THE GENUS *LEPIDOCHITONA* GRAY, 1821 (MOLLUSCA: POLYPLACOPHORA) IN THE NORTHEASTERN PACIFIC OCEAN (OREGONIAN AND CALIFORNIAN PROVINCES)

by

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Eernisse, D. J.: The genus *Lepidochitona* Gray, 1821 (Mollusca: Polyplacophora) in the northeastern Pacific Ocean (Oregonian and Californian Provinces).

Zool. Verh. Leiden 228, 7-v-1986: 1-53, map, pls. 1-7, figs. 1-72. - ISSN 0024-1652.

Key words: Polyplacophora; *Lepidochitona;* northeastern Pacific; key; new species.

The systematics of the northeastern Pacific *Lepidochitona* from the Californian and Oregonian Provinces (western continental United States) is presented and discussed. Three new species are described: *L. caverna* spec. nov. and *L. berryana* spec. nov. from California, and *L. fernaldi* spec. nov. from Washington and Oregon. These species are compared in most detail to the nominal species *L. dentiens* (Gould, 1846), *L. hartwegii* (Carpenter, 1855), *L. thomasi* (Pilsbry, 1898) and *L. keepiana* Berry, 1948.

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INTRODUCTION

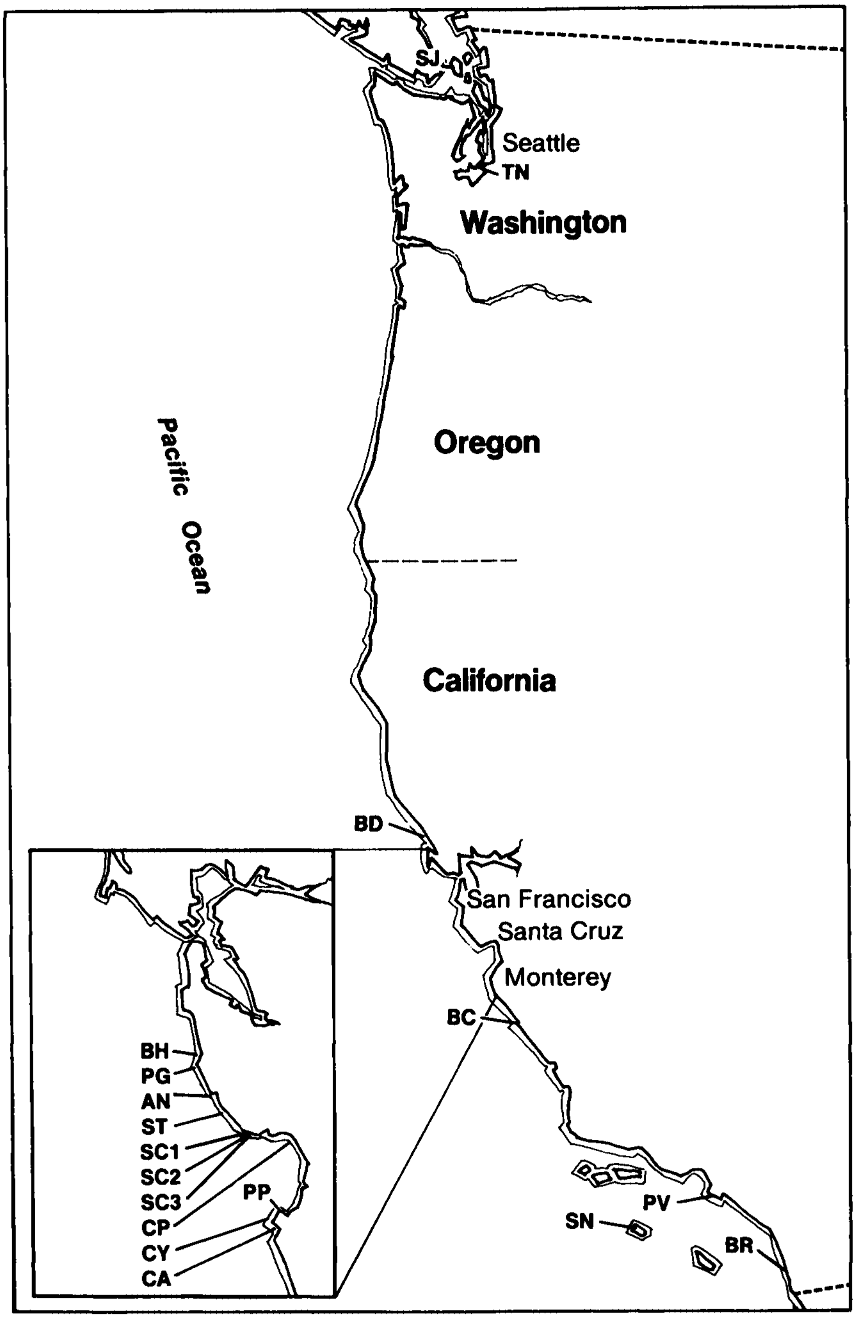
Northeastern Pacific members of the genus *Lepidochitona* Gray, 1821 have been considered in detail several times in the last century, most recently by Kaas and Van Belle (1981) and Ferreira (1982). Despite these valuable contributions, considerable confusion has remained. This revision reexamines misunderstood species in this group, and adds descriptions of three new species.

Kaas and Van Belle (1981) and Ferreira (1982) provide comprehensive historical treatments of the nomenclature of the genus *Lepidochitona*, and although Kaas and Van Belle's work concerns primarily European members of the genus, discussions of eastern Pacific species are included. As many of these authors' conclusions have been adopted, the historical treatment included here is not exhaustive.

As presently understood, there are 21 species in the genus *Lepidochitona* (or *Lepidochitona* s.s. in Van Belle, 1975-78, 1983) worldwide. Besides the nine European species treated by Kaas and Van Belle (1981), a single species, *L. turtoni* (Ashby, 1928), is known from the southeastern Atlantic, and two species, *L. liozonis* (Dall & Simpson, 1901) and *L. rosea* Kaas, 1972, are known from the Caribbean Sea and vicinity.

The remaining nine species are all restricted to the eastern Pacific Ocean, and all nine occur in the Oregonian and Californian Provinces (Newall, 1949; Valentine, 1966) of the northeastern Pacific. The geographical scope of this work is limited to these Provinces, an area approximately bounded by the borders of the western continental United States (U.S.). The map shows the primary study sites visited in the course of this work. Two of the nine species have not been described here, since they can not be confused with the new species described herein. They are: *L. beanii* (Carpenter, 1857), occurring from Perú to southern California, and *L. lowei* (Pilsbry, 1918), known only from southern and central California (Ferreira, 1982). Both these species are, however, included in a dichotomous key provided at the end of this work. Although Ferreira (1982) contends that *Trachydermon flectens* Carpenter, 1864 is also a *Lepidochitona*, I prefer to follow Kaas & Van Belle (1980) and Van Belle (1983) in grouping this species with the four other recognized species of *Dendrochiton* Berry, 1941.

Fossil specimens identified to *Lepidochitona* appear as early as the Eocene in Europe (Malatesta, 1962; Kaas and Van Belle, 1981), including all 13 extinct species of *Lepidochitona* recognized by Van Belle (1981). By contrast, only Pleistocene records are available from North America (see Ferreira, 1982). Previous identifications of these West Coast fossil specimens to extant species could potentially be confounded by the additional three morphologically similar species described herein.



Map. Primary Study Sites: SJ = San Juan Island (Mar Vista); TN = Tacoma Narrows; BD = Bodega Head; BH = Bean Hollow (Arrojo de los Frijoles); PG = Pigeon Pt.; AN = Año Nuevo Pt.; ST = Scott Creek; SC1 = Auburn Ave., Santa Cruz; SC2 = Stockton Ave., Santa Cruz; SC3 = Pt. Santa Cruz; CP = Soquel Pt., Capitola; PP = Pt. Pinos; CY = Cypress Pt.; CA = Carmel; BC = Landels-Hill Big Creek Reserve; PV = Palos Verdes, Los Angeles; SN = San Nicolas Island; BR = Bird Rock, La Jolla.

ORIGINAL DESCRIPTION:	*Chiton hartwegii* Cpr., 1855	*Chiton dentiens* Gld., 1846	*Lepidochitona keepiana* Berry, 1948
NAMES USED HERE:	*Lepidochitona hartwegii*	*Lepidochitona dentiens*	*Lepidochitona keepiana*
NAMES USED: 1892-1983:			
Pilsbry, 1892-93	*Tonicella (Cyanoplax) hartwegii*		*Ischnochiton dentiens*
Pilsbry, 1894a	*Trachydermon (Cyanoplax) hartwegii*	*Trachydermon (Cyanoplax) raymondi*	
Thiele, 1909	*Cyanoplax hartwegii* and *Trachydermon hartwegii*	*Cyanoplax raymondi* *Trachydermon raymondi* and *T. dentiens* (Sitka, Alaska)	
Thiele, 1910	*Trachydermon hartwegii*		
Berry, 1917b		*Cyanoplax raymondi*	
Packard, 1918	*Trachydermon hartwegi*	*Trachydermon raymondi* and *Ischnochiton dentiens* (?)	
Dall, 1921; Oldroyd, 1924, 1927	*Lepidochitona (Cyanoplax) hartwegii*	*L. (Cyanoplax) raymondi*	*L. (Lepidochitona) dentiens*
Johnson & Snook, 1927	*Lepidochitona (Trachydermon) hartwegii*	*L. (Trachydermon) raymondi*	
Light's Manual, 1941 (1st ed.)	?	*Lepidochitona raymondi*	
Smith, 1947	*Cyanoplax hartwegii*	*Cyanoplax raymondi*	*Lepidochitona dentiens*
Berry, 1948		*Cyanoplax dentiens*	*Lepidochitona keepiana*

Light's Manual, 1954 (2nd ed)	*Cyanoplax hartwegii*	*Cyanoplax raymondi* and *Cyanoplax dentiens*	
Palmer, 1958		*Cyanoplax dentiens*	
Burghardt & Burghardt, 1969	*Cyanoplax hartwegii*	*Cyanoplax dentiens*	*Lepidochitona keepiana*
McLean, 1969, 1978	*Cyanoplax hartwegii*		*Lepidochitona keepiana*
Abbott, R. T., 1974	*Cyanoplax hartwegii*	*Cyanoplax raymondi* and *Lepidochitona dentiens*	
Smith, 1975 in Light's Manual (3rd ed.)	*Cyanoplax hartwegii*	*Cyanoplax dentiens*	
Haderlie & D. P. Abbott, 1980	*Cyanoplax hartwegii*	*Cyanoplax dentiens*	
Putman, 1980	*Cyanoplax hartwegii*	*Cyanoplax dentiens*	*Lepidochitona keepiana*
Kaas & Van Belle, 1981	*Lepidochitona* (*L.*) *hartwegi*	*Lepidochitona* (*L.*) *dentiens*	*Lepidochitona* (*L.*) *keepiana*
Ferreira, 1982	*Lepidochitona hartwegii*	*Lepidochitona dentiens*	*Lepidochitona keepiana*
Kozloff, 1983		*Lepidochitona dentiens*	

Table 1: History of name changes for three species of *Lepidochitona* (1892 to 1983)

HISTORY

The genus *Lepidochitona* (type-species *Chiton marginatus* Pennant, 1777 = *Chiton cinereus* Linnaeus, 1767) was first proposed by Gray (1821). The name *Lepidochitona* was not commonly used until Iredale (1914) reinstated it to replace *Trachydermon* Carpenter, 1864: 649, which Iredale argued was preoccupied (see Berry, 1917b: 245; 1918: 12; Palmer, 1958: 285; Ferreira, 1982: 97 for discussions).

Although northeastern Pacific members of *Lepidochitona* have received considerable attention, there has been considerable name confusion for even the more common species. For example, table 1 presents the history of names that have been used in both systematic and selected natural history works for three species of *Lepidochitona*; these three species alone have been assigned to no fewer than five genera since Pilsbry (1892-93). Moreover, prior to Berry (1948), most workers mistakenly attributed Gould's *Chiton dentiens* to the wrong species. As is evident from table 1, two basic classifications have been advocated for this group of chitons. These differ in whether or not the name *Cyanoplax* Pilsbry, 1892-93: 44 (type-species *Chiton hartwegii* Carpenter, 1855) merits generic status. As stated by Smith (1947: 8): "Both Dall and Thiele have rather cumbersome classifications that make liberal use of Sections. Berry uses a simpler arrangement by considering *Tonicella*, *Cyanoplax*, and *Lepidochitona* all of generic rank, which seems reasonable, considering the differences between these groups on the west coast of North America." Smith, however, did not elaborate the differences between *Lepidochitona* and *Cyanoplax*, and this is a difficult issue.

As discussed by Ferreira (1982: 97), Pilsbry's (1892-93) diagnosis of *Cyanoplax* is insufficient to distinguish *Cyanoplax* from *Lepidochitona* Gray, 1821 as presently diagnosed. *Cyanoplax*, the name alluding to the bluish color of the valve interior (Pilsbry, 1894a), was originally proposed as a subgenus in *Tonicella* Carpenter, 1873, but has not been referred to this genus since (see Pilsbry, 1892-93: xxv). Pilsbry compared *Cyanoplax* with the genera *Chaetopleura* Shuttleworth, 1853, *Tonicella*, and *Trachydermon* (the latter name corresponding roughly to *Lepidochitona* as presently diagnosed). Pilsbry (1892-93: 44) states that (*L. hartwegii*) "might be considered a *Trachydermon* were it not for the peculiar blunt teeth, ambient gills and almost scaleless girdle." Following recent authors, I do not consider the peculiarities of the teeth, the gills, and the elements of the girdle different enough from *Lepidochitona* to warrant full generic status. *L. hartwegii* attains adult sizes more than twice as large as other species considered here, but large size itself is hardly a useful generic character. Likewise, Thiele (1909: 18) found Pilsbry's characterization of the thick and large valves of *Cyanoplax* to be no more than a species-specific character.

Pilsbry (1892-93), Dall (1921), Berry (1948), and Smith (1966) all made attempts to group *L. hartwegii* and *L. dentiens* (as presently understood) together but separate from *L. keepiana*, which they all considered to be closer to the European *L. cinerea* (Linnaeus, 1767). For instance, Pilsbry (1892-93: 74) states: (*L. keepiana*) "is closely allied to *cinereus* L. . . . ." In describing *L. keepiana*, Berry (1948: 15) also noted this similarity: "(*L. keepiana*) is associated with no very close relatives in our waters, the nearest probably being the various species of *Cyanoplax* and *Tonicella*. On geographic grounds its reference to *Lepidochitona* does not appear to be too happy, although at the present time it is difficult to suggest a better association for it." The division of *Lepidochitona* into smaller, phylogenetically meaningful groups will probably require a detailed comparison of a wide range of characters, as well as other members of the genus, and members of closely related genera. Until such work is attempted, it is appropriate to include all seven species discussed here in *Lepidochitona*.

SYSTEMATICS

Seven intertidal species of *Lepidochitona* from the Pacific Coast of western North America are described. The following abbreviations are used:

ANSP = Academy of Natural Sciences at Philadelphia
BMNH = British Museum (Natural History), London
CAS = California Academy of Sciences, San Francisco
DJE = D. J. Eernisse, priv. coll., Friday Harbor, Washington
DMNH = Delaware Museum of Natural History, Greenville
K = P. Kaas, priv. coll., now in RMNH, Leiden
LACM = Los Angeles County Museum, Los Angeles
RMNH = Rijksmuseum van Natuurlijke Historie, Leiden
SDNH = San Diego Natural History Museum
USNM = United States National Museum, Washington D.C.
VB = R. A. Van Belle, priv. coll., Sint-Niklaas, Belgium

The classification listed below differs from that proposed by Van Belle (1975-78, 1983) by regarding the three subgenera included by him in *Lepidochiton* (*Lepidochitona* s.s., *Dendrochiton* Berry, 1911, and *Spongioradsia* Pilsbry, 1893-94) at generic rank. Consequently, the diagnosis of *Lepidochitona* employed here would correspond to the diagnosis for *Lepidochitona* s.s. provided in Kaas & Van Belle (1981).

Family Ischnochitonidae Dall, 1889

Subfamily Lepidochitoninae Iredale, 1914

Lepidochitona Gray, 1821

Lepidochitona Gray, 1821: 234. Type: *Chiton marginatus* Pennant, 1777 = *Chiton cinereus* Linnaeus, 1767 by monotype. (See Kaas & Van Belle, 1981 for synonymies.)

Lepidochitona hartwegii (Carpenter, 1855)
(figs. 2, 12, 13, 29, 39, 40, 56, 65; table 1)

Chiton hartwegii Carpenter, 1855: 231.
Trachydermon hartwegii (Carpenter). — Pilsbry, 1892-93: 46 (with *Chiton nuttalli* in synonymy); Thiele, 1909: 16, pl. 2, figs. 26, 27.
Cyanoplax hartwegii (Carpenter). — Palmer, 1958: 263, Pl. 27, figs. 8-10; Pl. 28, figs. 8-15; Haderlie and Abbott, 1980: 417, pl. 131; Putman, 1980: 54.
Lepidochitona hartwegii (Carpenter). — Kaas & Van Belle, 1980: 58; 1981: 6.
Lepidochitona hartwegii (Carpenter). — Ferreira, 1982: 100.
Chiton nuttalli Carpenter, 1855: 231.

Material. — Lectotype and paralectotype (Redpath Museum No. 68) (designated by Ferreira, 1982: 102) of *Chiton hartwegii* Carpenter, 1855. Type-locality: Monterey (California). Four Possible syntypes of *Chiton nuttalli* Carpenter, 1855, including: BMNH 1861(65).5.20.102 (holotype in Palmer, 1958: 265); BMNH 1855.3.14.24 from "Santa Barbara" (California); and two specimens from "Monterey" (California) (BMNH unregistered). All intact dry specimens with only girdle and valves remaining.

Collections housed in CAS and LACM were examined, as well as my own extensive collections (approx. 800 specimens total) from the following localities: Santa Cruz (Santa Cruz Co.), many sites between Pacific Grove to Carmel, especially Point Pinos (Monterey Co.), San Nicolas Is. (Ventura Co.), Palos Verdes (Los Angeles Co.), and Bird Rock (San Diego Co.).

Shell (figs. 2, 12, 13, 29, 56). — Body oval shaped, occasionally exceeding 4 cm in length (largest specimen examined 45.1 mm in length). Valve profile low; side slopes slightly convex. Mucro central; post-mucronal slope flat to slightly convex.

Warty granules on tegmentum scattered among smaller round granules of uniform shape and spacing. Sculpturing especially irregular on lateral portions of valves. Lateral areas not raised otherwise. Tegmentum color normally drab olive green, often with dark longitudinal stripes on either side of the central areas. Articulamentum light blue except in juveniles. Insertion teeth of posterior valve thick and rugged, radiating outward (slit formula 8/12 - 1 - 8/12). Eaves spongy.

Girdle (figs. 65a-d). — Elements uniform in size, composed of juxtaposed (not imbricating) dorsal corpuscules (about 45 μm long, 18 μm wide), marginal spicules (about 120 μm long, 22 μm wide), and ventral transculent spicules (about 55 μm long, 20 μm wide). The dorsal girdle surface frequently banded by alternating light and dark colors, spotted with light-colored oval 'pores' (areas lacking corpuscules, about 20 corpuscules across).

Radula (figs. 39, 40). — First lateral teeth much shorter than median tooth with stout cup-shaped blades. Major lateral teeth tricuspid, each with central denticle nearly three times longer and wider than outer denticles.

Gills. — Holobranchial, with about 28-35 gill pairs in specimens over 10 mm in length.

Distribution. — The northernmost verified record is Battle Rock, Port Orford, Oregon (42° 43'N, 124° 31'W; DJE 0333-1). The southernmost verified record is Punta Abreojos, Baja California, Mexico (26° 45'N; 113° 40'W; CAS 3977).

L. hartwegii is extremely common south of Point Conception, California, both on the mainland and on the offshore islands. Its distribution in northern waters is much less continuous. Although it is common in the vicinity of the Monterey Peninsula (type-locality), it is absent, or extremely rare, at other localities in central California. I have not observed this species north of Santa Cruz, despite extensive searches. Verified specimens have been taken, however, from Sausalito, California (Marin Co.; CAS 3971) and at a few locations in southern Oregon, including the Battle Rock record (see above).

Although Oldroyd (1924, 1927) lists the northern range limit as Forrester Island, Alaska, and Kozloff (1974: 46) lists this species in his key for Puget Sound, the San Juan Archipelago, and the Straits of Juan de Fuca, I know of no specimens from these areas.

Habitat and ecology. — As discussed by Robb (1975), on the Monterey Peninsula, *L. hartwegii* commonly occurs in at least three habitat types, all relatively high in the intertidal. It is most abundant in areas of low wave action under the brown fucoid alga *Pelvetia fastigata* (J. G. Agardh) De Toni, where it is found together with limpets and *Mopalia muscosa* (Gould, 1846) on otherwise nearly bare rock. Under *Pelvetia* it can occur in densities exceeding 25 per square meter. Robb found that *P. fastigata* comprised 80 percent of the total gut contents of all specimens collected from this habitat. This diet is unusual for a marine herbivore because fucoid algae including *P. fastigata* contain high levels of tannins, secondary compounds which many molluscan grazers find unpalatable (Steinberg, 1985).

Higher in the intertidal, *L. hartwegii* is found in crevices which provide a moist, shady, and wave-sheltered environment, and in some high tidepools with sufficient crevices and protection from exposure. According to Robb, individuals in habitats lacking the algal cover of *P. fastigata* eat a mixture of macroscopic algae, including species of *Hildenbrandia*, *Gigartina*, *Petrocelis*, *Endocladia* and *Cladophora*.

In southern California *L. hartwegii* is especially common in high tidepools, where it can occur in extremely high densities. Like many other chiton species, *L. hartwegii* is most active at night, presumably to escape predation by visual predators such as birds. The cover of *P. fastigata* in the Monterey area acts as a refuge from gull predation (DeBevoise, 1975).

I have observed free spawning in this species in the lab on several occasions, including one mass spawning event (Eernisse, 1984a). Fertilization is external, and as in other species which have been observed to spawn gametes freely into the plankton (Pearse, 1979; Eernisse, 1984a), actively swimming trochophore larvae hatch from their egg capsules within about two days after fertilization. Such a larva is at first pelagic, but as its foot develops, gradually becomes creeping. After hatching, approximately five to seven days are required before a larva appears capable of metamorphosis (pers. observ.).

Juvenile specimens of *L. hartwegii* (under 10 mm in length) are exceptionally difficult to locate in the field. On the Monterey Peninsula they occur in extremely cryptic, inaccessible habitats, such as the underside of barnacle hummocks in relatively high tidepools. Juveniles are rarely found under *P. fastigata.*

Remarks. — It is well accepted that *Chiton nuttalli* Carpenter, 1855 is a synonym of *Chiton hartwegii* Carpenter, 1855. Pilsbry (1892-93), Smith and Gordon (1948), Palmer (1958) and Ferreira (1982) have all proposed this synonymy. Confusion related to the identity of the syntypes of *Chiton nuttalli* has previously been discussed by Palmer (1958: 265).

In referring to the specimens before him, Carpenter (1855: 232) stated that "A small specimen in Mr. Cuming's collection was passed over as the young of *C. hartwegii*; but a fine one in Mr. Nuttall's collection distinctly displays the points of difference above indicated, which at present appear of specific value..." As suggested by Palmer, the specimen (BMNH 1861.5.20.102) which had been isolated as the "Type", and was figured by Palmer (Plate 27, fig. 11) as the "holotype", is possibly the small specimen that "was passed over", but it is probably not the specimen Carpenter described as the type because it does not fit the published measurements and is not localized. (There is no indication this specimen is from Santa Barbara, as stated by Palmer.) Carpenter gave "Monterey" as the type-locality.

Solene Morris (BMNH; pers. comm., July 30, 1981) has furnished new information on possible syntype specimens of *C. nuttalli* in the British Museum. "I have located not only the specimen.....*Chiton nuttalli* Carpenter (BMNH 1861.5.20.102), which may possibly be one of the syntypes, but is most certainly of historic importance since it was presented to the Museum 'by the executors of the late Mr. Nuttall'. Another specimen (BMHN 1855.3.14.24) from the Nuttall Coll., previously sent to the Museum by Mr. Nuttall, loc. Santa Barbara, is more likely the specimen mentioned by Carpenter as in the Nuttall Coll. Two additional specimens from the Cuming Coll., labeled 1855), from Monterey (unregistered), are most probably the other mentioned specimens. None of the four specimens exactly fits the published measurements. However, the largest of the two Cuming Coll. specimens is closest: length: (not coiled) 31.70 mm; width: 19.05 mm; height: 5.55 mm. These two specimens come from the published locality."

Accordingly, this large specimen from the Cuming Coll. should be tentatively regarded as the type, not the specimen figured by Palmer. However, the identity of Carpenter's type is far from certain, because the specimen does not fit Carpenter's measurements precisely (publ. dimensions: length 26.6 mm, width 20.3 mm; height 6.1 mm, converted to mm from polls). The smaller specimen in the Cuming Coll. fits the length dimension more closely (25.1 mm) but is much too narrow (16.1 mm). Because of the lack of firm evidence that any of these specimens were actually examined by Carpenter, all four of these specimens are here regarded as possible syntypes.

All four of these specimens appear to be *L. hartwegii*. These specimens can hardly be regarded as a "small form" of *L. hartwegii* (Smith and Gordon, 1948: 205) because they are all quite large, including the measurements of the 'type' given by Carpenter, and are too large to be confused with other species treated herein.

I was not able to examine the type lot for *Chiton hartwegii* Carpenter, 1855 (Redpath Museum, no. 68), which consists of three syntypes, two of which were figured by Palmer (1958). Ferreira (1982: 102) designated one of these figured specimens (Palmer, 1958: Pl. 27, figs. 8-10) as the lectotype, and the other two specimens as paralectotypes. The lectotype is partially disarticulated (loose valves i, vii, and viii), with dimensions of 15.4+ mm (attached valves) in lenght, and 10.3 mm width (Palmer, 1958: 352). This lectotype is too small to be the type indicated by Carpenter, especially in the width dimension (publ. dimensions: 31.9 mm length, 19.2 mm width, 4.6 mm height).

Lepidochitona caverna spec. nov.

(figs. 5, 18, 19, 32, 45, 46, 59, 68; plates 1A, 3B)

Trachydermon (Cyanoplax) raymondi Pilsbry. — Pilsbry, 1898a: 287 (in part); Heath, 1899: 569. Not *T. raymondi* Pilsbry, 1898a.

Trachydermon raymondi Pilsbry. — Heath, 1904: 257; 1905: 391; 1907: 10; Higley and Heath, 1912: 95; Christiansen, 1954: 66; Maxwell, 1983: 276. Not *T. raymondi* Pilsbry, 1898a.

Lepidochiton raymondi (Pilsbry). — Jakovleva, 1952: 14; Kussakin, 1960: 1149. Not *T. raymondi* Pilsbry, 1898a.

Lepidochitona raimondi (Pilsbry). — Fischer-Piette, 1960: 1766. Not *T. raymondi* Pilsbry, 1898a.

Lepidochitona raymondi (Pilsbry). — Dell, 1962: 513. Not *T. raymondi* Pilsbry, 1898a.

Cyanoplax dentiens (Gould). — (?) Glynn, 1965: 45; Smith, 1966: 434; Gomez, 1975: 28; Pearse 1979: 29; Abbott & Hollenberg, 1980: 418 (in part). Not *L. dentiens* (Gould, 1846).

Lepidochitona hartwegii (Carpenter). — Ferreira, 1982: 102 (in part). Not *L. hartwegii* (Carpenter, 1855).

Type-material. — The holotype (RMHN 9175, Plates 1A, 3B) and one complete paratype (RMNH K5055, fig. 5) have been deposited in the Rijksmuseum van Natuurlijke Historie, another (disarticulated) paratype in the coll. VB (figs. 18, 19, 32, 45, 46, 59, 68). Additional paratypes will be deposited in the BMNH, USNM, ANSP and CAS.

Approximately 600 specimens (not part of the type-series) have been observed from the type-locality and two other locations along West Cliff Drive in Santa Cruz (Santa Cruz Co.); Pt. Santa Cruz and Stockton Avenue. I also reared in the lab over 1000 additional specimens, descended from animals originally collected in Santa Cruz. Specimens were also collected at Pt. Pinos and Cypress Pt. (Monterey Co.). I also examined two lots collected by Harold Heath (ANSP 72125, 72126). ANSP 72125 consists of 16 *L. dentiens* (two partially disarticulated, one disarticulated valves only), and 17 *L. caverna* (one partially disarticulated). ANSP 72126 consists of seven *L. dentiens* (five partially disarticulated, one loose valves only) and ten *L. caverna* (two partially disarticulated). These lots are further discussed below. I am unaware of other collections of this species. Searches both north and south of Monterey Bay and in east Santa Cruz have failed to produce this species.

Type-locality. — Intertidal sea cave near Auburn Ave., Santa Cruz, California (36°57'N 122°03' W; leg. D. J. Eernisse, March 3, 1984), collected from the roof of the cave at a moderately high tidal level.

Diagnosis. — Irregular warty granules scattered on valve surfaces, especially in lateral areas. Gills merobranchial. Maximum body length about 14 mm.

Description of holotype (plates 1A, 3B). — Animal intact, preserved in ethanol; between oval-elongate and oval in body outline; 6.6 mm in length, 4.3 mm in width, and 1.2 in height.

Valve profile relatively low. Intermediate valves strongly beaked, broadly rectangular in shape; side slopes convex. Mucro about central; post-mucronal slope approximately flat. Eaves spongy. Tegmentum sculptured with warty irregular granules spaced among more or less regular, diamond-shaped granules. Warty sculpturing most pronounced in lateral areas; these areas not raised otherwise. Tegmentum green with white and black markings on both sides of central areas. Articulamentum blue.

Girdle narrow (each side about 10 percent of total width), with alternating light and dark color-banding. Dorsal surface clothed with small, stout, non-imbricating, closely-spaced corpuscules, about 60 μm long and 25 μm wide. Girdle fringed with marginal spicules, about 100 μm long. Ventral surface covered with normally obtuse, striated scales (about 60 μm long), arranged in regular radiating rows.

Each gill row extending about 80 percent of foot length, with 20 gill plumes on left side, viewed from below. Right gill row partially damaged.

Range of morphological variation. — Maximum length observed 13.9 mm, but most specimens do not exceed 12 mm in length. Body outline usually oval-elongate (fig. 5), occasionally (as in holotype) approaching an oval outline.

Primary color of tegmentum invariably green for all specimens observed at the type-locality (and at most other sites). Local color variation, however, does occur. For instance, in a sea cave near the type-locality (SC2), burgundy-colored individuals were common. Adult specimens always marked with consistent complex patterns of secondary colors, especially white, black and blue (fig. 5). Juveniles (less than 4 mm in length) differ by their much darker coloration on all valves except the fifth; this valve is frequently marked with a white chevron.

Tegmental sculpturing always irregular, as in holotype. Mucro position always more or less central, with an approximately flat post-mucronal slope.

Articulamentum light blue and/or green. Insertion teeth generally flattened and radiating outwards on terminal valves, forming only a slight arc at the posterior margin of tail valve; lateral teeth sharp (slit formula range 8/12 - 1 - 8/13).

Girdle elements (figs. 68b,d) usually with similar dimensions to those described for holotype. Scattered among the dorsal elements are occasional narrow, slightly bent spicules (about 40μm long), sheathed in small chitonous cups (fig. 68b). These spicules difficult to see in most specimens examined.

Median tooth of radula dilated towards anterior blade (fig. 45). Tridentate cusps of major lateral teeth, each with an extremely broad, slightly concave median denticle (fig. 46).

Each gill row extends about 80 to 90 percent of foot length; composed of 15 to 22 gill pairs in specimens longer than 6 mm (the number increasing with size).

Distribution — The northernmost locality of *L. caverna* is the typelocality. The southernmost verified record was collected at Cypress Pt. (36°35'N, 121°59'W; DJE 0427-1).

Habitat and ecology. — *L. caverna* can be locally abundant, but is known from relatively few localities. This secretive species has been found in three intertidal sea caves in the Santa Cruz area, as well as in similar microhabitats at Pt. Santa Cruz. These habitats are small dark overhangs with protected cracks and crevices at an upper mid-tidal level. On the Monterey Peninsula this species has been collected in a habitat similar to that described by Heath (1899, 1905, 1907) for *T. raymondi*, leading me to the conclusion that Heath was probably observing *L. caverna* (see below). Heath described both a brooding reproductive behavior and a hermaphroditic reproductive condition in the specimens he examined. My own observations, as well as those of Pearse and Lindberg (1980), have supported these findings (Eernisse, 1984a).

L. caverna is locally common at Pt. Pinos (South Side) and Cypress Pt., especially in the vicinity of high tidepools and as with *L. thomasi* and *L. fernaldi*, in association with barnacles and anemones. At Pt. Santa Cruz and at Pt. Pinos I have also found *L. caverna* nestled in the pallial grooves of *Nuttallina californica* (Reeve, 1847). Gomez (1975) noted such an association with *N. californica* for small chitons he identified as *Cyanoplax dentiens*. Gomez was probably observing *L. caverna*, because this is the only species commonly found under *N. californica* at Pt. Pinos where Gomez made his observations (pers. observ.). The inability of Gomez to find this association at other Monterey Peninsula localities further supports this view, because *L. caverna* is only locally abundant in this area. I believe the association is less specific than indicated by Gomez, perhaps because he was unaware of other cryptic microhabitats occupied by this species.

L. caverna can be reared in the laboratory if a continuous splashing of sea water is provided so that the unsubmerged animals never dry out completely. The addition of *Nuttallina californica* facilitates artificial rearing conditions, perhaps because it grazes the macroscopic algae and keeps the algae from overgrowing the substrate surfaces, thereby providing grazing space for *L. caverna.*

Etymology. — The name *"caverna"*, meaning 'cave', is used in reference to the intertidal sea cave at the type-locality.

Discussion. — As in *L. hartwegii*, the tegmentum of *L. caverna* consistently has irregular warty granules scattered among otherwise regular sculpturing. This feature is not found in other Pacific species of *Lepidochitona*. However, I disagree with Ferreira's (1982: 100) identification of specimens I collected from the type-locality for *L. caverna.* Although Ferreira contends these are small specimens of *L. hartwegii*, I believe they are *L. caverna* and clearly distinct from *L. hartwegii.* Tegmentum sculpturing is superficially similar in the two species, but when specimens of similar size are compared, it is apparent that the tegmental granules are much less dense in *L. caverna. L. caverna* also differs in its much smaller body size, shorter gill row (with fewer gill pairs), and other features described by Eernisse (1984a), including electromorph, egg hull morphology, and reproductive distinctions.

Remarks. — It is my belief that *L. caverna* is the species Heath (1905, 1907) and Higley and Heath (1912) knew as *T. raymondi*, a hermaphroditic brooder occurring in high tidepools on the Monterey Peninsula. Dr. Arthur Bogan (ANSP) provided two lots of '*Trachydermon raymondi*', collected by Heath, in the ANSP collections. These are likely the specimens sent to Pilsbry (Pilsbry, 1898a), that were thought lost (Ferreira, 1982: 100). Examination of these two lots supports my suggestion that Heath's hermaphroditic brooder is not conspecific with *T. raymondi* Pilsbry (=*L. dentiens* (Gould)). As summarized above, over half of the 50 specimens in these two lots were unquestionably *L. caverna.* Apparently, Heath was collecting both *L. caverna* and *L. dentiens*, unaware they were distinct. Likewise, Pilsbry examined and apparently even partially disarticulated three specimens of *L. caverna*, but failed to recognize their distinctness from *L. dentiens.* This is surprising since these specimens clearly display the warty granules on the lateral margins of the valves, which Pilsbry (1894a) stressed as diagnostic for *L. hartwegii.* If Pilsbry concluded that these were merely juvenile *L. hartwegii*, as Ferreira (1982: 100) contends, it is curious that he did not label them as such.

Judging from his first report of brooding in *L. caverna*, Heath (1899: 628) may have been less than certain what name to use. Although earlier in his work (1899: 569) Heath had included the identification provided by Pilsbry (1898a), he does not use this name in his text. For example, in describing the tendency for brooded larvae to remain near their parents, Heath writes "It probably belongs to the genus *Trachydermon* and as in the case of *Ch. polii* [= ?*Lepidochitona corrugata* (Reeve, 1848)] carries its eggs in the mantle furrow. In several instances I have found scores of small *Chiton* within a very small distance of the parents, showing that the free-swimming stage could have been only of the briefest duration."

Although Heath several times mentions that this species is fairly abundant in certain localities, it should also be stressed that few if any chiton collectors have equaled Dr. Heath's careful collecting methods, especially with minute post-larval stages (see Berry, 1917a: 76). Without such care, *L. caverna* is likely to pass unnoticed.

In Santa Cruz, the sea cave population at the type-locality was first discovered by William G. Wright, and studied by Drs. D. R. Lindberg and J. S. Pearse, as reported in Pearse (1979), Pearse and Lindberg (1980), and Ferreira (1982: 102). The initial conclusions of Pearse and Lindberg, regarding seasonal patterns of sex changes, have not been confirmed in my own studies, which included more detailed histological and laboratory observations (Eernisse, 1984a). It is probable that the "large males" they observed were specimens of another species such as *L. dentiens*, which I have occasionally found in this sea cave.

Lepidochitona dentiens (Gould, 1846)
(figs. 1, 10, 11, 28, 37, 38, 55, 64; plates 2, 3A, 4; table 1)

Chiton (Onythochiton) dentiens Gould, 1846: 145; 1852: 321, pl. 28, figs. 433, 433a, 433b; 1862: 242; Johnson, 1964: 67.
Cyanoplax dentiens (Gould). — Berry, 1948: 13 (*Trachydermon raymondi* Pilsbry in synonymy); Smith, 1977: 224; Haderlie & Abbott, 1980: 418 (in part), pl. 131.
Lepidochitona dentiens (Gould). — Ferreira, 1982: 98 (in part); Kozloff, 1983: pl. 9.
Cyanoplax dentiens cryptica Kues, 1974: 297.
Ischnochiton pseudodentiens Carpenter, 1864: 530. New name for *Chiton dentiens* Gould.
Trachydermon (Cyanoplax) raymondi Pilsbry, 1894a: 46. — (?) Pilsbry, 1894b: 57.

Material. — Holotype (USNM 5824) of *Chiton dentiens* Gould, 1846 (plate 2a, b), Puget Sound (Washington State); dry specimen, 4.7 mm length, curled, partially disarticulated with loose valves i, ii, and iii. Syntypes (2) of *Trachydermon* (*Cyanoplax*) *raymondi* Pilsbry, 1894a (ANSP 65027) "San Francisco" (California); one of the syntype specimens intact (22.8 mm length) herein designated lectotype (plate 3A); other specimen partially disarticulated (loose valves i, ii, iii, and viii) herein designated paralectotype (plate 4A-F). Holotype (SDNH 51310) of and paratypes of *Cyanoplax dentiens cryptica* Kues, 1974 (CAS 53589; USNM 735015), published locality "Bird Rock, La Jolla, California."; holotype intact preserved in alcohol, two paratype specimens (CAS 53589) (both disarticulated) appear from labels to have been collected at "Devil's Slide, on *Eisenia*."

The collections housed in CAS and LACM were examined, as well as over 800 specimens from the following localities: Alaska: Sitka (Sitka Borough). Washington: Mar Vista Resort, San Juan Is. (San Juan Co,); Tatoosh Is. (Clallam Co.). Oregon: Fossil Pt., Coos Bay (Coos Co.). Harris Beach and Gold Beach (both in Curry Co.). California: Bodega Head (Sonoma Co.); Arroyo de los Frijoles (Bean Hollow), Pigeon Point, Año Nuevo Point (all in San Mateo Co.) Scott Creek (Santa Cruz Co.); and Landels-Hill Big Creek Reserve (Monterey Co.).

Shell (figs. 1, 10, 11, 28, 37, 38, 55). — Oval-elongate shape. Valve profile low to medium; side slopes convex. Animal rather small, maximum observed length 27.3 mm, but most specimens do not exceed 20 mm. Mucro more or less central; post-mucronal slope generally flat to slightly convex (more rarely slightly concave, especially in southern California specimens). Valves beaked.

Tegmentum sculpturing composed of uniform round granules arranged in regular patterns on all valve surfaces. Lateral areas weakly defined, not raised. This species is characterized by its unusually variable coloration patterns, although certain patterns seem to reappear frequently. The more common colors involved in these complex multicolored patterns on the tegmentum include (but are not limited to) green, burgundy, light or dark brown, white, red, and blue. If all of the specimens from a particular locality have similar coloration, the species is probably not *L. dentiens.*

Articulamentum variously colored, usually light blue, green or golden. Sutural laminae rounded; insertion teeth of posterior valve mostly regular, flattened, projecting radially (slit formula 7/11 - 1 - 7/13). Eaves spongy, slit rays defined by small pores.

Girdle (figs. 64a-d). — Dorsally clothed with stout, distally-pointed, not imbricating corpuscules, about 50-75 μm long, 25 μm wide. Margin of girdle fringed with elongate spicules about 120μm long. Ventral surface covered with translucent, longitudinally ribbed lanceolate or rectangular scales. Girdle usually banded by alternating light and dark colors, or scattered light spots.

Radula (figs. 37, 38). — First lateral teeth narrowed distally. Tridentate cusps of major lateral teeth with the median denticle roughly twice as long and wide as the outer denticles; sides convex.

Gills. — Specimens over 8 mm length with about 20-28 gill pairs; each gill row extending approximately 85 percent of foot length.

Distribution. — Ferreira (1982:99) lists Boswell Bay, Hinchinbrook Island, near Prince William Id., Alaska (60°24'N, 146°08'W; CAS 39424) as the northernmost verified record, and Puerto Santo Tomas, Baja California, Mexico (31°34'N, 116°40'W; LACM 67-2) as the southernmost record.

L. dentiens is one of the most abundant chitons found along the outer exposed coast of the western U.S. north of Pt. Conception, California. It is often overlooked, however, because of its small size and cryptic habits. Putman (1982) describes this species as relatively common in San Luis Obispo County, California, near Pt. Conception. To the south this species is thought to be increasingly rare (Berry, 1948). I have collected two specimens at Palos Verdes (DJE 0121-1), but records from southern California are extremely scattered and often need further verification, including the present southernmost record. As concluded by Ferreira (1983), records of *L. dentiens* on Socorro Is., Mexico by Pilsbry (1898b) should be attributed to *L. keepiana.* Southern California specimens are particularly difficult to identify. Although girdle elements and tegmental sculpturing are similar to central and northern California specimens of *L. dentiens*, the possibility that unrecognized southern California species are present with similar morphology to *L. dentiens* can not be ruled out at this time.

In the northern part of the range of *L. dentiens* relatively few collecting records exist, perhaps due to the inconspicuous nature of this species. It seems likely that *L. dentiens* is common on at least the outer Pacific Coast from central California to Alaska, where the habitat is favorable. Unlike the southern

California specimens, all collections I examined from the northern regions (Oregon, Washington and Alaska) closely resembled specimens collected in central California. In comparing *L. dentiens* from central California I am impressed by remarkable similarities rather than large intraspecific variation. Previous difficulties in identifying this species could have resulted from the inclusion of other species in collections.

Habitat and ecology. — *L. dentiens* can be found in a variety of habitats, ranging from low to high intertidal, and thus makes characterization of a typical habitat difficult. It can be extremely common in the very low intertidal in densities occasionally exceeding 50 chitons per square meter. Here it occurs especially on large crusts of *Petrocelis*, on *Egregia* holdfasts, on "bare" rock surfaces, and in cracks and crevices. Localities where it has been noted in high densities include all the localities listed for my collections above. However, it is largely absent within Monterey Bay, California, including the rocky intertidal of the Santa Cruz area. Likewise, it does not seem to extend far into the protected coast portions of Washington and British Columbia, including Puget Sound, the published type-locality. It does, however, occur in some protected areas, including Argyle Lagoon on San Juan Island, Washington, where it is found on the undersides of small rocks.

Although densities are greatest in the low intertidal, *L. dentiens* is not restricted to this zone. Large individuals can be quite common higher in the intertidal. For instance, on the west side of San Juan Island, Washington, *L. dentiens* living in association with the '*Endocladia-Balanus* association' in absence of juveniles in the high intertidal suggests an upward vertical migration with increasing size. Glynn (1965) reported relatively high densities of *L. dentiens* living in association with the '*Endocladia-Balanus* association'in Monterey Bay, but it is possible that he was referring to *L. caverna* spec. nov.

Kues (1974) described *L. dentiens cryptica* from the San Diego, California area living on the holdfasts of *Eisenia*, a shallow subtidal kelp. His description of the highly restricted habitat and consistent coloration contrast with the characteristic variable habitat and coloration of this species that I have documented.

In the lab in central California, I have observed many free spawning events for this species between January and May (Eernisse, 1984a). When fertilization was successful, larvae developed with characteristics similar to those described for *L. hartwegii.*

Remarks. — The name *Ischnochiton pseudodentiens* was proposed by Carpenter (1864) for the type of Gould's *Chiton dentiens*. As explained by Palmer (1958: 265), Carpenter noted the fact that Gould had mistaken spots for denticles in his original description, and incorrectly supposed a new name was required. Dr. Rosewater (USNM) kindly supplied me with three specimens which Carpenter likely used in association with his name "*pseudodentiens*." These specimens have no type status, as is clear from the wording of Article

72(d) of the ICZN. However, because Carpenter apparently replaced the original label for the type-specimen with his own when he prepared labels for these other specimens, it is possible that a mix-up occurred.

The authenticity of the specimen presently regarded as holotype (USNM 5824) is relatively certain, based on the close correspondence to Gould's published dimensions, and from comparison of the specimen to his later published figures (1852: pl. 28), despite inaccuracies in these figures. Specifically, Gould (or his engraver, Joseph Drayton) greatly exagerated the contour of the tegmental surface, by drawing three distinct nodules (the infamous 'denticles') in the lateral region of each intermediate valve. As plate 2A,B of the presumed holotype illustrate, these three nodules simply correspond with color and slight contour peculiarities of this particular specimen. Carpenter's label, presently with the presumed holotype specimen (USNM 5824), lists "Oregon" instead of the published locality. Puget Sound was at that time considered to be part of the Oregon Territory, so this is not necessarily an inconsistency.

One of Carpenter's "*pseudodentiens*" specimens (USNM 4154) lists the collecting-locality as Puget Sound, Gould's published type-locality. Another possibility is that this specimen with the correct locality and Carpenter's identification as "*Trachydermon dentiens* Type. Gld.", leg. Kennerley, is the true type, but there are major problems with this view. This specimen, dry with no soft parts remaining (save a small radula fragment and girdle), is a mere 2.7 mm in length, nowhere near the dimensions published by Gould (length 5.1 mm, width 3.8 mm, converted to mm from polls). As is apparent from its girdle, it is not even a *Lepidochitona*, since it displays rather large girdle scales as in *Ischnochiton*. Berry apparently arrived at a similar conclusion, since he stated "certainly not a type" on a label with this specimen.

Carpenter's other two specimens of "*pseudodentiens*" (USNM 14917/15269; San Pedro, Calif.) are even less likely to have been Gould's type. Again the locality is confused, since USNM catalogues list locality 15269 as "San Diego - San Pedro." There is no mention of San Diego on labels with the specimens. There are also identification problems. A relatively large specimen, partially disarticulated, is clearly *L. dentiens* as diagnosed here in all respects. The second specimen (intact) appears most likely to be *L. keepiana*, although the distinctive girdle features of this species are obscured by poor preservation. Thus, Carpenter's lot for "*pseudodentiens*" is composed of three distinct species.

As is evident from table 1, *Chiton dentiens* has often been referred to as *Trachydermon raymondi*. Berry (1948) and Smith (1977) convincingly established *Trachydermon raymondi* Pilsbry, 1894a as a synonym of *C. dentiens*. After examining Gould's holotype and Pilsbry's two syntypes, I concur with this synonymy. The type lot of *T. raymondi* consists of two dry specimens. One of these is intact, with 22.8 mm length, 10.2 mm width, and 3.8 mm height, and roughly fits the dimensions of the specimen for which Pilsbry listed "Length 23, breadth 11 mm (type; San Francisco)." The other specimen is of similar size and could also be the listed specimen. It is partially disarticulated, with loose valves i, ii, iii, and viii, and measures 10.1+ mm length (attached valves), 10.5 mm width, and 2.6 mm height. I herein designate the intact syntype as lectotype, and the partially disarticulated specimen as a paralectotype. Both of these specimens are unusually large for *L. dentiens*; meristic features of these specimens should not be used to typify the species. I was misled at first by shape differences displayed by these specimens relative to more typical *L. dentiens* until I included other unusually large specimens in my comparisons and was thus able to attribute shape differences to the natural allometric changes associated with increasing size. Comparisons with 10 smaller specimens also collected by W. J. Raymond at "San Francisco" (CAS 020465), supported this view.

The holotype and paratypes of *Cyanoplax dentiens cryptica* Kues, 1974 were examined and they appear quite different from *L. dentiens* specimens from central California. I do not agree with Ferreira (1982: 99), who considers *C. dentiens cryptica* to be a synonym of *L. dentiens*, that the distinctions noted by Kues are "well within the intraspecific range of variation of *L. dentiens*." However, until more specimens from southern California are examined, I am reluctant to change the assessment of Kues (1974: 297) who reasons that "the exact relationships of this San Diego group to (*L. dentiens*) must wait until more information is available concerning the nature of (*L.*) *dentiens* in the southern part of its range." It is possible that this form could represent a distinct species.

Lepidochitona thomasi (Pilsbry, 1898a)
(figs. 8, 24, 25, 35, 51, 52, 62, 71; plates 5, 6, 7A)

Nuttallina thomasi Pilsbry, 1898a: 288. — Heath, 1899: 37, 1905: 257; Higley & Heath, 1912: 95; Dall, 1921: 190; Oldroyd, 1927: 867; Smith, 1947: 16; Smith & Gordon, 1948: 206; Christiansen, 1954: 66; Thorpe in Smith, 1966: 438; Burghardt & Burghardt, 1969: 32, pl. 4, fig. 67; Abbott, 1974: 400; Smith, 1975: 464; Pearse, 1979: 48; Davis, et al., 1979: 43.
Nuttalina thomasi (Pilsbry). — Kussakin, 1960: 1149.
Nuttallochiton thomasi (Pilsbry). — Fischer-Piette & Franc, 1960: 1770.
Lepidochitona thomasi (Pilsbry). — Eernisse & Pearse, 1980: 926; Eernisse, 1983: 18; Edwards, et. al., 1984: 56.
Lepidochitona dentiens (Gould). — Ferreira 1982; 99 (in part). Not *L. dentiens* (Gould, 1846).

Material. — Lectotype (plates 5A, 6A) and paralectotype (plates 5B, 6B, 7A) of *Nuttallina thomasi* Pilsbry, 1898a (ANSP 7190 and A4652 - alc. coll.) (designated by Ferreira, 1982: 99), type-locality: " 36°36'N 121°56'W (Vicinity of Lover's Point)/Pacific Grove, Monterey, California"; leg. H. Heath, "In small tidepools, 4-8 feet above mean tide mark."

Between 1978 and 1984 I examined approximately 500 individuals of *L. thomasi* at the Landels-Hill Big Creek Reserve, (36°04'N 121°36'W; Monterey Co., California). I have also collected several specimens, near the type-locality, at Pt. Pinos and Cypress Point (Monterey Co.). Nearly all other known specimens identified as *N. thomasi* Pilsbry are at the CAS, but this collection consists of only 17 specimens, as follows (pres. in alcohol unless otherwise indicated): 2 specimens (dry), "Pt. Pinos" (CAS 032291); 1 specimen, "Pt. Lobos" (CAS 000530); 1 specimen, (CAS 011436); 2 specimens, Soberanes Pt. (36°27'N 121°56'W; CAS 011433); 5 specimens (all dry and disarticulated), "Mouth of Malpaso Cr. (Monterey Co.)" (CAS 032291); 5 specimens (3 dry, incl. 1 disarticulated), "7-9 mi.

S. of Yankee Pt. (Monterey Co.) on corallines in shelter of *Postelsia palmaeformis*," (CAS 011437, 014144); 1 specimen, "Hopkins Marine Station, Pacific Grove" (CAS 014143). I have also examined a single specimen at LACM, "Intertidal, Pacific Grove, Monterey" (LACM 59-12).

Shell (figs. 8, 24, 25, 35, 62). — Oval-elongate shape; generally flattened and small, usually not exceeding 16 mm length (maximum observed length 18.5 mm). Valve profile low; slopes convex. Intermediate valves beaked when not eroded. Mucro nearly terminal in most specimens; post-mucronal slope corresponds more or less with vertical posterior margin. Consequently, posterior portion of tail valve blunt and thickened, with thick rugged insertion teeth directed ventrally or even slightly anteriorly (especially lateral teeth). Slit formula 8/11 - 1 - 8/13.

Valve surfaces typically heavily eroded. Tegmental sculpturing (when it can be observed) composed of regular, well-spaced granules, not raised substantially. Tegmentum and dorsal girdle elements both dark brown (if not eroded to the underlying blue articulamentum); tegmentum often streaked with curving white markings.

Girdle (figs. 71a-d). — Broad and dark, distinctively clothed dorsally with both short, stout corpuscules (about 35μm long, 15μm wide), and much longer blunt thickened corpuscules (about 120μm long, 35μm wide), giving the girdle a spiny or rough appearance (plate 7a). Marginal spicules also about 120μm in lenght, but more pointed distally. Girdle underside covered with lanceolate scales, about 40μm long and 15μm wide.

Radula (figs. 51, 52). — First lateral teeth about as long as the median tooth; dilated slightly towards the anterior blade. Major lateral teeth cusps tridentate, each with median denticle about twice as wide and long as outer denticles.

Gills. — Specimens over 6 mm length with about 20-28 gill pairs; each gill row extending approximately 90 percent of foot length.

Distribution. — Northernmost record for *L. thomasi* is Pescadero Point (San Mateo County) (Smith and Gordon, 1948). Type-specimens from Pacific Grove area are the next-most northern verified record. The southernmost verified specimen was collected at Landels-Hill Big Creek Reserve (DJEO405-1) near Oystercatcher Point (see Eernisse, 1984b). Since this rather limited range corresponds with the transition zone between the Oregonian and Californian Provinces, *L. thomasi* may qualify as a "short-range endemic" species as defined by Newman (1975).

Habitat and ecology. — *L. thomasi* inhabits the upper midintertidal zone, and although it has been collected in areas of extreme exposure (e.g. the Big Sur coastline), its tendency to nestle into cracks and under barnacle hummocks may protect it from direct wave shock. It has long been known that females of *L. thomasi* brood their offspring (Heath, 1905). The reproductive behavior of *L. thomasi* and its consequences are discussed by Eernisse (1984a).

The extremely sporadic records for *L. thomasi* over the last century are likely due to both its patchy occurrence and its tendency to inhabit microhabitats in most places inaccessible to all but the most destructive collecting techniques. Histological sections reveal diatoms in their guts and it is likely that *L. thomasi* feeds on the film of diatoms and other microscopic plants that coat intertidal surfaces.

The eroded condition of the tegmentum as displayed by the lecto- and paralectotype (plate 5A, B) is typical in this species, although occasional individuals can be found with uneroded tegmentum surfaces, such as the individual illustrated in figure 8. In my experience, such uneroded specimens are found in the most protected microhabitats, suggesting that physical scouring is responsible for the erosion. I have also observed that animals with eroded valves can repair their tegmentum surface in lab conditions. Similar observations have been made with *Nuttallina californica*, another species which is typically heavily eroded. It is interesting that *L. dentiens* is rarely found eroded; why this is so remains a perplexing question.

Remarks. — Besides details of reproduction described by Heath (1905), Higley and Heath (1912), and a description of the syntypes by Ferreira (1982: 99), no one has added to Pilsbry's original diagnosis, which still is generally sufficient to characterize *L. thomasi*. Further description was necessary, however, to distinguish this species from *L. fernaldi* spec. nov., described herein. I consider Ferreira's (1982: 99) synonymy of *N. thomasi* Pilsbry with *L. dentiens* (Gould) to be incorrect. Although this species is clearly a *Lepidochitona* rather than a *Nuttallina*, it is distinct from *L. dentiens*.

Ferreira (1982: 99) based his designation of lectotype and paralectotype on only the dry portion of the type lot. He was apparently unaware of the syntype specimen (A4652), referred to on labels with the dry lot, which has been preserved in alcohol since its collection by Heath. This specimen is partially disarticulated, with loose valves i, vii, and viii kept with the dry lot (ANSP 7190). These are the three valves Ferreira designated paralectotype so, following this designation, the remaining alcoholic parts (plates 5A, 7A) complete the paralectotype. The lectotype specimen (plates 5B, 6B) was dry and also partially disarticulated, but the loose valves are i, v, vii, and viii, not i, vi, vii, and viii as listed by Ferreira (1982: 99).

Permission was granted to biopsy a small portion of the gonad tissue in the lecto- and paralectotype in hopes of finding intact eggs that could be used for egg hull comparisons. This required rehydration of the lectotype and it was left in the rehydrated state, as requested by the ANSP. Unfortunately, eggs were not found (ironically, both of Heath's specimens appear to have been males).

Lepidochitona fernaldi spec. nov.
(figs. 4, 16, 17, 31, 43, 44, 58, 67; plates 1B, 7B)

Type-material. — The holotype (RMNH 9176; plates 1B, 7B) and one paratype (RMNH K5054) have been deposited in the Rijksmuseum van Natuurlijke Historie; another paratype, dried and disarticulated has been placed in the VB collection (figs. 16, 17, 31, 43, 44, 58, 67). Additional paratypes will be deposited in the BMNH, USNM, ANSP, and CAS.

Approximately 500 specimens (not part of the type-series) have been observed from the type-locality and other locations along the west side of San Juan Island. I collected additonal specimens in association with anemones and barnacles living on boulders in the intertidal from the west side of The Narrows, Tacoma, Washington (47°16'N 122°30'W). I was originally aware of *L. fernaldi* from only the vicinity of the type-locality. The collecting efforts of Mr. Roger N. Clark have expanded the known distribution of this species to include Tacoma Narrows and four locations in southern Oregon. It seems likely that *L. fernaldi* will turn up in similar habitats in nearby areas.

Type-locality. — Mar Vista Resort, San Juan Island, Washington (48°03'N 123°05'W; leg. D. J. Eernisse; August 20, 1982); on the sides of the barnacle *Semibalanus cariosus* (Pallas, 1788) adjoining the anemone *Anthopleura elegantissima* (Brandt, 1835) at the fringe of high tidepools.

Diagnosis. — Mucro nearly terminal; post-mucronal slope nearly vertical. Gill row extending less than 70 percent of foot length, with not more than 17 gill plumes on each side. Maximum body length about 15 mm.

Description of holotype (plates 1B, 7B). — Animal intact, preserved in ethanol; oval-elongate in body outline; 9.4 mm in length, 5.6 mm in width, and 1.4 mm in height.

Valve profile relatively low. Mucro position nearly terminal; post-mucronal slope nearly vertical; posterior margin of tail valve thickened. Intermediate valves beaked; valve slopes convex; eaves quite spongy. Tegmentum sculptured with well-spaced, rather large, uniform granules. Color dark brown, with white lateral portions on fifth valve. Articulamentum blue.

Girdle wide (each side about 18 percent of total width); rough appearing; dorsally clothed with dark brown elongate blunt corpuscules. Elements not imbricating and variable in size, to about 70 μm in length, and about 35 μm in diameter. Girdle fringed with marginal spicules, about 120 μm in length; ventral surface covered with striated lanceolate scales, about 50 μm in length.

Each gill row short, extending about 60 percent of foot length, with 14 gill plumes on left side (ventral view), and 12 on right.

Range of morphological variation. — Maximum length observed 17.0 mm, but most specimens do not exceed 12 mm in length. Body outline always oval-elongate (fig. 4), but adults generally less elongate than juveniles.

At the type-locality, tegmental coloration nearly always dark brown, frequently with white markings (especially on fifth valve). Valve surfaces, however, frequently heavily eroded to underlying blue articulamentum. Most of larger girdle elements also dark brown. At Tacoma Narrows, both tegmental and girdle coloration typically lighter brown, with more extensive white and tan markings on tegmentum, and patches of white girdle elements scattered irregularly among the more numerous brown elements.

Tegmental sculpturing, when uneroded, consistently as described for holotype. Likewise, mucro position (fig. 58) generally posterior as in holotype, although profile of posterior valve is so low in some intact specimens that mucro appears scarcely elevated. Disarticulation reveals a thickened posterior margin even in these specimens.

Articulamentum variously colored, usually light blue in adults and golden in juveniles. Sutural laminae generally rounded or rectangular (figs. 10, 11). Posterior valve insertion teeth rugged and irregular; central teeth projecting ventrally; lateral teeth slightly anteriorly. Central region of posterior valve ventral surface depressed, bounded by a more posterior, heavy articulamentum ridge; insertion slit rays, therefore, not apparent. This ridge much less pronounced in juvelines. Slit formula range 9/12-1-9/12.

Range of girdle element size (figs. 67a-d) usually similar to that of holotype. Tridentate cusps of major lateral radular teeth (figs. 43, 44), each with a broad, convex median denticle about twice as long and wide as outer denticles. Gill rows characteristically short, extending from 55 to 70 percent of foot length; composed of 11 to 17 gill pairs in specimens longer than 6 mm (the number increasing with size).

Distribution. — Specimens from the type-locality are presently the northernmost confirmed record for *L. fernaldi.* A single specimen from Harris Beach, one mile north of Brookings, Oregon (Curry Co.; 42°03'N 124°18'W; DJE 0634-1) has been designated the southernmost verified record.

Habitat and ecology. — *L. fernaldi* tends to be local, but like other brooding species, can be locally abundant. I have observed this species in densities exceeding 100 per square meter in tidepools at the type-locality, and similar densities at the Tacoma Narrows, but such dense groupings are not found in all places they might be expected. *L. fernaldi* lives in association with barnacles (usually *Semibalanus cariosus*) and the anemone, *Anthopleura elegantissima.* Anemone clones frequently live in close contact with the crenulated surfaces of barnacles, and *L. fernaldi* takes advantage of both the many depressions and crevices on the barnacle's plates and the cover and dampness provided by anemones. This protected microhabitat occurs relatively high in the intertidal. For instance, this species is especially abundant near the edges of tidepools at about +1.8 to +2.5 m at the type-locality. At Tacoma Narrows, the 'barnacle-anemone' association occurs on large intertidal boulders.

As described by Eernisse (1984a), at the type-locality *L. fernaldi* is characterized by a simultaneous hermaphroditic condition, and as in *L. thomasi*, is a brooder. Brooding is especially common in the winter and spring. The limited benthic dispersal of brooded offspring appears to account for the high densities found in certain favorable localities, although at least some planktonic dispersal ability is likely.

Etymology. — I take pleasure in naming this new species after the late Dr. Robert L. Fernald, whom I was visiting when specimens of this new chiton were first collected. Dr. Fernald was a friend and constant source of advice and encouragement, and I remember him fondly. He was very interested in chitons, and as a teacher of invertebrate reproduction at Friday Harbor Laboratories, the association of his name with a species with interesting reproductive attributes seems especially appropriate.

Discussion. — I consider *L. fernaldi* to be distinct from *L. thomasi* (Pilsbry), based on the former's clearly shorter gill row with fewer gill plumes, and differences in girdle elements. Elsewhere, I have also documented differences in electromorph patterns, body size, and reproductive differences, including an unusual hermaphroditic condition found only in *L. fernaldi* (Eernisse, 1984a). However, there is no question that *L. thomasi* is a close relative, especially in view of the striking similarity of egg hull patterns in these two species (Eernisse, 1984a); this relationship is further supported by overall morphological similarity and habitat. For instance, both have valves of similar shape, especially the posterior valve, with a nearly terminal mucro position. Both have an overall uniform, dark appearance, especially of the girdle, which has a somewhat 'spiny' appearance in both (less so in *L. fernaldi*). Both brooding species lay elongate rod-shaped egg masses. Both can be found in association with the same species of barnacle and anemone in high tidepools. Radular and some electromorph characters (Eernisse, 1984a) are also similar in both.

As with *L. thomasi*, it is necessary to distinguish this species from *L. dentiens* (Gould), which it closely resembles. Besides major reproductive, electrophoretic, and egg hull differences discussed by Eernisse (1984a), *L. fernaldi* can be diagnosed by its uniformly dark 'slightly spiny' girdle; similar-appearing, often eroded valves; a blunt nearly terminal mucro; fewer gills and shorter gill row; slightly orange foot; smaller size; and restricted habitat. Although large *L. dentiens* occur in moderate densities in the same tidepools as *L. fernaldi* at the type-locality, *L. fernaldi* has not been found in the lower intertidal where *L. dentiens* reaches its highest densities.

Lepidochitona keepiana (Berry, 1948)

(figs. 3, 14, 15, 30, 41, 42, 57, 66; table 1)

Lepidochitona keepiana Berry, 1948: 13-15. — McLean, 1969: 61; fig. 34.3 (reprinted 1978); Burghardt & Burghardt, 1969: 19, pl. 2, figs. 24-25; Abbott, 1974: 397; Putman, 1980: 70; 1982 365. Ferreira, 1982: 107; 1983: 307; Hertz, 1984: 8.

Ischnochiton (*Trachydermon*) *dentiens* (Gould). — Pilsbry, 1892-93: 73; pl. 8, figs. 61-65; 1894: 65, pl. 15, fig. 26. Not *L. dentiens* (Gould, 1846), fide Berry, 1948: 15.

Lepidochitona dentiens (Gould). — Berry, 1922: 410; tbl. 1, pl. 1, figs. 7-9. Not *L. dentiens* (Gould, 1846), fide Berry, 1948: 15.

Material. — Holotype: S. S. Berry coll., Cat. No. 11992; figured in Hertz, 1984: 8. Paratypes: S. S. Berry coll., Cat. No. 3978; SDNH T.S. 18. Type-locality: Newport Bay, Orange County, California (33°37'N 117°56'W). The existence of additional paratypes at other institutions and private collections listed by Berry (1948) has not been confirmed.

Approximately 200 specimens were collected and examined on two occasions at Palos Verdes, Los Angeles County, California (33°43'N 118°20'W). Also examined were the collections at CAS and LACM. *L. keepiana* appears to be sporadically common in southern California and Baja California, Mexico.

Shell (figs. 3, 14, 15, 30, 57). — Animal rather small, maximum length about 16 mm; distinctly oval in shape. Valve profile relatively high; slopes straight; valves not beaked. Mucro anterior; post-mucronal slope concave.

Tegmentum covered with uniform round granules arranged in regular longitudinal patterns especially in central areas. Jugum acute; lateral areas defined but only very slightly raised. Color of tegmentum variable, predominantly with lighter colors such as beige, orange, yellow, or white, but occasionally dark green or brown.

Articulamentum translucent or white; sutural laminae short and triangular. Insertion teeth of terminal valves thin and numerous, radiating outwards (slit formula 9/13 - 1 - 10/14). Eaves thin and not spongy.

Girdle (figs. 66a, c, d). — Dorsally clothed with distinct small stout corpuscules, up to about 60 μm long and 20-30 μm wide. These corpuscules appear round from a dorsal view; closely-packed but not imbricating. Girdle fringed with striated marginal spicules, about 130 μm long; undersurface has translucent, often imbricating scales about 40 μm long.

Radula (figs. 41, 42). — Tridentate cusps of major lateral teeth each with the median denticle only slightly larger than the outer denticles.

Gills. — Specimens over 6 mm in length with about 14-18 gill pairs, each gill row extending approximately 90 percent of foot length.

Distribution. — Ferreira, (1982: 108) lists northernmost record at Otter's Point (36°38'N 121°54'W), and southernmost locality from Rancho Socorro (30°20'N 115°45'W; LACM 66-3).

L. keepiana appears to be much less common in central California. I have taken specimens of *L. keepiana* in high- to mid-intertidal pools at Cayucos (San Luis Obispo Co.), north of Point Conception. Ferreira (1982) reports this species from the subtidal of the Monterey Peninsula region, including the northernmost record.

Habitat and ecology. — *L. keepiana* occurs most commonly under small stones in the low intertidal to shallow subtidal, especially in sandy areas with some degree of protection from wave exposure. Its habitat seems to resemble that of *L. cinerea* (Linnaeus) in Europe (pers. observ.); it is also morphologically similar to this species. Despite the fact that *L. keepiana* can be one of the most abundant chitons in the southern California fauna, its ecology remains largely unknown. One possible reason for this ignorance is that many of the localities where this species was collected earlier in this century, including the type-locality, have been substantially modified or made inaccessible by development.

Discussion. — Pilsbry (1892-93: 73) first provided a detailed description of *L. keepiana*, including comparison with the European *L. cinerea*, under the mistaken supposition that the specimens he was examining were Gould's *Chiton dentiens*. Berry's description of *L. keepiana* in 1948 cleared up this confusion and provided detailed comparisons of the morphology of *L. keepiana* with the more northerly *L. dentiens*. Ferreira (1982: 108) recently provided an excellent compilation of features which differ in these two species. Briefly summarized, *L. keepiana* differs in its lighter color, white articulamentum, straight side slopes, more carinate jugum, different tegmental sculpturing, slightly more anterior mucro, narrower sinus, more numerous and less regular insertion teeth, larger girdle scales, absence of minute orifices in ray slits, and less spongy eaves. These differences can be extended in large part to comparisons of *L. keepiana* with *L. thomasi*, *L. fernaldi*, and *L. caverna*, all which resemble *L. dentiens* to a greater degree. An exception are the bright blue dots or lines which can often be found in *L. dentiens* but not in *L. thomasi* or *L. fernaldi*. In addition, the posterior valve of *L. thomasi* and *L. fernaldi* generally lacks minute orifices on the ray slits, except in small individuals, and displays markedly irregular insertion teeth.

Lepidochitona berryana spec. nov.
(figs. 9, 26, 27, 36, 53, 54, 63, 72; plate 1C)

Type-material. — The holotype (RMNH 9174; plate 1C) and two paratypes (RMNH K5053; fig. 9) have been deposited in the Rijksmuseum van Natuurlijke Historie. Another paratype, dried and disarticulated, has been placed in VB coll. (figs. 26, 27, 36, 53, 54, 63, 72). Additional paratypes will be deposited in the BMNH, USNM, ANSP and CAS.

Approximately 250 specimens (not part of the type-series) have been observed from the type-locality and from localities north of Santa Cruz including Davenport Landing (Santa Cruz Co.), Año Nuevo Pt. (San Mateo Co.), and Pigeon Pt. (see below). A single specimen was collected in southern California, at Palos Verdes (Los Angeles Co.). No previous collections of this species are known to me, with the exception of a single specimen taken in southern Monterey Co. (Sand Dollar Beach, Los Padres Nat. Forest; DMNH 36683) by Dr. Barry Roth, and identified by Spencer Thorpe as *Lepidochitona* sp.

Type-locality. — Soquel Pt., Santa Cruz (36°58'N 121°58'W; Santa Cruz Co.; leg. D. J. Eernisse, February 1984), California, occurring on small stones submerged in shallow water during the lowest low tides.

Diagnosis. — Mucro slightly anterior; post-mucronal slope concave. Intermediate and posterior valves beaked; valve slopes straight; eaves not spongy. Articulamentum translucent or white. Maximum number of insertion slits on each terminal valve about 10; insertion teeth uniform and broad. Maximum body length about 15 mm. Tegmentum rust-colored with bright blue zig-zagging lines.

Description of holotype (plate 1C). — Animal intact, preserved in ethanol; oval-elongate in body outline; 9.8 mm in length, 6.0 mm in width, and 2.0 mm in height.

Valve profile relatively high; side slopes straight. Mucro somewhat anterior; post-mucronal slope concave. Intermedial and tail valves beaked. Eaves not spongy. Tegmentum colored with bright blue jagged lines on a rust-colored background, spotted with some white and dark areas, and a prominent white post-mucronal stripe. Tegmentum sculptured with closely-packed, well-defined diamond-shaped granules arranged in regular patterns. Articulamentum translucent white.

Girdle smooth appearing, with dense granular texture; banded by alternating light and dark colors. Dorsal surface clothed with minute distally-pointed non-imbricating corpuscules (about 30 μm long, 14 μm wide); corpuscules in sutures slightly larger (about 45 μm long, 20 μm wide). Girdle fringed with marginal spicules (about 80 μm long); undersurface covered with distally-pointed scales (about 60 μm long, 15 μm wide).

Each gill row extending about 75 percent of foot length, with 14 gill plumes on left side of foot (ventral view), and 17 on right.

Range of morphological variation. — Maximum length observed 14.1 mm. Body outline always oval-elongate (fig. 9).

Coloration of tegmentum consistent; nearly all individuals colored similar to holotype, especially in the typical pattern of bright blue jagged lines on a rust-colored background. Occasional individuals (about five percent) differ from this pattern by displaying only a single color on one or more valves; always one of primary colors found in typically marked individuals, and often linked to an absence of tegmental sculpturing on the same valve(s). Besides this deviation, tegmental sculpturing of all observed individuals similar to that of holotype. Likewise, girdle coloration and range in girdle element size (fig. 72) similar to that described for holotype.

Mucro generally slightly anterior, post-mucronal slope concave in all adult specimens, to approximately flat in some juveniles (less than 5 mm length). Intermediate and tail valves beaked; valve slopes consistently flat; eaves not spongy.

Articulamentum always translucent to white; sutural laminae broadly rounded (fig. 26). Insertion teeth on terminal valves uniform and broad; slit rays defined by small pores (slit formula range 8/10 - 1 - 8/11).

First lateral teeth of radula (fig. 53) with broad anterior blades tapering gradually to a much narrower base. Tridentate cusps of major lateral teeth, each with median denticle about twice as long and wide as outer denticles (fig. 54).

Each gill row extending from 75 to 90 percent of the foot length; composed of 14-20 gill pairs in specimens longer than 6 mm (the number increasing with size).

Distribution. — Rare, occurring at least as far north as Pigeon Pt. (south side) (37°11'N 122°24'W; San Mateo Co., DJE 0207-1) and as far south as Palos Verdes (33°43'N 118°20'W; Los Angeles Co., Calif.; DJE color slide 0221-1).

Habitat and ecology. — *L. berryana* is similar to *L. keepiana* in its habitat, living most commonly in sandy, protected localities where it is most often found attached to small stones (especially those covered with encrusting coralline algae) in the low intertidal and shallow subtidal. The type-locality is a protected, wide, flat rocky platform, situated inside Monterey Bay facing south, away from the predominate northwesterly swells. At other localities in more exposed outer coast situations this species is restricted to sites with an unusual degree of protection, such as behind the shelter of Año Nuevo Island at Año Nuevo Pt., or behind sea stacks on the south side of Pigeon Pt. *L. dentiens* has not been found at the type-locality of *L. berryana* but is about as common as *L. berryana* at Año Nuevo Pt. and Pigeon Pt. I have observed free spawning on several occasions in this species (see Eernisse, 1984a).

Etymology. — This species is named in honor of the late Dr. S. Stillman Berry of Redlands, California, who contributed many publications on living and fossil chitons of the West Coast, including work on *Lepidochitona*.

Discussion. — *L. berryana* seems to have escaped notice, perhaps because of its sporadic distribution and similar appearance to other species. My early suspicion that this was a distinct species from *L. dentiens* proved correct after examination of electromorph and egg hull characters (Eernisse, 1984a). More detailed morphological comparisons led me next to suspect that I might be observing a northern from of *L. keepiana*, perhaps one of the "very pretty and often bizarre color-forms" referred to by Berry (1948). This was conceivable because Berry listed Pacific Grove (Monterey Co.) as the northernmost recorded range for *L. keepiana*. But this view was rejected after more detailed biochemical and anatomical examination. In addition, a single small specimen of *L. berryana*, collected at the same time as roughly 200 *L. keepiana* at Palos Verdes (Los Angeles Co.), matched unambiguously the central California *L. berryana* electromorph patterns (Eernisse, 1984a), rather than those for *L. keepiana* or *L. dentiens*. As is evident from a color slide of this individual (DJE color slide 0221-1), it displays the same color patterns diagnostic of the central California populations, giving me greater confidence in ascribing importance to this normally variable character.

The consistent color pattern displayed by *L. berryana* sets it apart from *L. dentiens* and *L. keepiana*, both of which are extremely variable in their coloration. *L. berryana* can be distinguished from *L. dentiens* and the three brooding species (*L. caverna*, *L. thomasi*, and *L. fernaldi*) by its characteristic color pattern, its white articulamentum, straight side slopes, more carinate jugum, more elevated and anterior mucro, noticably concave post-mucronal slope (not as pronounced in juveniles), lack of spongy eaves, fewer insertion teeth on the head valve, and distinctive egg hull and electromorph patterns (see Eernisse, 1984a).

Several features can be used to distinguish *L. berryana* from *L. keepiana*. The generally more oval-elongate body shape of *L. berryana* contrasts sharply with the oval shape of *L. keepiana*. *L. berryana* also differs from this latter species in its coloration. Both the consistency of pattern and the presence of bright blue jagged lines set it apart. There is also a clear difference in size of the dorsal girdle scales and there are consistently fewer insertion teeth in both the head and tail valves of *L. berryana*. The intermediate valves of *L. berryana* also have a pronounced beak, which is only found in occasional juvenile specimens of *L. keepiana*. Egg hull and biochemical characters are also unambiguous diagnostic features (Eernisse, 1984a).

KEY TO THE NORTHEASTERN PACIFIC *LEPIDOCHITONA*

The West Coast *Lepidochitona*, most often assigned to the genus *Cyanoplax*, have received considerable attention in the last century (see Table 1; Haderlie and Abbott, 1980; Ferreira, 1982, for reviews). A combination of factors, including small size, inconspicuous nature, patchy distribution, and complex patterns of morphological variation permitted three species to go unnoticed until the current work. Herein, I considered the systematics of three new species and the four previously described species with which they are likely to be confused. The following key should enable workers to identify all nine members of this genus known to occur on the Pacific Coast of North America.

This key is especially useful as a supplement to Allyn G. Smith's 1975 key to the intertidal chitons of central California (Light's Manual, 3rd ed.). It can replace step 16 in that key (p. 462) and will cover not only the species of *Lepidochitona* found in central California, but can also identify *L. fernaldi*, which is known to occur only in Washington and Oregon, and *L. beanii* (Carpenter, 1857), which is known to range from Perú to southern California (Ferreira, 1982: 103).

Because *L. fernaldi* and *L. dentiens* are the only species of *Lepidochitona* known from Washington, a simplified version (with *L. thomasi* removed) at step 7 is generally adequate for the Pacific Northwest (see also Kozloff, 1985).

The southern California fauna includes chiton species not in Smith's key (see McLean, 1978; Putman, 1980), for example, the additional species of *Lepidochitona*, *L. beanii* (figs. 7, 22, 23, 34, 49, 50, 61, 70) and *L. lowei* (Pilsbry, 1918) (figs. 6, 20, 21, 33, 47, 48, 60, 69) (syn. *C. fackenthallae* Berry, 1919), the latter species ranging from San Diego to the Monterey Peninsula (Smith, 1947), and apparently living exclusively on the holdfasts of kelp. This key will serve adequately for these two and for four other species of *Lepidochitona* also known to occur in southern California.

1. Dorsal girdle surface with long (greater than 500 μm) hyaline spicules, interspersed or bunched at the sutures in groups of three to four .... *L. beanii*
- Dorsal girdle surface without long hyaline spicules 2
2. Mucro slightly anterior; post-mucronal slope decidedly concave, especially in adult (> 5 mm length) specimens. Eaves not spongy. Side-slopes of

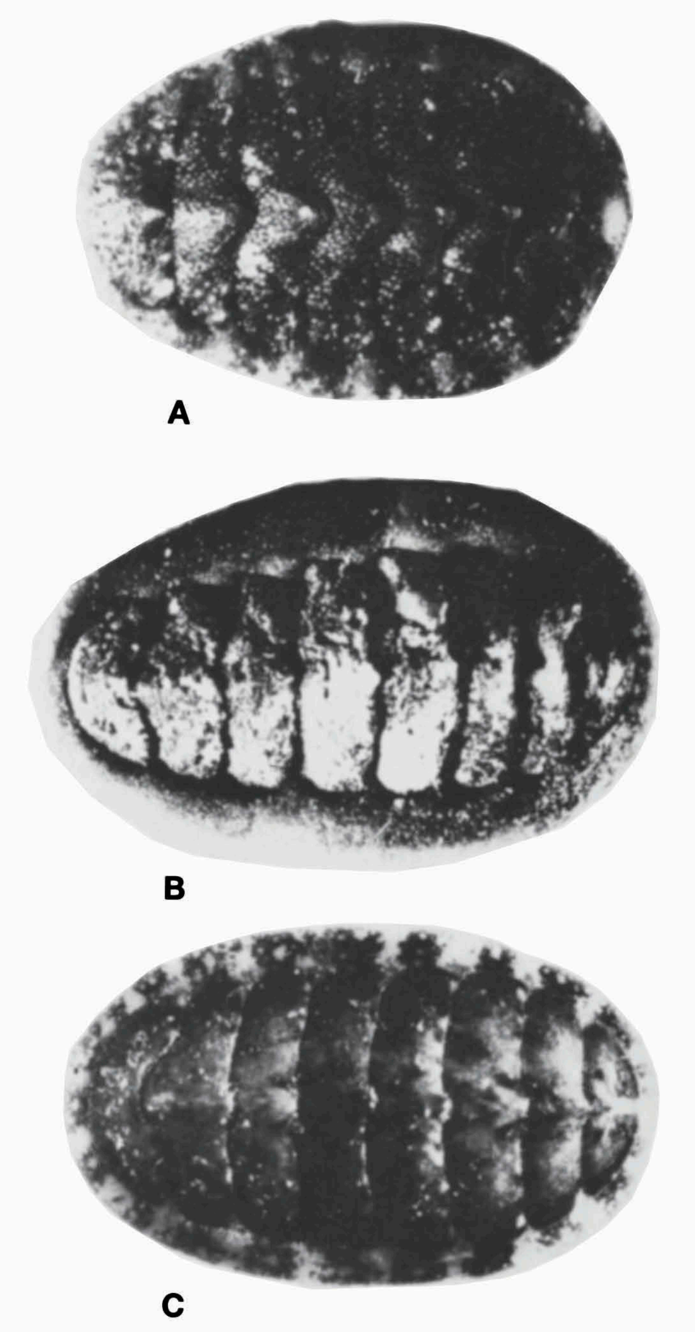


Plate 1. Holotype specimens of (A) *Lepidochitona caverna* spec. nov.; (B) *L. fernaldi* spec. nov.; (C) *L. berryana* spec. nov.

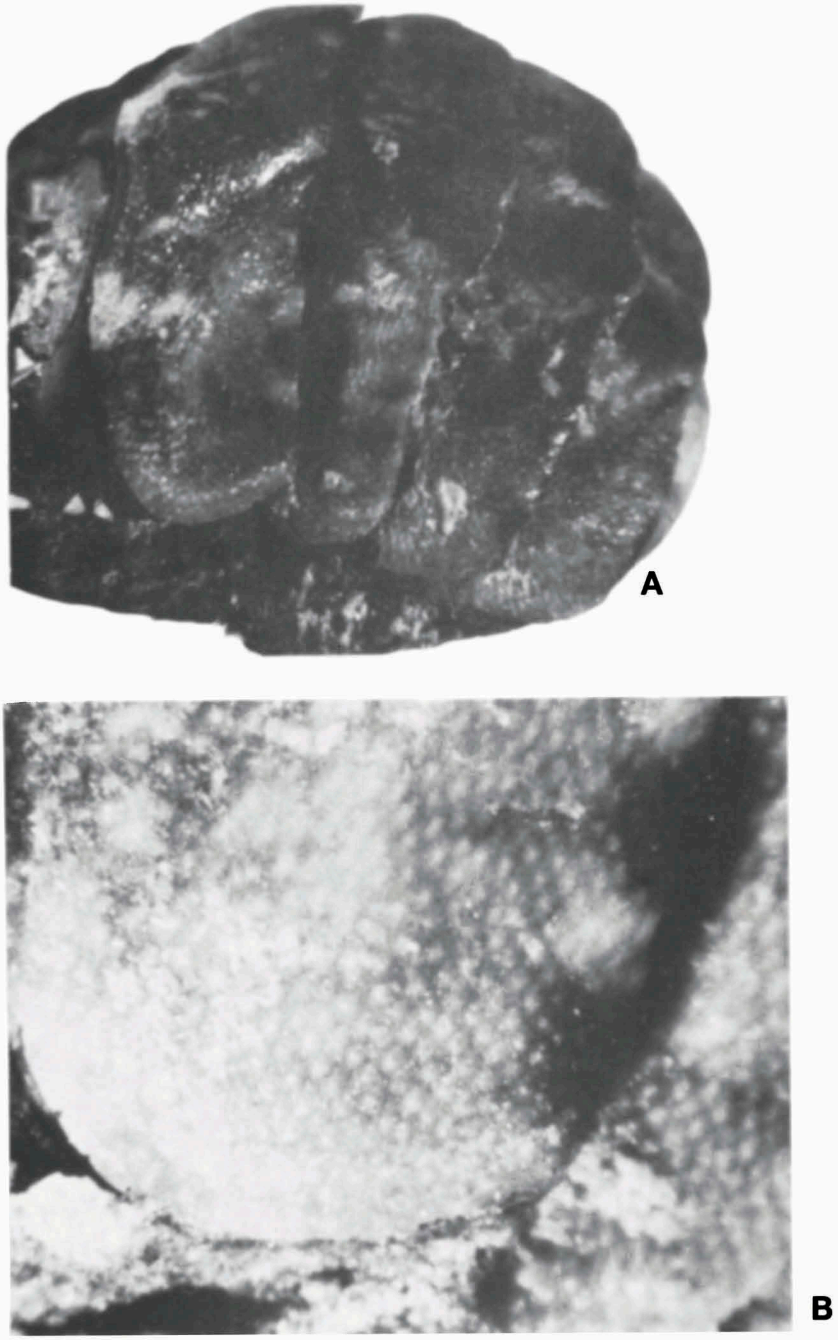


Plate 2. *Chiton dentiens* Gould holotype (A) and close-up (B).

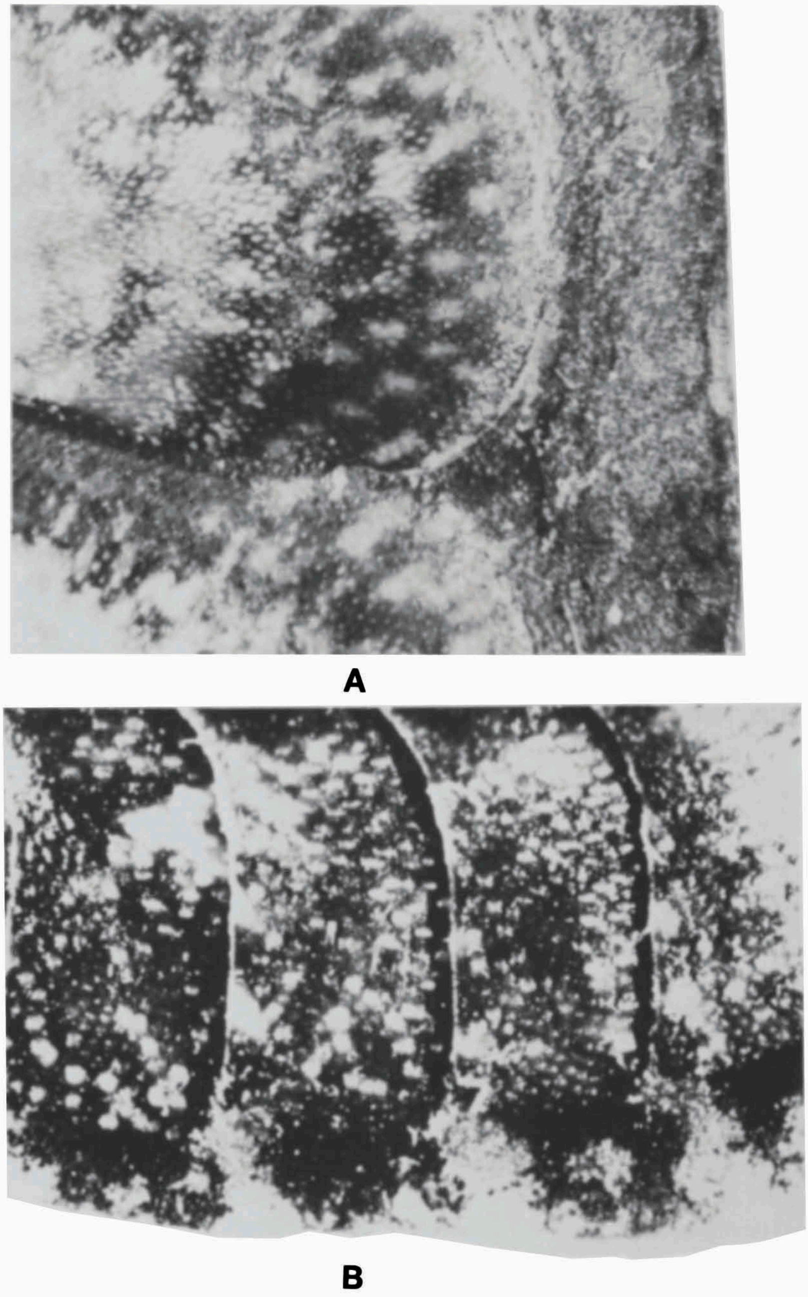


Plate 3. Close-up views of intermediate valves and girdle — (A) *Trachydermon raymondi* Pilsbry lectotype; (B) *Lepidochitona caverna* spec. nov. holotype.

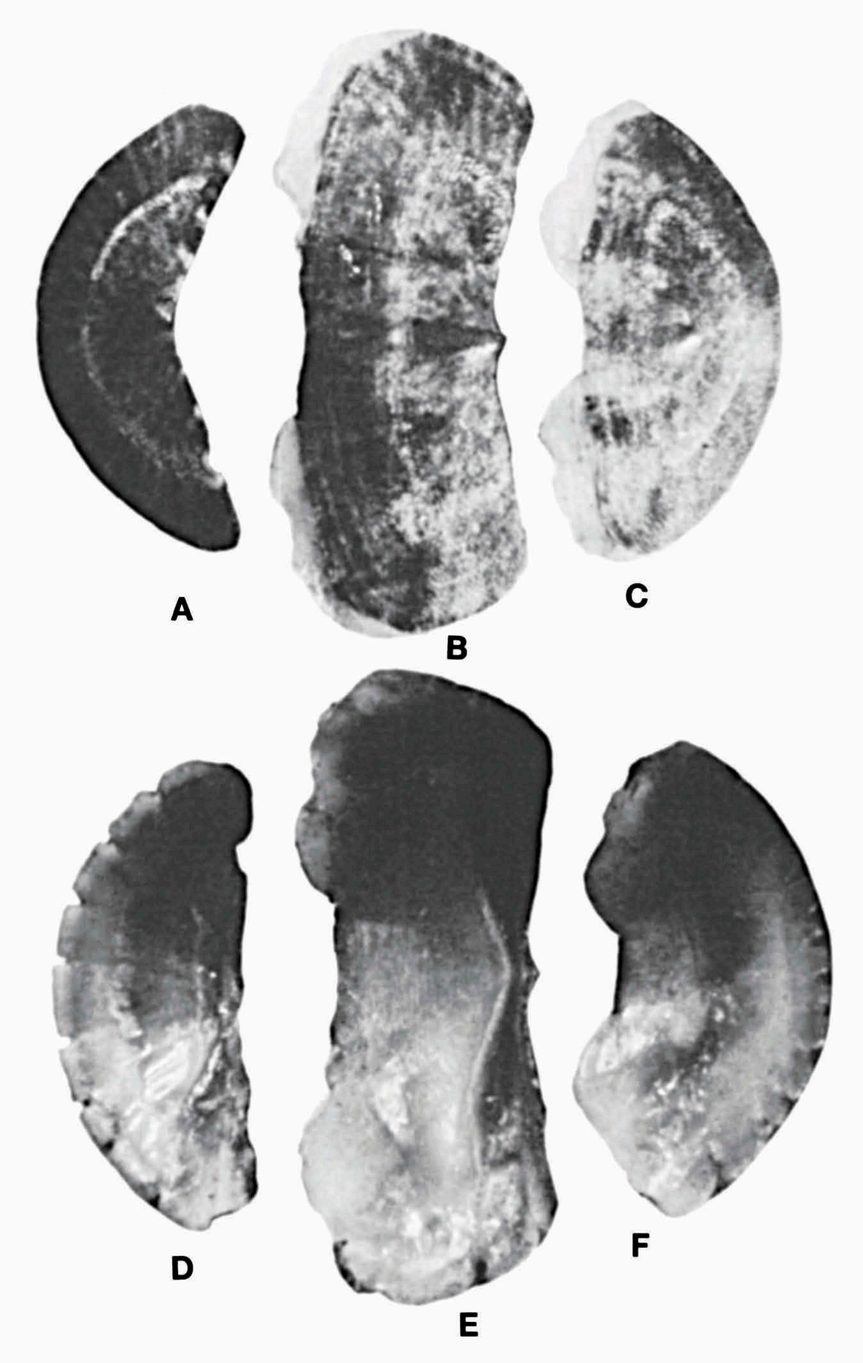


Plate 4. *Trachydermon raymondi* Pilsbry paralectotype (disarticulated valves i, ii, and vii) — (A-C) dorsal view; (D-F) ventral view.

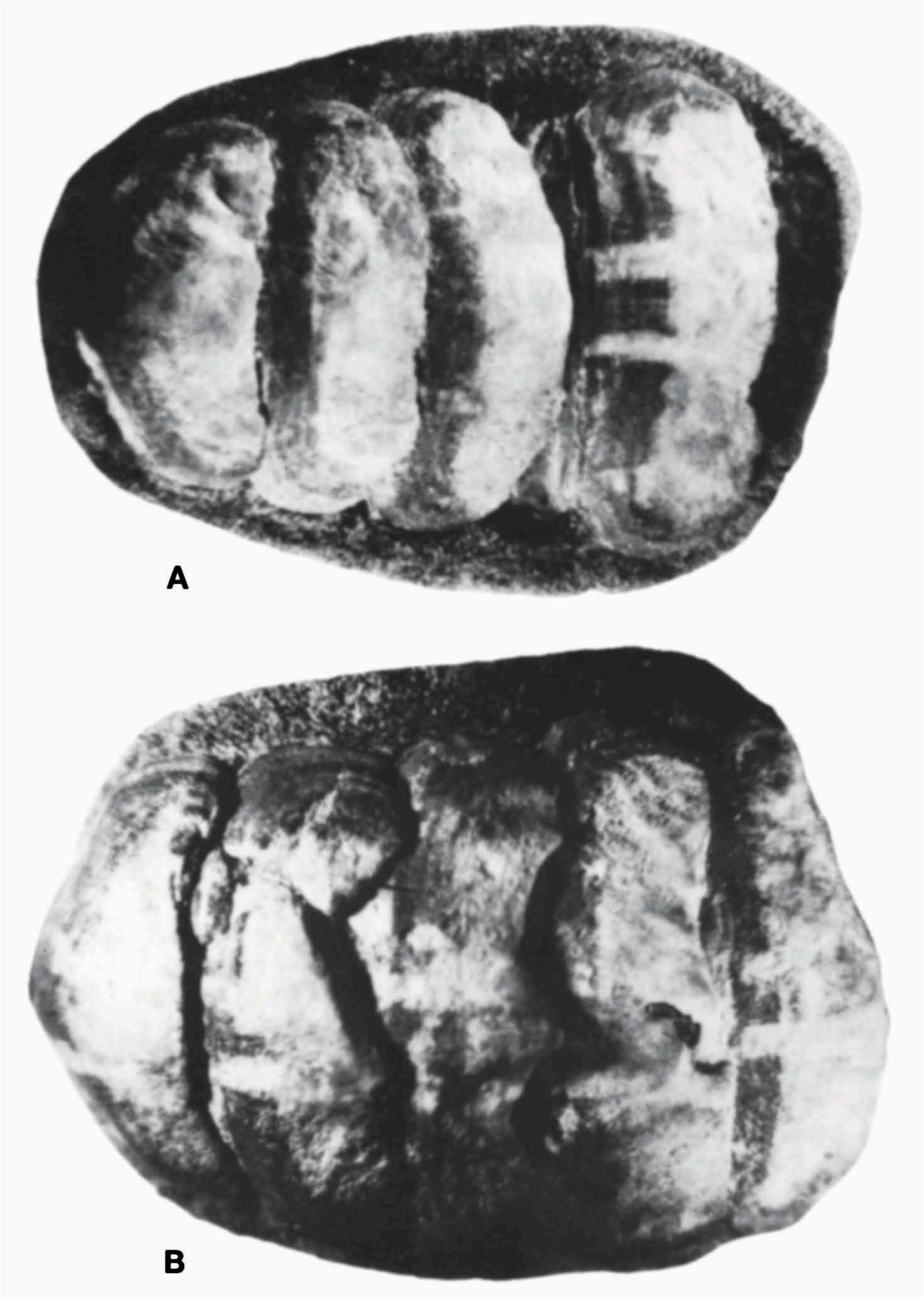


Plate 5. *Nuttallina thomasi* Pilsbry — (A) lectotype; (B) paralectotype (disarticulated valves for both specimens shown in Plate 6).

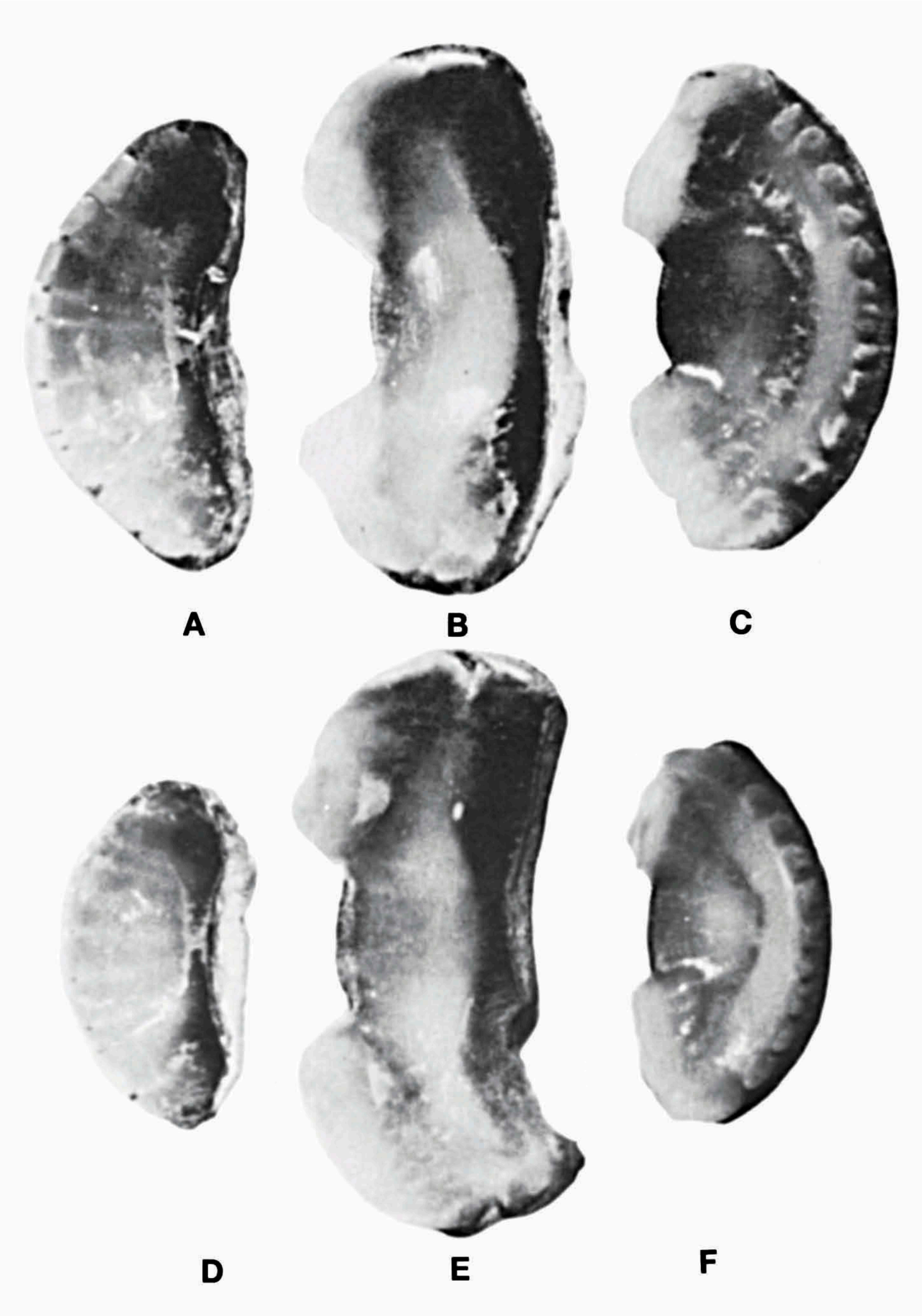


Plate 6. *Nuttallina thomasi* Pilsbry — (A) lectotype (disarticulated valves i, v, and viii, ventral view); (B) paralectotype (disarticulated valves i, vii, and viii, ventral view).

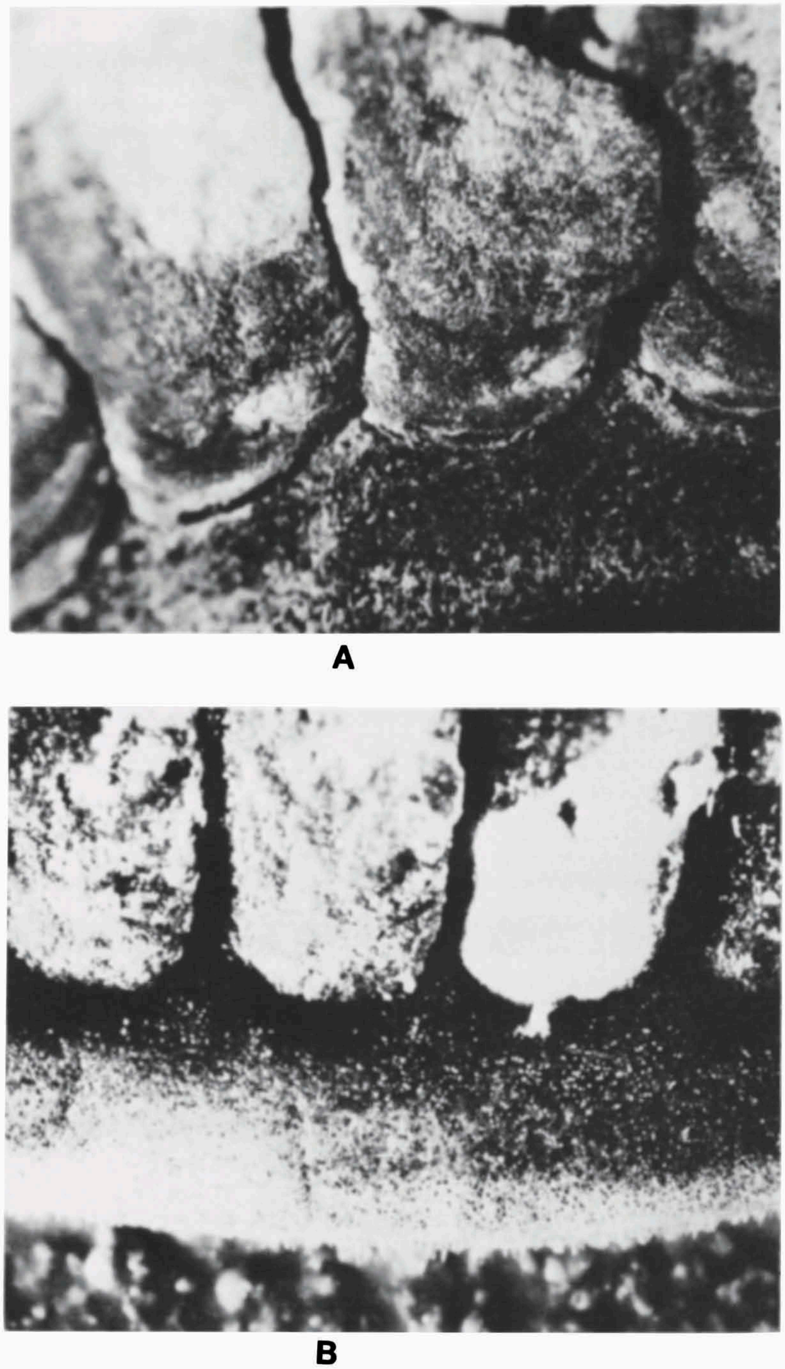
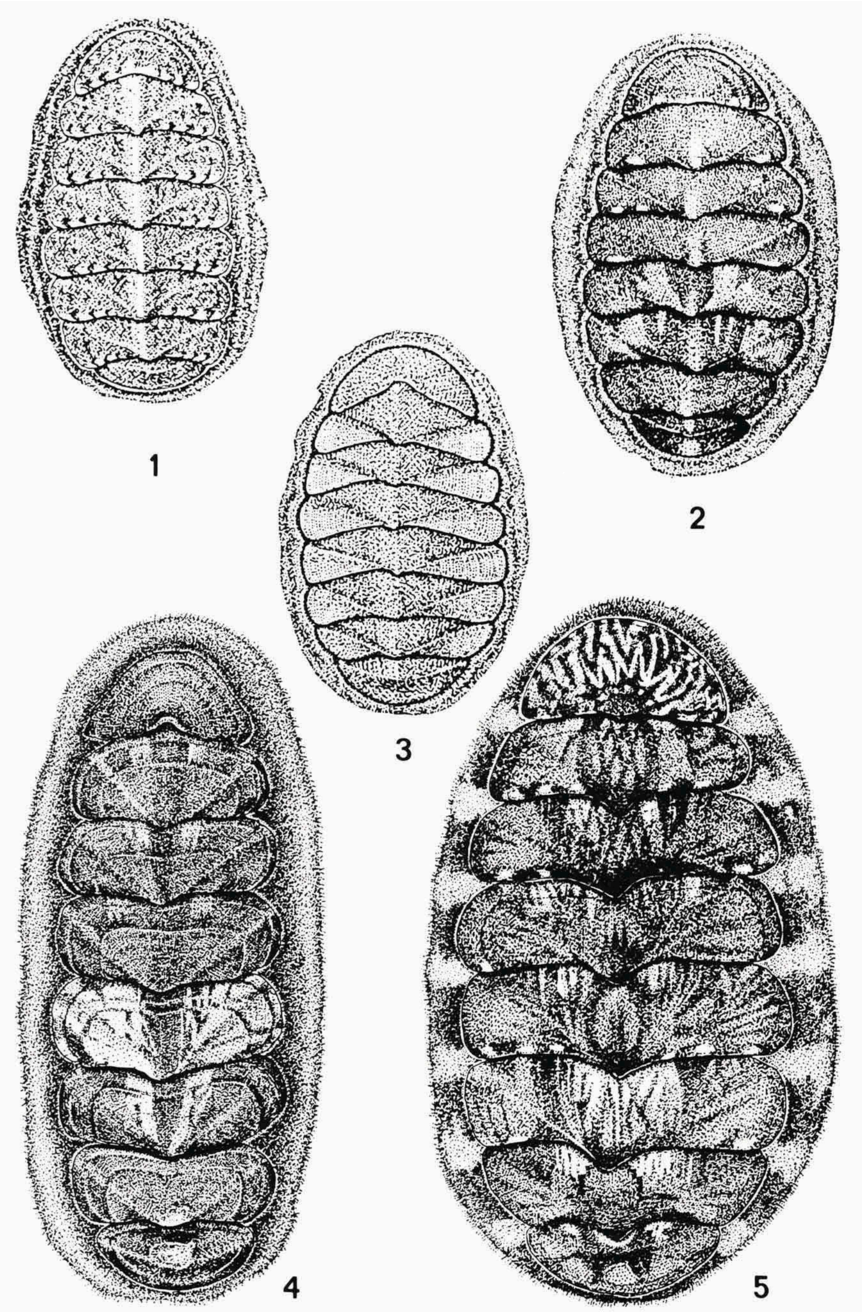
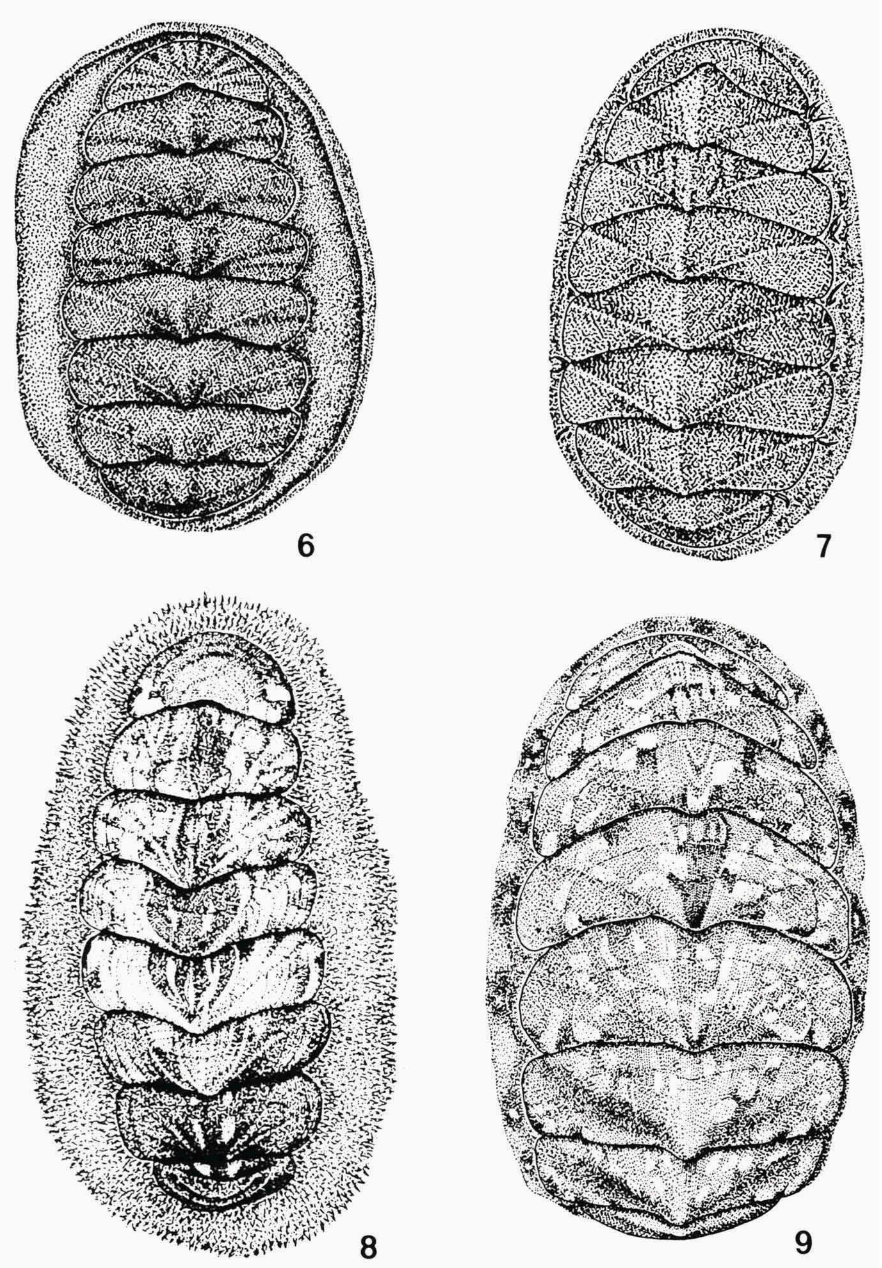


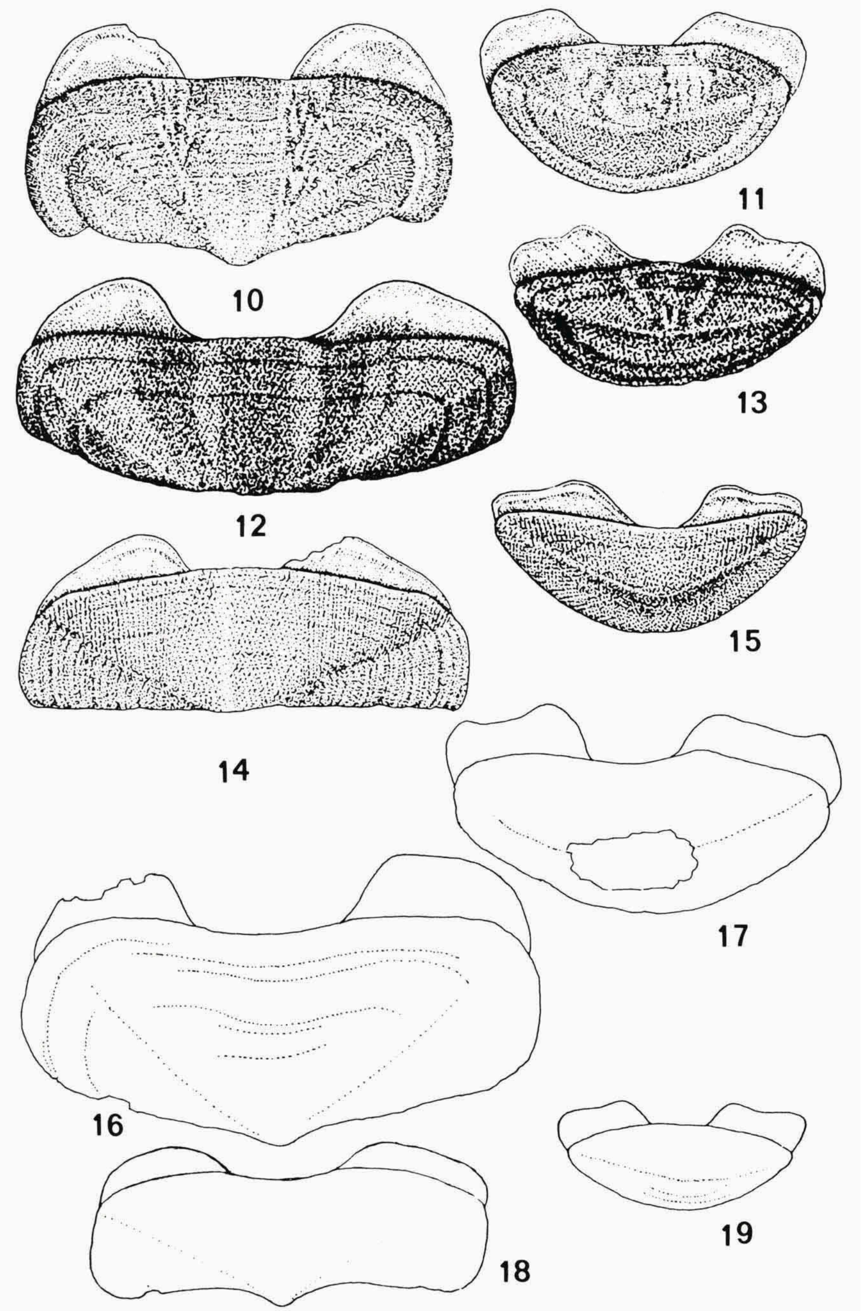
Plate 7. Close-up views of intermediate valves and girdle — (A) *Nuttallina thomasi* Pilsbry paralectotype; (B) *Lepidochitona fernaldi* spec. nov. holotype.



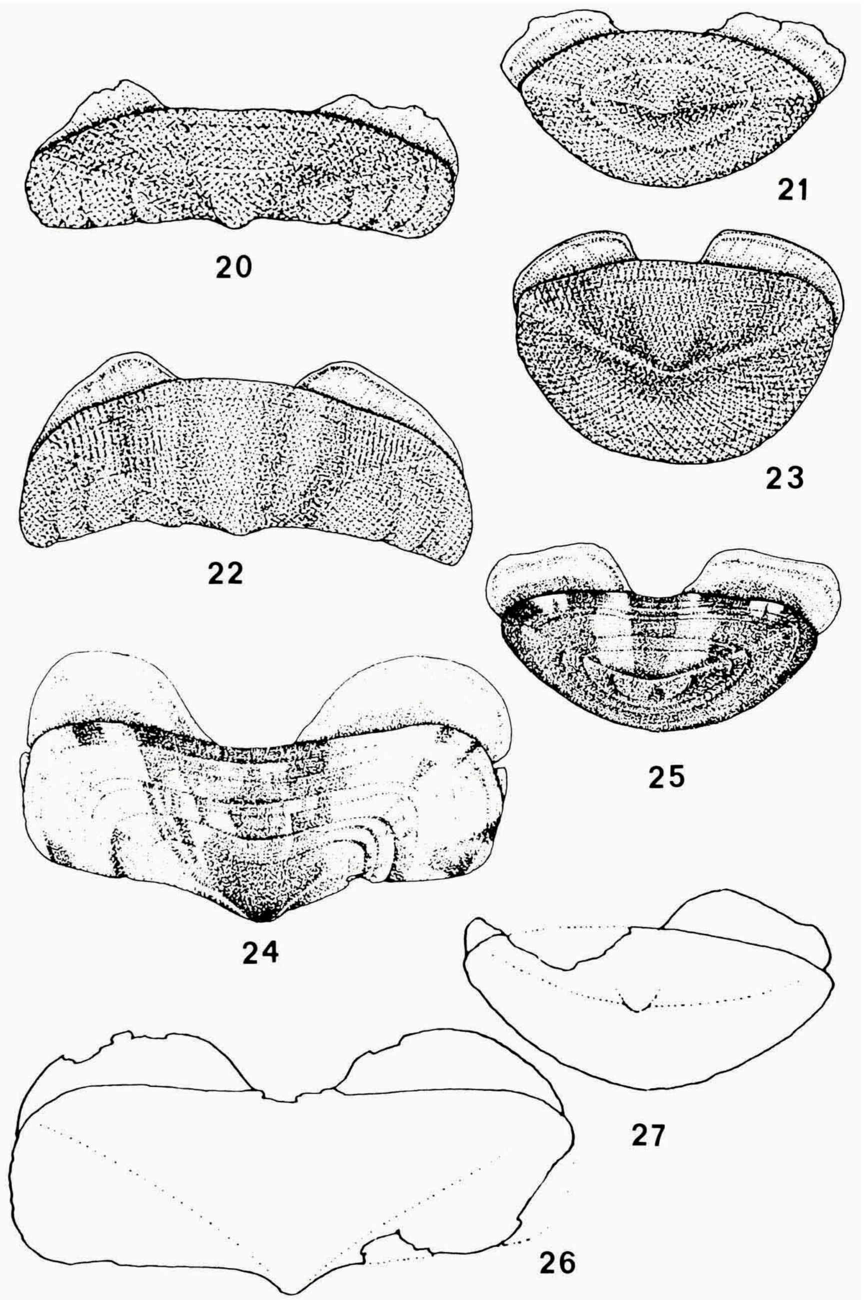
Figs. 1-5. Complete specimens (dorsal view) of: 1, *Lepidochitona dentiens* (Gould, 1846), × 3.95; Cape Alava, Washington, W. E. Rice leg., VB 2555b. 2, *L. hartwegii* (Carpenter, 1855), × 2.82; Pt. Fermin, San Pedro, California, J. Williams leg., VB 2515b. 3, *L. keepiana* Berry, 1948, × 3.95; Newport Bay, California, E. P. Chace leg., VB 2623b. 4, *L. fernaldi* spec. nov., × 7.9; W. San Juan Is., San Juan Co., Washington, D. J. Eernisse leg., RMNH K 5054. 5, *L. caverna* spec. nov., × 8.4; W. Santa Cruz, Santa Cruz Co., California, D. J. Eernisse leg., RMNH K 5055.



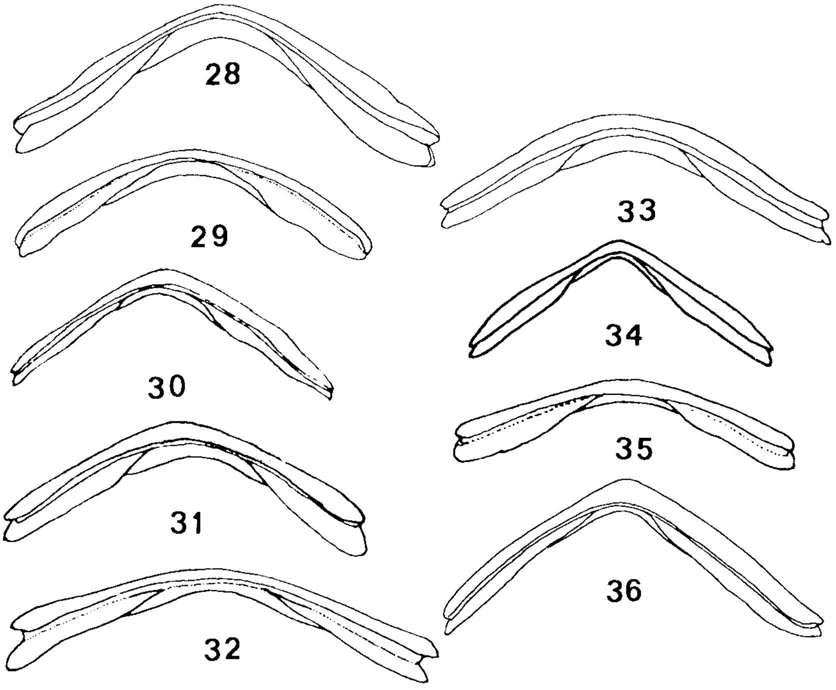
Figs. 6-9. Complete specimens (dorsal view) of: 6, *L. lowei* (Pilsbry, 1932), × 4.2; San Pedro, California, E. P. Chace leg., VB 2671b. 7, *L. beanii* (Carpenter, 1857), × 8.4; Bahia de San Francisquita, Gulf of California, A. J. Ferreira leg., K 4894. 8, *L. thomasi* (Pilsbry, 1898), × 8.4; Big Creek, Monterey Co., California, D. J. Eernisse leg., K 4997. 9, *L. berryana* spec. nov., × 8.4; 41st Ave, Santa Cruz Co., California, D. J. Eernisse leg., RMNH K 5053.



Figs. 10-19. Intermediate valve (iv-vi) and tail valve (viii) of: 10-11, *L. dentiens* (Gould, 1846), × 11.3; Olympic Peninsula, Washington, S. Welty leg., VB 2555a. 12-13, *L. hartwegii* (Carpenter, 1855), × 5.64; Shell Beach, California, G. Burghardt leg., VB 2515a. 14-15, *L. keepiana* Berry, 1948, × 7.9; San Onofre, California, D. Myhre leg., VB 2623a. 16-17, *L. fernaldi* spec. nov. × 16; W. San Juan Is., San Juan Co., Washington, D. J. Eernisse leg., VB. 18-19, *L. caverna* spec. nov., × 16; W. Santa Cruz, Sant Cruz Co., California, D. J. Eernisse leg., VB.



Figs. 20-27. Intermediate valve (iv-vi) and tail valve (viii) of: 20-21, *L. lowei* (Pilsbry 1918), × 11.3; Pt. Fermin, California, E. P. Chace leg., VB 2617a. 22-23, *L. beanii* (Carpenter, 1857), × 16.5; San Felipe, Gulf of California, E. P. Chace leg., VB 2631a. 24-25, *L. thomasi* (Pilsbry, 1898), × 16.5; Big Creek, Monterey Co., California, D. J. Eernisse leg., VB 2751b. 26-27, *L. berryana* spec. nov., × 11.3; 41st Ave, Santa Cruz Co., California, D. J. Eernisse leg., VB.



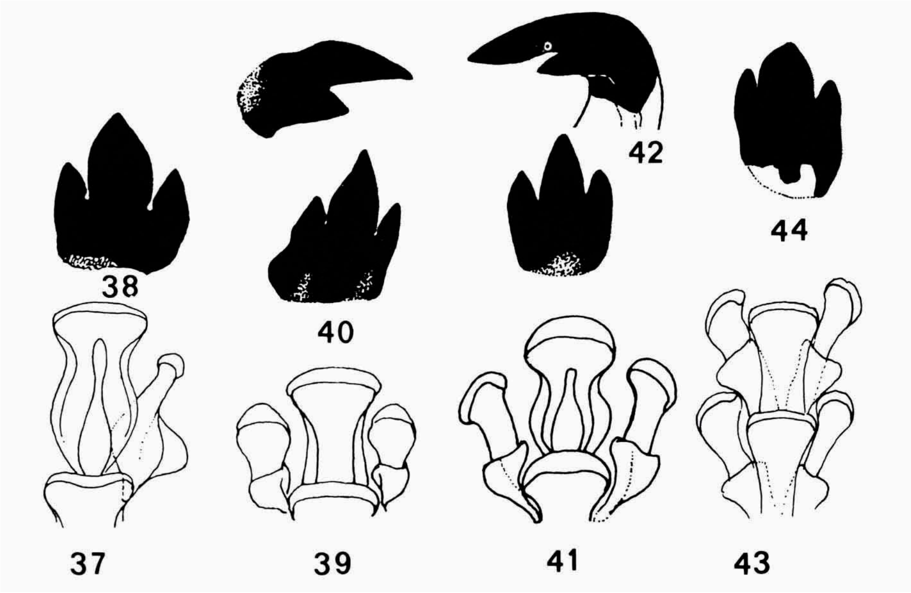
Figs. 28-36. Rostral view of intermediate valve, camera lucida sketch, (same data as for figs. 10-27) of: 28, *L. dentiens* (Gould, 1846), X 7.9. 29, *L. hartwegii* (Carpenter, 1855), X 3.95. 30, *L. keepiana* Berry, 1948, x 5.93. 31, *L. fernaldi* spec. nov., x 11.58. 32, *L. caverna* spec. nov., x 11.59. 33, *L. lowei* (Pilsbry, 1918), x 7.9. 34, *L. beanni* (Carpenter, 1857), x 11.61. 35, *L. thomasi* (Pilsbry, 1898), x 11.62. 36, *L. berryana* spec. nov., x 7.9.

intermediate valves straight. Articulamentum translucent white............3

Mucro central to near posterior margin; post-mucronal slope approximately flat to slightly convex, occasionally slightly concave. Eaves spongy. Side slopes of intermediate valves convex. Articulamentum colored, usually blue or golden..4

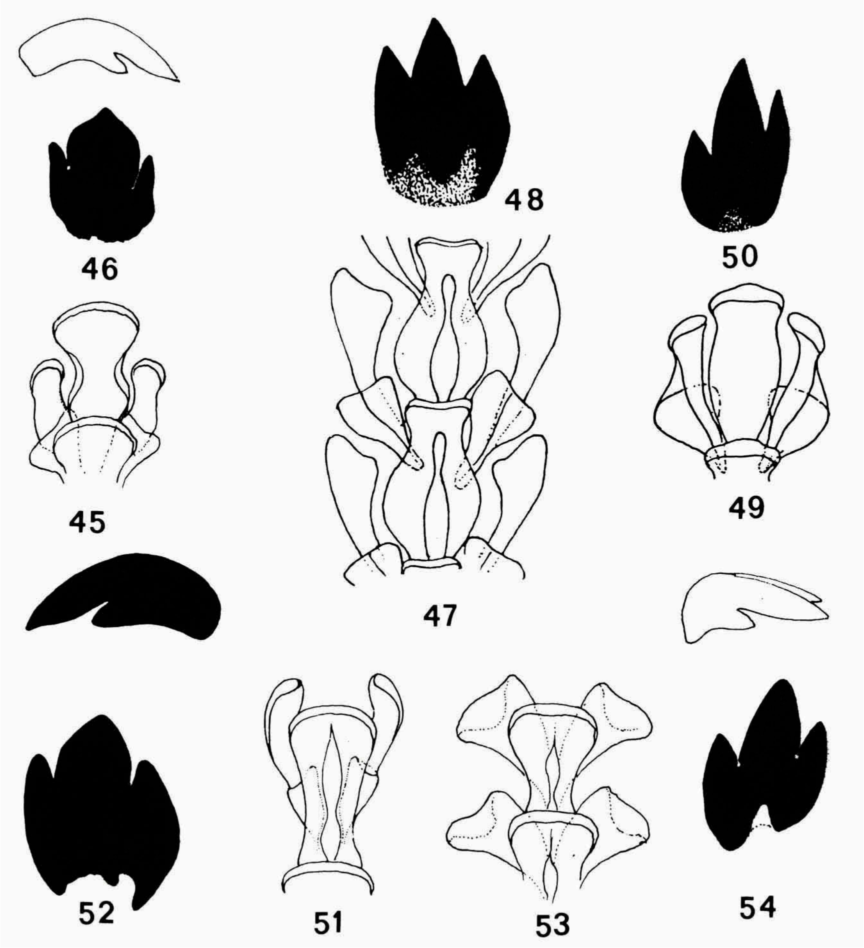
3. Dorsal girdle elements visible as very small stout spicules (about 125 μm long). Intermediate valves beaked only in juveniles (> 5 mm length). Usually eroded or unbeakened in larger specimens. Slit formula 9/13 - 1 - 10/14. Tegmentum coloration variable, but never with blue lines or spots ....*L. keepiana*

– Dorsal girdle elements extremely minute (about 30 μm long stout spiculoid granules). Valves 2 to 8 beaked. Slit formula 8/10 - 1 - 8/11. Tegmentum invariably colored rusty orange, with bright blue zig-zagging lines, also with small patches of white and black, often with a white stripe projecting posteriorly from the mucro..*L. berryana*



Figs. 37-44. Central and first lateral radula teeth = cusp of major lateral tooth (same data as for figs. 10-27) of: 37-38, *L. dentiens* (Gould, 1846), × 330. 39-40, *L. hartwegii* (Carpenter, 1855), × 330, 41-42, *L. keepiana* Berry, 1948, × 235. 43-44, *L. fernaldi* spec. nov., × 330.

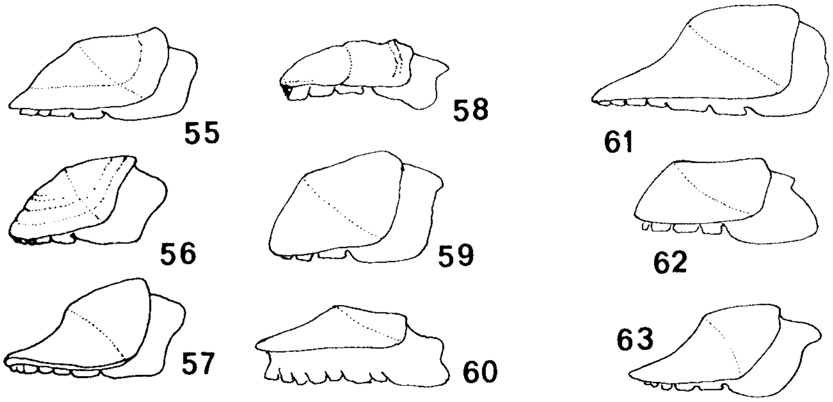
4. Lateral areas of intermediate valves with irregular, warty granules scattered among otherwise regular granular sculpturing. Color usually greenish or olivaceous 5
– Tegmental sculpturing of regular and evenly spaced granules, sometimes heavily eroded. Color various 6
5. Gills holobranchial, about 25 per side in specimens about 1 cm in length, to about 35 per side in adults from 2 to over 4 cm length. Frequently exceeding 15 mm in length. Body profile broadly oval. Dorsal elevation low. Color olivaceous with lack markings on both sides of central areas .... *L. hartwegii*
– Gills merobranchial, extending about 80 to 90 percent of foot length, 10 to 22 per side. Often brooding eggs in these pallial grooves. Small adult size, not exceeding 15 mm length. Body profile usually oval-elongate. Dorsal elevation medium. Color green or more rarely maroon with white markings that are usually most pronounced on both sides of valve 5 .... *L. caverna*
6. Head valve with radiating ribs, body outline oval and extremely broad .... *L. lowei*
– Head valve without ribs, body outline oval-elongate with nearly parallel sides 7
7. Mucro nearly central, posterior margin not greatly thickened. Insertion teeth of posterior valve flattened and approximately regular, directed



Figs. 45-54. Central and first lateral radula teeth = cusp of major lateral tooth (same data as for figs. 10-27) of: 45-46, *L. caverna* spec. nov., × 330. 47-48, *L. lowei* (Pilsbry, 1918), × 235. 49-50, *L. beanii* (Carpenter, 1857), × 330. 51-52, *L. thomasi* (Pilsbry, 1898), × 330. 53-54, *L. berryana* spec. nov., × 330.

outwards. Slit rays of this valve defined by pores in the articulamentum. Tegmental granules densely packed, valves rarely eroded. Coloration complex and extremely variable, usually with blue flecks. Girdle generally light, often with darker bands alternating with light areas, or with light spots; never spiny appearing. Not brooding; mature eggs about 210 μm in diameter surrounded by transparent cone-shaped projections. Most common in low intertidal, although present in high tidepools....... *L. dentiens*

– Mucro nearly terminal so that posterior margin is thickened. Insertion teeth of posterior valve stout and irregular, lateral teeth directed ventrally.



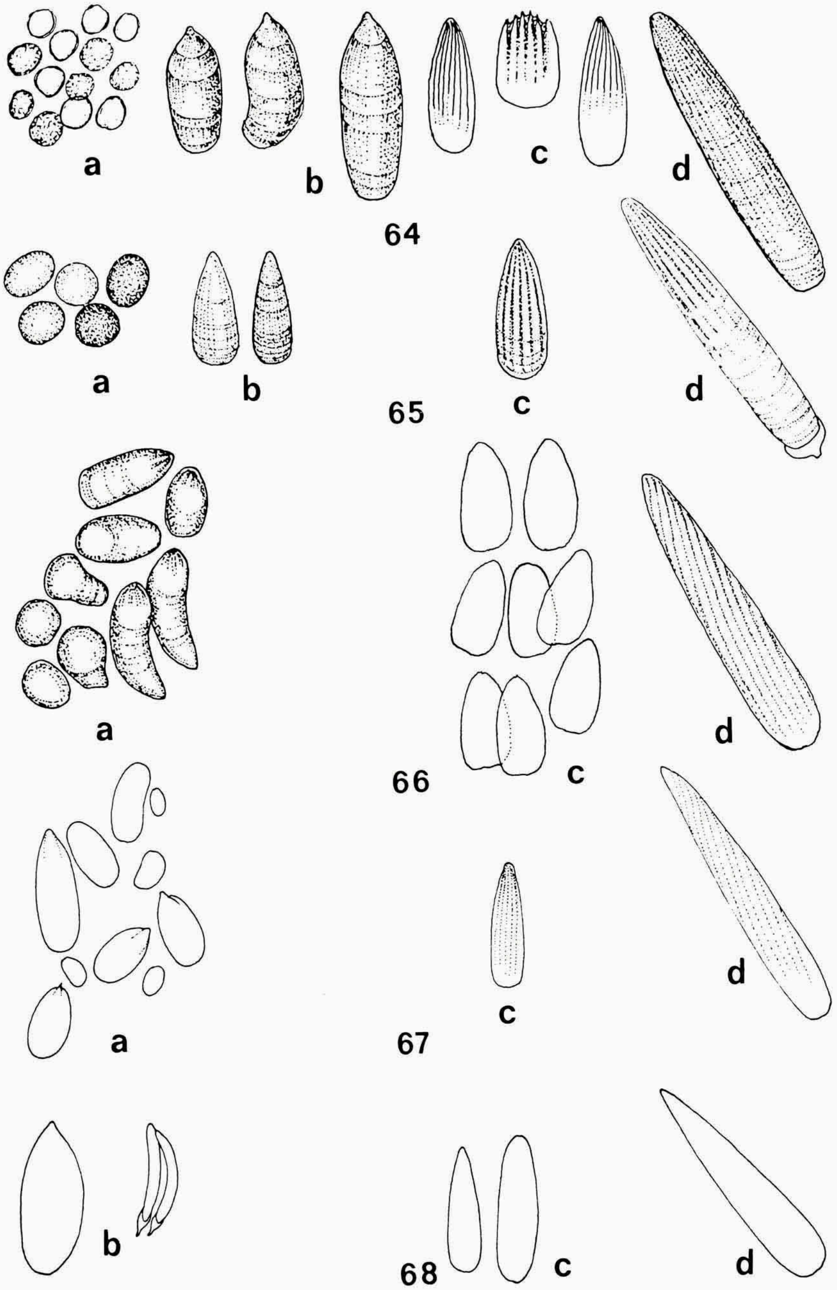
Figs. 55-63. Lateral view of valve viii, camera lucida sketch (same data as for figs. 10-27) of: 55, *L. dentiens* (Gould, 1846), × 7.9. 56, *L. hartwegii* (Carpenter, 1855), × 6.57, *L. keepiana* Berry, 1948, × 7.9. 58, *L. fernaldi* spec. nov. (Eernisse del.) 59, *L. caverna* spec. nov. (Eernisse del.) 60, *L. lowei* (Pilsbry, 1918),× 11.85.61, *L. beanii* (Carpenter, 1857),× 16.5.62, *L. thomasi* Pilsbry, 1898),× 7.9.63, *L. berryana* spec. nov., × 7.9.

Slit rays of this valve apparent only in juveniles, with central area in ventral view depressed in larger specimens. Valves often eroded, tegmental sculpturing, when apparent, composed of even but well spaced granules. Color of tegmentum generally dark, without blue flecks. Girdle generally dark or, when light, relatively uniform in color. Often brooding rod-shaped egg masses composed of smooth eggs about 260 to 280 µm in diameter. Foot often shows orange tint in living specimens. Restricted to high intertidal. Locally abundant 8

8. Dorsal girdle "spiny," with some elongate spicules, about 120 µm long, 30 µm wide, with blunt distal ends, scattered among much shorter stout spicules, about 30 µm long, and half as wide. Gill row extending 85 to 95 percent of foot length, with 18 to 30 gills per side, increasing with size .... *L. thomasi*

– Dorsal girdle elements more even in size, composed of stout elongate spicules usually not exceeding 75 µm length. Gill row extending only 60 to 75 percent of foot length, with 8 to 17 gills per side, again increasing with size .... *L. fernaldi*

Figs. 64-68. Girdle elements, respectively, a. dorsal calcareous corpuscules or spicules in situ, b. do., isolated, c. ventral scales, d. marginal spicules (same data as for figs. 10-27) of: 64, *L. dentiens* (Gould, 1846), a × 165, b - d × 330. 65, *L. hartwegii* (Carpenter, 1855), a-d, × 330. 66, *L. keepiana* Berry, 1948, a-d × 330. 67, *L. fernaldi* spec. nov., a-d, × 330. 68, *L. caverna* spec. nov., a-d, × 330.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ACKNOWLEDGEMENTS

For the loan of specimens in their care, I am indebted to: Drs. Barry Roth and Daphne F. Dunn (CAS), Dr. James H. McLean (LACM), Dr. Arthur E. Bogan (ANSP), Dr. Joseph Rosewater (USNM), Dr. Solene Morris (BMNH), Mr. Anthony D' Attilio (SDNH), and Dr. Russell H. Jensen (DMNH), Mr. Roger N. Clark also provided many useful specimens.

I was also extremely fortunate to have the many fine drawings in this work prepared by Mr. Piet Kaas (RNMH). His generosity is surpassed only by his ability to clearly see and draw chitons. He and his collaborator, Mr. R. A. Van Belle, of Sint-Niklaas, Belgium, were also extremely helpful in various other aspects of this work, as was Dr. Antonio J. Ferreira (CAS).

Several people provided useful comments on my manuscript, including: Dr. John S. Pearse (Univ. Calif., Santa Cruz), Drs. Barry Roth and Michael T. Ghiselin (CAS), Dr. David R. Lindberg (Univ. Calif., Berkeley), and Ms. Dorothy F. Sly (Sonoma, Calif.).

This work partially fulfilled the requirements for my Ph. D. dissertation at the Univ. Calif., Santa Cruz. I thank Dr. William Doyle, Director of the Institute of Marine Sciences, UCSC, for partial support during my graduate studies. Grants were also received from the Western Society of Malacologists, and the American Museum of Natural History (Lerner-Gray Fund for Marine Research). Final revisions of this manuscript were completed while supported by a postdoctorate fellowship from Friday Harbor Laboratories, University of Washington, Dr. A. O. D. Willows, Director.

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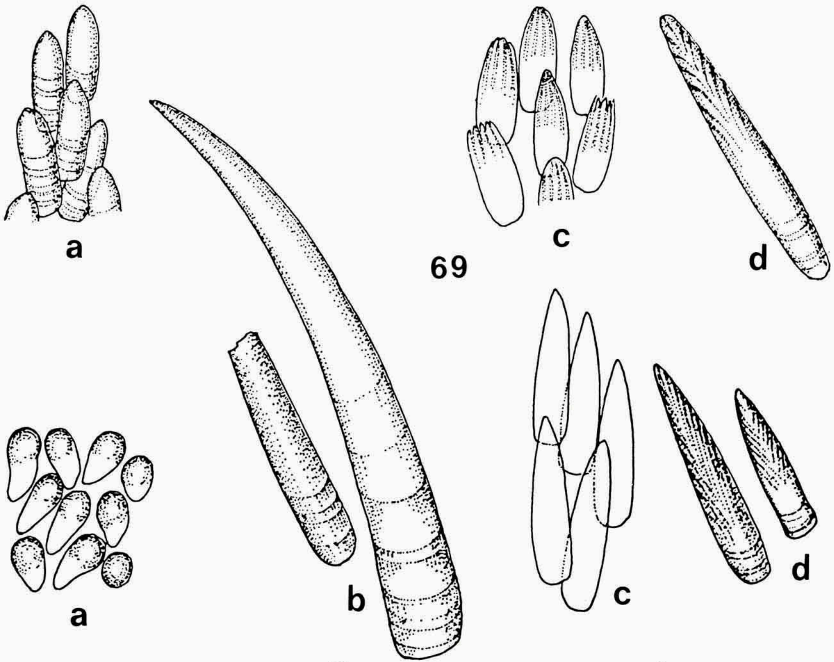
Figs. 69-72. Girdle elements, respectively, a. dorsal calcareous corpuscules or spicules in situ, b. do., isolated, c. ventral scales, d. marginal spicules (same data as for figs. 10-27) of: 69, *L. lowei* (Pilsbry, 1918), a-d, × 330. 70, *L. beanii* (Carpenter, 1857), a-d, × 330 (b small dorsal spicule and large intersegmental spine). 71, *L. thomasi* (Pilsbry, 1898), a, × 165, b-d, × 330. 72, *L. berryana* spec. nov. a-d, × 330.



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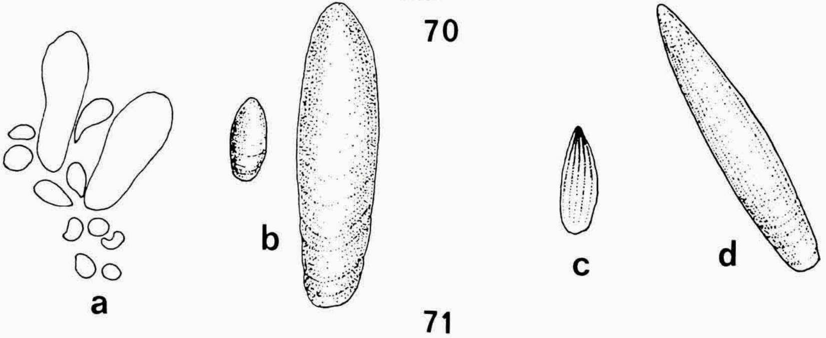

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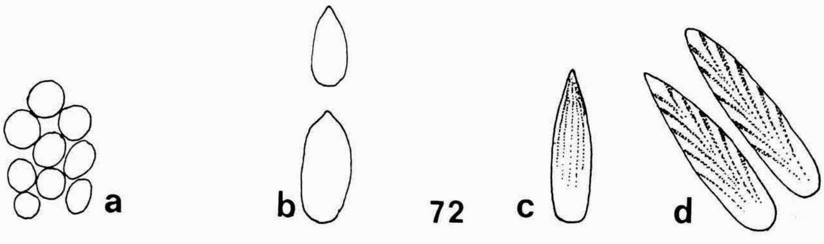

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