M. swanii</i>		305	Intermediate	15.18
13868	<i>Mopalia</i> sp. cf. <i>M. swanii</i>		305	Intermediate	15.19
13869	<i>Mopalia</i> sp. cf. <i>M. swanii</i>		305	Tail	15.20–15.21
13870	<i>Mopalia</i> sp. cf. <i>M. swanii</i>		305	Tail	15.22–15.23
13871	<i>Mopalia</i> sp. cf. <i>M. swanii</i>		305	Tail	15.24
13872	<i>Mopalia</i> sp. cf. <i>M. swanii</i>		305	Tail	15.25–15.26

## Appendix 2 [Continued]

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