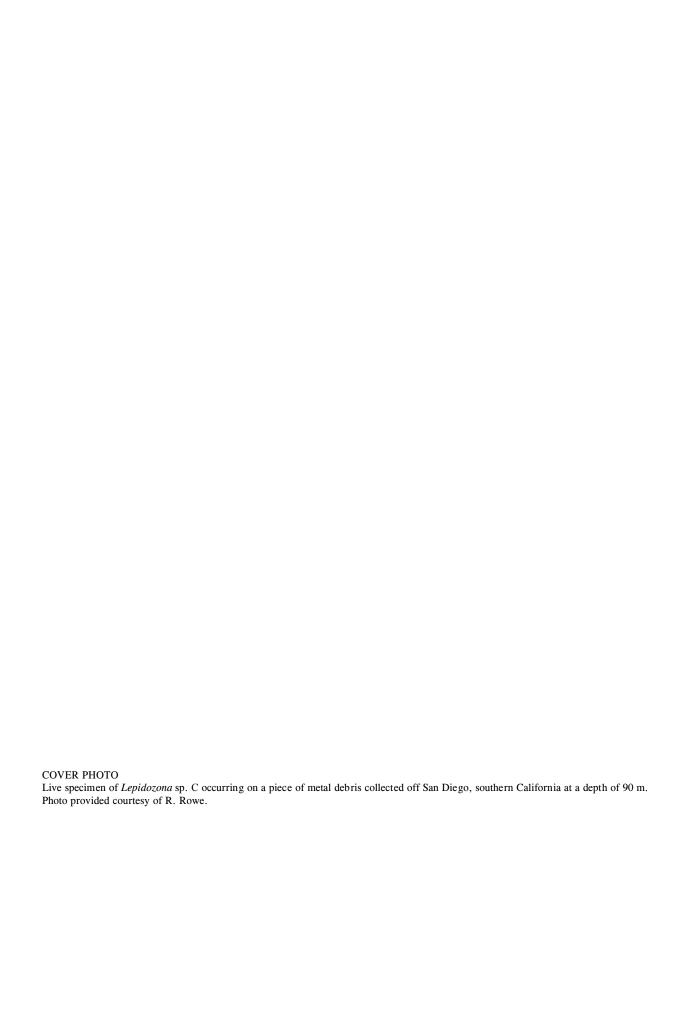
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Chitons (Mollusca: Polyplacophora)
Known from Benthic Monitoring Programs
in the Southern California Bight

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CHITONS (MOLLUSCA: POLYPLACOPHORA) KNOWN FROM BENTHIC MONITORING PROGRAMS IN THE SOUTHERN CALIFORNIA BIGHT

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Abstract: About 36 species of chitons possibly occur at depths greater than 30 m along the continental shelf and slope of the Southern California Bight (SCB), although little is known about their distribution or ecology. Nineteen species are reported here based on chitons collected as part of long-term, local benthic monitoring programs or less frequent region-wide surveys of the entire SCB, and these show little overlap with species that occur at depths typically encountered by scuba divers. Most chitons were collected between 30-305 m depths, although records are included for a few from slightly shallower waters. Of the two extant chiton lineages, Lepidopleurida is represented by Leptochitonidae (2 genera, 3 species), while Chitonida is represented by Ischnochitonidae (2 genera, 6-9 species) and Mopaliidae (4 genera, 7 species). The lepidopleurids Leptochiton rugatus and Hanleyella oldroydi are two of the most common chitons, accounting for ~35% of all SCB specimens, while a second recognized species of Leptochiton, L. nexus, is also reported. Lepidozona (Chitonida: Chitonina: Ischnochitonidae) is the most diverse genus in this study, represented by L. golischi, L. mertensii, L. radians, L. retiporosa, L. scrobiculata, and three provisional species (Lepidozona spp. A-C). Of these, L. retiporosa and L. scrobiculata are most common, together comprising ~29% of the chitons sampled. Callistochiton (Ischnochitonidae) is represented by C. palmulatus. Mopaliidae (Chitonida: Acanthochitonina) is represented by Dendrochiton gothicus, D. thamnoporus, Mopalia imporcata, M. lowei, M. phorminx, Placiphorella mirabilis, and Tonicella venusta. Details are presented of the distribution, abundance, size, and co-occurrence of the observed chiton species, and a key is provided to those species expected to live within the studied depths of the SCB. Additionally, several species not collected during this study but considered likely to occur or as dubious records are discussed.

Introduction

Chitons (Mollusca: Polyplacophora) are a diverse and ancient group of marine mollusks, which include more than 940 living (Schwabe, 2005; D. J. Eernisse, unpublished compilation) and about 430 fossil (Puchalsky et al., 2008) recognized species worldwide. Although chitons occur from the intertidal to deep ocean trenches, most faunal and ecological studies have focused on relatively shallow water species. For example, the chitons living in intertidal to shallow subtidal habitats along the ecologically diverse western coast of North America (West Coast) are fairly well known, having been covered in a number of regional or site specific natural history guides, taxonomic keys, or other useful sources (e.g., Burghardt & Burghardt,

1969; Brusca et al., 1971; Smith, 1975; Allen, 1976; Brusca & Brusca, 1978; McLean, 1978; Haderlie & Abbott, 1980; Putman, 1980; Kozloff, 1983, 1996; O'Clair & O'Clair, 1998; Slieker, 2000; Lamb & Hanby, 2005; Eernisse et al., 2007). In contrast, with the exception of the preliminary study by Eernisse (1998), no studies have specifically addressed the chiton fauna occurring at depths > 30 m of this region. This cutoff depth is visited only rarely by scuba divers and few of the species seen by divers or in the intertidal occur below 30 m.

More than 30 species of chitons representing 15 genera and six families are likely to occur in waters deeper than 30 m along the continental shelf and slope

of the Southern California Bight (SCB), which ranges from Point Conception, California, USA to Cabo Colonet, Baja California, México (see Table 1). Except for general geographic and bathymetric range information listed in monographs and other taxonomic works (e.g., Ferreira, 1978, 1979a, 1979b, 1982, 1983; Kaas & Van Belle, 1985a, 1985b 1987, 1990, 1994; Watters, 1990; Clark, 1994, 1999), little information is available concerning the presence of many species in these relatively deep southern California waters. Much of the shelf and slope benthos of the region is composed of soft sediments, which are the focus of several large benthic monitoring programs associated with major municipal wastewater outfalls (see City of Los Angeles, 2007, 2008; Orange County Sanitation District, 2007; City of San Diego, 2008a, 2008b; Los Angeles County Sanitation Districts, 2008). Although soft sediments are typically considered unsuitable habitat for chitons, the presence of various types of hard substrates scattered across the sea floor provides refuges for these animals and also exposes them to incidental capture by regular benthic or epibenthic sampling activities (e.g., Mullineaux, 1987; Eernisse, 1998). In southern California, these chiton microhabitats often include small rocks, rocky outcroppings or reefs, mollusk shells and shell fragments, as well as man-made debris such as bottles, cans, and larger pieces of glass, metal, plastic or even rubber (TDS, personal observation). This study summarizes the SCB benthic chiton fauna collected by the above monitoring programs over the past two decades or more.

Methods

Most of the chitons examined in this study were collected as part of the long-term ocean monitoring programs conducted by the City of San Diego, City of Los Angeles, Los Angeles County Sanitation Districts, and Orange County Sanitation District. Additional specimens were collected by these or other agencies during several large-scale regional monitoring projects that spanned the entire SCB. These bight-wide surveys included the 1994 Southern California Bight Pilot Project (SCBPP) and subsequent Bight'98, Bight'03 and Bight'08 regional monitoring efforts in 1998, 2003 and 2008, respectively (e.g., Bergen et al., 1998, 2001; SCBPP, 1998; Ranasinghe et al., 2003, 2007). Samples containing chitons were typically collected using

standard benthic sampling (e.g., Van Veen grabs) or trawling (e.g., otter trawl) gear and procedures. It is worth noting that this sampling has not targeted rocky areas, e.g., using biological (rock) dredge gear, and such future sampling could turn up additional chiton species.

All chitons collected were examined and identified using dissecting and compound microscopes. Body lengths were measured to the nearest 0.1 mm from the anterior-most margin of the girdle in front of valve I (head valve) to the posterior-most girdle margin behind valve VIII (tail valve) with the chitons flattened as much as possible. Lengths for excessively curled or damaged specimens were estimated.

Higher-level chiton systematics and phylogeny have been in a state of flux and the focus of subsequent research for a number of years (e.g., Smith, 1960; Kaas & Van Belle, 1980, 1985a, 1985b, 1987, 1990, 1994, 1998; Van Belle, 1983, 1985, 1999; Eernisse, 1984; Sirenko, 1993, 1997, 2006; Buckland-Nicks, 1995, 2008; Kaas et al., 1998; Okuso et al., 2003). The classification expressed in Table 1 follows Eernisse et al. (2007), which is supported by recent molecular studies by D. J. Eernisse (unpublished; see also Eernisse, 2004a, 2004b, 2006, 2007, 2008a, 2008b; Kelly & Eernisse, 2008; Vendrasco et al., 2008). This arrangement is similar to the recent system proposed by Sirenko (2006) but differs in its reassignment of Dendrochiton and Tonicella to Mopaliidae Dall, 1889, and not Tonicellidae Simroth, 1894, as in Sirenko's classification. Starobogatov & Sirenko (1975) derived Tonicellidae from Simroth's (1894: 321) "Tribus" (= tribe) Tonicelloidea without any proposed change in composition. Simroth (1894) clearly intended this taxon to correspond to one of three "Ischnochitoninae" lineages depicted in Pilsbry's earlier proposed phylogeny (reprinted in Simroth, 1894: 326). Tonicelloidea as envisioned by Pilsbry and Simroth grouped four disparate genera (including Tonicella) whose least inclusive grouping would presently correspond with Chitonida. In contrast, Sirenko's (2006) composition of Tonicellidae is similar to Lepidochitonidae Iredale, 1914, of other authors (e.g., Ferreira, 1982, or as subfamily within Ischnochitonidae in Kaas & Van Belle, 1985b). We use Lepidochitonidae here instead of Tonicellidae because Lepidochitonidae sensu Eernisse et al., 2007, is exclusive of Tonicella, which instead is considered part of Mopaliidae (see

Table 1. Systematics and bathymetric distribution of chitons likely to occur in waters deeper than 30 m in the Southern California Bight (SCB); classification follows Eernisse et al. (2007); * = species reported from SCB benthic monitoring programs; † = not included in key; I = intertidal.

Taxon/Species	Depth Range	Sources ‡
Class Polyplacophora Gray, 1821		
Order Lepidopleurida Thiele, 1910		
Suborder Lepidopleurina Thiele, 1910		
Family Leptochitonidae Dall, 1889		
Hanleyella Sirenko, 1973		
Hanleyella oldroydi (Bartsch MS, Dall, 1919) *	18 - 455 m	7, 10, 13, 24
Leptochiton Gray, 1847		
Leptochiton americanus Kaas and Van Belle, 1985	400 - 1400 m	13
Leptochiton cf. belknapi Dall, 1878	160 - 4206 m	15, 19, 23
Leptochiton nexus Carpenter, 1864 *	I - 144 m	7, 10, 13, 24
Leptochiton rugatus (Carpenter in Pilsbry, 1892) *	I - 458 m	7, 10, 13, 24
Leptochiton sp. *	116 m	23, 24
Deshayesiella Carpenter MS, Dall, 1879		
Deshayesiella spicata (Berry, 1919)	18 - 467 m	20, 23
Oldroydia Dall, 1894		
Oldroydia percrassa (Dall, 1894)	I - 730 m	7, 10, 13
Order Chitonida Thiele, 1910		
Suborder Chitonina Thiele, 1910		
Family Chaetopleuridae Plate, 1899		
Chaetopleura Shuttleworth, 1853		
Chaetopleura gemma Carpenter MS, Dall, 1879	I - 50 m	12, 15
Family Ischnochitonidae Dall, 1889		
Callistochiton Carpenter MS, Dall, 1879		
Callistochiton crassicostatus Pilsbry, 1893	I - 732 m	7, 9, 17, 18
Callistochiton decoratus Carpenter MS, Pilsbry, 1893	I - 72 m	7, 9, 17, 18
Callistochiton palmulatus Carpenter MS, Dall, 1879 *	I - 85 m	7, 9, 17, 18, 24
Lepidozona Pilsbry, 1892		
Lepidozona golischi (Berry, 1919) *	75 - 1281 m	1, 2, 7, 24
Lepidozona mertensii (von Middendorff, 1847) *	I - 100 m	7, 8, 15, 24
Lepidozona radians (Carpenter in Pilsbry, 1892) *	I - 150 m	7, 16, 24
Lepidozona retiporosa (Carpenter, 1864) *	I - 1463 m	7, 8, 15, 24
Lepidozona scabricostata (Carpenter, 1864) †	I - 1460 m	7, 8, 15
Lepidozona scrobiculata (von Middendorff, 1847) *	I - 200 m	5, 7, 8, 15, 24
Lepidozona willetti (Berry, 1917)	13 - 274 m	7, 8, 15
Lepidozona sp. A *	101 m	24
Lepidozona sp. B *	305 m	24
Lepidozona sp. C *	90 m	24
Stenoplax Carpenter MS, Dall, 1879		
Stenoplax corrugata (Carpenter in Pilsbry, 1892)	I - 107 m	15
Stenosemus von Middendorff, 1847		
Stenosemus stearnsii (Dall, 1902)	412 - 704 m	16
Suborder Acanthochitonina Bergenhayn, 1930		
Family Acanthochitonidae Pilsbry, 1893		
Acanthochitona Gray, 1821		
Acanthochitona avicula (Carpenter, 1864)	I - 36 m	21, 22

Table 1 (continued)

Saxon/Species	Depth Range	Sources ‡
Family Lepidochitonidae Iredale, 1914		
Lepidochitona Gray, 1821		
Lepidochitona beanii Carpenter, 1857	I - 230 m	6, 11, 14
Family Mopaliidae Dall, 1889		
Dendrochiton Berry, 1911		
Dendrochiton flectens (Carpenter, 1864)	I - 38 m	11, 14
Dendrochiton gothicus (Carpenter, 1864) *	I - 230 m	11, 14, 24
Dendrochiton semiliratus Berry, 1927	38 -141 m	11, 14
Dendrochiton thamnoporus (Berry, 1911) *	I - 38 m	11, 14, 24
Mopalia Gray, 1847		
Mopalia acuta (Carpenter, 1855)	I - 40 m	17
Mopalia imporcata Carpenter, 1864 *	I - 120 m	17, 24
Mopalia lowei Pilsbry, 1918 *	I – 17 m	17, 24
Mopalia phorminx Berry, 1919 *	18 - 183 m	17, 24
Placiphorella Carpenter MS, Dall, 1879		
Placiphorella mirabilis Clark, 1994 *	28 - 155 m	3, 17, 24
Placiphorella pacifica Berry, 1919	155 - 2000 m	3, 17, 23
Tonicella Carpenter, 1873		
Tonicella venusta Clark, 1999 *	I - 140 m	4, 24

[‡] Primary sources: (1) Berry, 1919a; (2) Berry, 1925; (3) Clark, 1994; (4) Clark, 1999; (5) Clark, 2004; (6) Eernisse, 1986; (7) Eernisse, 1998; (8) Ferreira, 1978; (9) Ferreira, 1979a; (10) Ferreira, 1979b; (11) Ferreira, 1982; (12) Ferreira, 1983; (13) Kaas & Van Belle, 1985a; (14) Kaas & Van Belle, 1985b; (15) Kaas & Van Belle, 1987; (16) Kaas & Van Belle, 1990; (17) Kaas & Van Belle, 1994; (18) Pilsbry, 1892–1893; (19) Schwabe, 2008; (20) Sirenko & Clark, 2008; (21) Slieker, 2000; (22) Watters, 1990; (23) R. N. Clark, personal communication; (24) present study.

above). Genera such as *Cyanoplax* and *Nuttallina* within Lepidochitonidae are common in southern California but are not addressed here because they are largely restricted to intertidal or shallow subtidal depths. Of the taxa considered subfamilies of Ischnochitonidae by Van Belle (1983; also Kaas & Van Belle, 1985-1998), we follow Eernisse et al. (2007) in considering Chaetopleuridae and Lepidochitonidae to be distinct from Ischnochitonidae while, unlike Sirenko (2006), we retain *Callistochiton* (part of Van Belle's Callistoplacinae) within Ischnochitonidae. Likewise, we recognize the priority of Leptochitonidae Dall, 1889 in

preference to Lepidopleuridae Pilsbry, 1892, and use it to also include *Oldroydia* and *Deshayesiella*, not separating these genera to Protochitonidae Ashby, 1925, as in Sirenko (2006). Based on preliminary molecular evidence, it is likely that the monotypic *Oldroydia* Dall, 1894, with type species *Lepidopleurus* (*Oldroydia*) percrassus Dall, 1894 (currently *Oldroydia* percrassa), could eventually be considered a junior synonym of *Deshayesiella* Carpenter MS, Dall, 1879, whose members are mostly found in the western Pacific (D. J. Eernisse, in preparation).

Key to Benthic Chitons of the Southern California Bight

1.	Lateral and pleural areas of intermediate valves distinct from jugal region, latero-pleural areas sculptured with numerous, elongate, teardrop-shaped pustules, jugum with deeply incised longitudinal striations; girdle with sutural tufts of very long, straight, smooth spicules
-	Valves not sculptured as above
2.	Girdle greatly expanded anteriorly, much wider around head valve than tail valve; mouth region with conspicuous cephalic lappets extending anteriorly; intermediate valves at least 4 times wider than long, depressed in lateral areas
_	Girdle not expanded anteriorly, equally wide around head and tail valves; mouth region surrounded by simple platform, without lappets; intermediate valves less than 4 times as wide as long, with straight or convex lateral areas
3.	Tegmentum of valves pinkish or greenish grey and streaked or speckled with white, brown or other colors
-	Tegmentum of valves colored solid white, although some orange or black deposits may be present
4.	Gill rows not separated by interspace, with left and right rows forming a nearly continuous arch surrounding the anus; gills merobranchial, restricted to about posterior third of pallial groove; disarticulated valves without insertion plates
-	Gill rows separated by distinct interspace, with left and right rows not reaching the anus; gills holobranchial, extending at least half or more the length of the pallial groove; disarticulated valves with insertion plates . 11
5.	Head valve, lateral areas of intermediate valves, and tail valve with randomly arranged, prominent, relatively tall tubercles; central areas with longitudinal rows of smaller, flatter pustules; dorsal girdle with tufts of long, smooth, calcareous needles up to 400 µm long scattered among shorter spicules Hanleyella oldroydi

^{*} Follows R. N. Clark (personal communication) in recognizing *Placiphorella pacifica* Berry, 1919, as a valid eastern Pacific species, although Kaas & Van Belle (1994) consider this a junior synonym of *P. atlantica* (Verrill & S. I. Smith, 1882).

 Valve sculpturing not as above, without prominent tubercles or pustules; girdle with or without long needlelike spines, but not usually in dense tufts if present Valves heavy with coarse, irregular sculpturing on end valves and latero-pleural areas of intermediate valves; jugal region usually distinct, forming a raised and relatively smooth ridge compared to latero-pleural areas; posterior edges of intermediate valves curved or distinctly beaked (V-shaped); girdle encroaches conspicuously between valves (- 50% valve width or more); dorsal girdle surface with scattered smooth, needlelike spicules up to 500 μm long (may be broken off) Valves thin with mostly fine, granulose sculpturing, with or without raised, round to oval granules; jugum not distinct; intermediate valves rectangular with more or less straight posterior edges and small or inconspicuous apices; girdle obes not encroach noticeably between the valves; girdle with or without long spicules Intermediate valves with "a long jugal area characteristically projecting forward for almost half the length of the tegmentum" (Sirenko & Clark, 2008: 1) and with a higher "ratio of jugal length to the length of the postmucronal area" (Sirenko & Clark, 2008: 4) than in the next choice Oldroydia percrassa Intermediate valves "lacking long, distinct and projecting jugal area" (Sirenko & Clark, 2008: 1), with a lower "ratio of jugal length to the length of the postmucronal area" (Sirenko & Clark, 2008: 1), with a lower "ratio of jugal length to the length of the postmucronal area" (Sirenko & Clark, 2008: 1) than in the previous choice Deshayesiella spiculas Tegmental sculpture of minute granules forming subgranulose riblets; riblets arranged into radiating series on head valve, lateral areas of intermediate valves and postmucronal area of tail valve, and into longitudinal rows on central areas and antenucronal area of tail valve Tegmental sculpture of		
jugal region usually distinct, forming a raised and relatively smooth ridge compared to latero-pleural areas; posterior edges of intermediate valves curved or distinctly beaked (V-shaped); girdle encroaches conspicuously between valves (-50% valve width or more); dorsal girdle surface with scattered smooth, needlelike spicules up to 500 μm long (may be broken off)	-	
distinct; intermediate valves rectangular with more or less straight posterior edges and small or inconspicuous apices; girdle does not encroach noticeably between the valves; girdle with or without long spicules 8 7. Intermediate valves with "a long jugal area characteristically projecting forward for almost half the length of the tegmentum" (Sirenko & Clark, 2008: 1) and with a higher "ratio of jugal length to the length of the postmucronal area" (Sirenko & Clark, 2008: 4) than in the next choice	6.	jugal region usually distinct, forming a raised and relatively smooth ridge compared to latero-pleural areas; posterior edges of intermediate valves curved or distinctly beaked (V-shaped); girdle encroaches conspicuously between valves ($\sim 50\%$ valve width or more); dorsal girdle surface with scattered smooth, needlelike spicules
tegmentum" (Sirenko & Clark, 2008: 1) and with a higher "ratio of jugal length to the length of the postmucronal area" (Sirenko & Clark, 2008: 4) than in the next choice	-	distinct; intermediate valves rectangular with more or less straight posterior edges and small or inconspicuous
"ratio of jugal length to the length of the postmucronal area" (Sirenko & Clark, 2008: 4) than in the previous choice	7.	tegmentum" (Sirenko & Clark, 2008: 1) and with a higher "ratio of jugal length to the length of the postmucronal
head valve, lateral areas of intermediate valves and postmucronal area of tail valve, and into longitudinal rows on central areas and antemucronal area of tail valve	_	"ratio of jugal length to the length of the postmucronal area" (Sirenko & Clark, 2008: 4) than in the previous
 9. Girdle distinctly spiculose, with long needlelike spines to 400 μm scattered dorsally amongst mostly short (~70 μm), oval, smooth spicules; postmucronal slope distinctly concave; black caps of major lateral teeth of radula bicuspid, moderately elongate, inner denticle much larger than outer denticle Leptochiton nexus Girdle not distinctly spiculose, but comprised dorsally of mostly rectangular, ribbed scales not longer than ~60 μm, although longer, ribbed spicules to 140 μm are occasionally evident, especially at the valve sutures; postmucronal slope generally straight, often vertical in southern California deep-water specimens, with or without small depression just below mucro; black caps of major lateral teeth of radula unicuspid, very long and sharply pointed	8.	head valve, lateral areas of intermediate valves and postmucronal area of tail valve, and into longitudinal rows
 (~70 μm), oval, smooth spicules; postmucronal slope distinctly concave; black caps of major lateral teeth of radula bicuspid, moderately elongate, inner denticle much larger than outer denticle Leptochiton nexus Girdle not distinctly spiculose, but comprised dorsally of mostly rectangular, ribbed scales not longer than ~60 μm, although longer, ribbed spicules to 140 μm are occasionally evident, especially at the valve sutures; postmucronal slope generally straight, often vertical in southern California deep-water specimens, with or without small depression just below mucro; black caps of major lateral teeth of radula unicuspid, very long and sharply pointed	_	Tegmental sculpture roughly granulose, with raised, well separated, round to oval granules 10
 ~ 60 μm, although longer, ribbed spicules to 140 μm are occasionally evident, especially at the valve sutures; postmucronal slope generally straight, often vertical in southern California deep-water specimens, with or without small depression just below mucro; black caps of major lateral teeth of radula unicuspid, very long and sharply pointed	9.	$(\sim 70 \ \mu m)$, oval, smooth spicules; postmucronal slope distinctly concave; black caps of major lateral teeth of
intermediate valves; tegmental sculpture of raised granules organized in chains, arranged longitudinally in central areas and more or less radially in lateral areas and on end valves; girdle covered dorsally with mostly blunt, striated spicules up to 100 µm, and longer, almost smooth needlelike spines up to 375 µm along edges of valves; black caps of major lateral teeth of radula bicuspid, inner denticle shorter than outer denticle	_	\sim 60 μ m, although longer, ribbed spicules to 140 μ m are occasionally evident, especially at the valve sutures; postmucronal slope generally straight, often vertical in southern California deep-water specimens, with or without small depression just below mucro; black caps of major lateral teeth of radula unicuspid, very long and
round granules, arranged quincunxially and not in chains; girdle covered dorsally with elongate, bluntly pointed scales or spicules, $\sim 100-150~\mu m$ long, each scale with 3-4 riblets; black caps of major lateral teeth of radula	10.	intermediate valves; tegmental sculpture of raised granules organized in chains, arranged longitudinally in central areas and more or less radially in lateral areas and on end valves; girdle covered dorsally with mostly blunt, striated spicules up to $100~\mu m$, and longer, almost smooth needlelike spines up to $375~\mu m$ along edges of valves; black caps of major lateral teeth of radula bicuspid, inner denticle shorter than outer denticle
	_	round granules, arranged quincunxially and not in chains; girdle covered dorsally with elongate, bluntly pointed scales or spicules, $\sim 100\text{-}150~\mu m$ long, each scale with 3-4 riblets; black caps of major lateral teeth of radula

 $[\]dagger$ *Leptochiton* cf. *belknapi* may represent two similar, but distinct nominal species in SCB waters according to R. N. Clark (personal communication): *L. belknapi* Dall, 1878, and *L. mesogonus* Dall, 1902.

11.	Girdle covered dorsally with strongly imbricating oval to nearly rectangular-shaped scales, or conical scale-like spicules or corpuscles
_	Girdle without imbricating scales or spicules, dorsal surface covered with minute, non-overlapping corpuscles, giving a granular or sandy appearance, with or without short pointed spicules, slender spines, dendritic bristles or flexible hairs
12.	Head and tail valves with very heavy, prominent ribs
_	Head and tail valves without prominent ribs, although there may be distinct radiating rows of globular tubercles
13.	Tail valve bulging prominently above other valves, shaped like a fist (may not be developed in small specimens), mucro anterior and not raised relative to highly convex postmucronal slope; head valve sculptured with about 9 massive, pustulose radial ribs separated by wide sulci, posterior ribs often bifurcated; lateral areas of intermediate valves highly raised, sculptured similar to head valve with 2 radial ribs separated by narrow groove; girdle covered dorsally with small, oval, imbricating scales ($\sim 70 \times 130 \mu m$), each with 10-12 fine riblets
_	Tail valve not prominently bulging, mucro subcentral to terminal and higher than postmucronal slope; head valve with about 7 or 11 radial ribs; girdle scales with 5-8 broad ribs or 10-14 sharp riblets
14.	Mucro high and terminal, postmucronal slope nearly vertical; head valve with about 7 stout ribs separated by wide sulci, radial ribs diverging into pustular to scalloped subribs; lateral areas of intermediate valves highly raised and sculptured similar to head valve, with single strong radial ridge diverging laterally into 3-4 subribs; girdle covered dorsally with small, oval, imbricating scales ($\sim 90 \times 160 \mu m$), each with 5-8 broad ribs
-	Mucro of intermediate height and subcentral, postmucronal slope straight to slightly convex; head valve with about 11 scalloped ribs without subribs, ribs separated by narrow, relatively shallow sulci; lateral areas of intermediate valves raised and sculptured similar to head valve with 2 distinct scalloped radial ribs; girdle covered dorsally with oval, imbricating scales (~140 x 220 µm), each scale with 10-14 sharp riblets
15.	Head valve, postmucronal area of tail valve, and raised lateral areas of the intermediate valves with 4-6 irregular, concentric corrugations; girdle covered dorsally with small, taller than wide ($\sim 96 \times 72 \mu m$), slightly bent, ribbed, round-topped scales
_	Valves without irregular concentric corrugations, although a few weak growth lines may be present 16
16.	Imbricating girdle elements juxtaposed, whitish, glossy, much taller than wide (up to 430 x 160 µm); tegmentum of head valve, lateral areas, and postmucronal area of tail valve sculptured with fine, beaded, divaricating radial riblets; apophyses not connected by a jugal lamina (requires disarticulation)
_	Girdle elements armor like, consisting of strongly overlapping, usually wider than tall, oval to rectangular shaped scales; tegmentum not as above, either smooth with weak granulations or strongly sculptured with various types of ridges and/or tubercles; apophyses connected by a jugal lamina that is notched where it connects on each side (requires disarticulation)

17.	Tegmentum of all valves appearing almost uniformly smooth with weak, granular sculpturing; color variable, often mottled with olive, brown, orange, yellow, or occasionally white; girdle scales approximately rectangular, wider than tall ($\sim 270 \times 170 \ \mu m$), each scale with about 12 fine striations Lepidozona radians
_	Tegmentum distinctly sculptured with various combinations and arrangements of raised pustules, tubercles, pits and ridges, often arranged in radial or longitudinal rows; head valve, lateral areas of intermediate valves, and postmucronal area of tail valve usually similarly sculptured and distinct from central areas
18.	Central areas of intermediate valves with longitudinal to arching diagonal rows of distinct but shallow pits, but without conspicuous longitudinal ridges; end valves and lateral areas of intermediate valves with obsolete radial rows of minute, sparsely set, round, usually bead-like tubercles; girdle scales relatively small, nearly as tall as wide ($\sim 144 \times 120 \ \mu m$), with faint longitudinal striations; color often uniform brown or reddish-brown and mottled with white in southern California specimens, but also occasionally tan or apricot
_	Central areas of intermediate valves with distinct longitudinal ridges that may or may not extend across the jugum, sometimes latticed and appearing pitted between; girdle scales usually wider than tall, small ($\sim 100~\mu m$) to large ($\sim 450~\mu m$), with or without striations, and with or without nipples at top
19.	Tegmental sculpture of head valve, lateral areas of intermediate valves, and postmucronal area of tail valve highly variable, without raised, neatly separated tubercles, but usually with irregular pustules arranged in radial ribs, elongated pustules along posterior sutures usually protruding to give a serrated appearance; central areas of intermediate valves with well-spaced, longitudinal ridges extending across the jugum, often latticed in between; girdle scales rectangular (\sim 180 x 130 μ m), slightly convex with distinct longitudinal striations; tegmentum color variable, usually of greens or browns
_	Tegmentum of end valves and lateral areas not as above, sculptured with neatly separated tubercles of various sizes and shapes (minute and round, button-like, globular, digitate), sutural ribs not appearing serrated; central areas with closely set or well-spaced longitudinal ridges, with or without distinct latticing 20
20.	Tegmentum of end valves and lateral areas of intermediate valves sculptured with small, neatly separated, roundish (bead-like) tubercles
-	Tegmentum of valves without small bead-like tubercles, but sculptured with relatively large button-like (flat and round), globular or digitate tubercles
21.	Tegmentum mostly microgranulose, with sparsely set bead-like tubercles arranged in ill-defined radial rows, distance between tubercles at least several times their width (~5 tubercles per row); central areas with closely set, often beaded, longitudinal ridges without distinct cross-hatching; girdle scales oval, moderately convex, with distinct longitudinal striations; color mostly a uniform orange brown, with or without creamy white banding
_	Tegmentum of end valves and lateral areas sculptured with radiating ribs separated by fine distinct grooves or sulci, each rib bearing numerous, closely set bead-like tubercles, distance between tubercles 1-3 times their width (\sim 6-12 tubercles per row); central areas with distinct cross-hatching between longitudinal ribs; girdle scales strongly convex or bulbous, with faint longitudinal striations, and crowned with a ribbed nipple (often broken off)

[‡] Lepidozona golischi formerly synonymized with L. scabricostata (Carpenter, 1864) (see Ferreira, 1978; Kaas & Van Belle, 1987), but considered in Clark (2008) and herein as a distinct species (L. scabricostata not included in key).

22.	Central areas of intermediate valves appearing deeply pitted with longitudinal ridges distinctly cross-hatched; tegmentum with widely spaced digitate tubercles or closely set flat or slightly raised round tubercles; girdle scales only slightly convex with distinct longitudinal striations
-	Central areas not pitted, without distinct cross-hatching, although faint horizontal latticing may be apparent between the prominent longitudinal ridges; tegmental sculpture of closely set, button-like or globular to digitate tubercles, distance between tubercles about 1-2 times their width; girdle scales relatively large (>400 μm), strongly convex, with or without weak striations, and crowned with a ribbed nipple (often broken off) 24
23.	Tegmentum of end valves and lateral areas of intermediate valves sculptured with radiating rows of well-separated, digitate tubercles, distance between tubercles at least several times their width; tegmentum and girdle coloration of banded reddish-browns and tans (color based on single specimen) Lepidozona sp. A
-	Tegmentum of end valves and lateral areas sculptured with relatively flat or slightly raised, round, closely set tubercles, distance between tubercles about 1-2 times their width; tegmentum and girdle coloration mostly tan to light orange with perhaps a darker jugal ridge (color based on single specimen) Lepidozona sp. B
24.	Head valve, lateral areas of intermediate valves, and posterior region of tail valve sculptured with rows of tall, globular to sometimes digitate tubercles; longitudinal ridges prominent throughout central areas, clearly extending across jugum; girdle scales typically smooth or with nearly obsolete longitudinal striations; color generally reddish-brown and blotched with lighter or darker tones Lepidozona mertensii
_	Head valve, lateral areas, and posterior region of tail valve sculptured with rows of numerous, flattened, button-like tubercles; longitudinal ridges of central areas becoming faint or obsolete across the jugum; girdle scales usually with faint longitudinal striations apparent; color reddish-brown with white banding on some posterior valves (color based on single specimen)
25.	Girdle nude dorsally with microscopic elements appearing uniformly granular or sandy, without conspicuous spicules, spines, bristles, or hairs
-	Girdle with conspicuous dorsal spicules, spines, bristles, or hairs scattered variably over a more or less granular or sandy surface
26.	Central areas of intermediate valves sculptured with 12-16 fine lateral riblets on each side, the remainder of the tegmentum evenly microgranulose; tegmentum color variable but mostly greens or rede
-	Tegmental sculpture smooth throughout; tegmentum color typically orange or pink, end valves and lateral areas with white zigzag lines, pleural areas with 2-5 large white flammules, although colors may be faint
27.	Girdle beset dorsally with spicules of different sizes and shapes or slender, hyaline spines, without conspicuous bristles or hairs
-	Girdle beset dorsally with dendritic processes, bristles or flexible hairs
28.	Tegmentum sculptured with conspicuous, raised, spherical tubercles arranged in radiating, branching rows on head valve and lateral areas of the intermediate valves, and forming beaded lirae in central areas; girdle covered with spicules or spines of different types and sizes (smooth or ribbed, slender or thick, curved or straight); tegmental color usually orange, rarely green, often with tiny black pigment spots, tail valve often black and spotted with white

_	Tegmentum smooth to the naked eye, microgranulose, color variable; girdle with long (>500 μ m), slightly curved, slender hyaline spines or spicules interspersed or occurring in bunches of 3-4 at sutures
29.	Tegmentum evenly microgranulose, head valve and lateral areas of intermediate valves appearing smooth, central areas with or without fine longitudinal riblets
-	Tegmentum coarsely sculptured, with or without strong radial, pustulose ribs
30.	Central areas with longitudinal riblets or grooves; girdle with tufts of plumose setae, with or without stalked calcareous processes; setae restricted to sutures only or occurring both near the sutures and as a supramarginal row around the girdle
_	Central areas smooth, without riblets; girdle without distinct tufts of plumose setae, but with isolated corneous setae or hairs up to $1000~\mu m$ long that bear stalked, calcareous spicules arising from a groove along one side; setae located near sutures and around end valves, but not in a supramarginal row Dendrochiton flectens
31.	Plumose setae without stalked calcareous spicules, consisting of tufts of long, curved, yellowish hairs surrounding a single thicker, branching bristle; setal tufts located near sutures, around the end valves, and as a supramarginal row; postmucronal slope concave
_	Plumose setae with stalked calcareous spicules, consisting of tufts of 3-6 fragile, branching, horny processes up to 1000 µm long; setal tufts present only at the sutures; postmucronal slope straight
32.	Head valve with 8 weak, thread-like radiating ribs, tegmentum of head valve and lateral areas of intermediate valves pitted by oblique, curved decussations, central areas with numerous fine, longitudinal lirae; girdle densely covered with small, stout, blunt-topped spicules up to $55 \times 14 \mu m$, and sparsely scattered long, hollow, grooved chitinous setae with 2 series of shorter, stalked, chitinous hairs arising from the grooves <i>Mopalia acuta</i> §
-	Head valve with prominent, annulated to nodulose radial ribs, intermediate valves sculptured similarly with the 2 heaviest ribs defining the extent of each lateral area; girdle setae not as above
33.	Girdle setae wispy, many as long as the girdle is wide, each with sparse lateral branches; central areas of intermediate valves with distinct longitudinal riblets, between which is a dense lattice of irregular, much finer lateral subribs; head valve with about 8-10 heavy radiating ribs, interspersed by one or more radiating rows of shorter but distinct pustules, similar rows of short pustules between the heavy defining ribs of the lateral areas; mucro subcentral
-	Girdle setae relatively stout, appearing bushy with dense lateral branches, although branching may be less pronounced in juveniles; central areas with or without distinct longitudinal riblets; mucro nearly terminal
34.	Setae with slender, usually recurved, bristles arranged in numerous indistinct rows, setal shaft visible between bristles, bristles angled away from setal shaft at their attachment point; central areas with distinct longitudinal riblets, between which are much finer lateral subribs; head valve with about 10 annulated, cordlike, or almost smooth radial ribs, lateral areas bounded by similar diagonal and sutural ribs, transverse nodules defining the annuli of the radial ribs fused and not separated, interspaces between radial ribs sculptured with mostly coalesced granules not arranged in radial rows

§Follows Eernisse et al. (2007) in treating *Mopalia acuta* (Carpenter, 1855) as a somewhat deeper water species distinct from the similar *M. plumosa* Carpenter *in* Pilsbry, 1893, which was formerly considered a junior synonym of *M. acuta*.

Results

We report 19 species of chitons from mostly deepwater habitats ranging throughout the SCB, including 16 described and three provisional (undescribed) species (Table 2). A fourth possible new species is also reported based on a single small juvenile. The chitons reported were collected between 1988 and 2009 at 66 different sampling sites ranging from northern Baja California to the northern Channel Islands and Point Conception (Figure 1, Appendix A). Several species are distributed widely throughout the region, while others are so far restricted to one or a few locations. Most individuals were collected from depths between 30 and 305 m, which were the primary focus of this study. Records for a few species collected from slightly shallower waters (9-18 m) by SCB benthic monitoring programs are also included because we expect these will eventually be found in deeper water. As in Eernisse (1998), we found the chiton fauna at the depths sampled herein to be largely distinct in comparison to the species commonly found in either shallower or deeper waters. Information is presented below for each species regarding their relative abundance, size, geographic distribution, bathymetric range, and co-occurrence with other chitons in the region.

Family Leptochitonidae Dall, 1889

Hanleyella oldroydi (Bartsch MS, Dall, 1919) (Plate 1, Figure 2)

Hanleyella oldroydi is reported to occur along the West Coast from Kosciusko Island, Alaska to Cabo San Quintin, Baja California at depths ranging from 18 to 455 m (Ferriera, 1979b; Baxter, 1983; Kaas & Van Belle, 1985a; Eernisse, 1998). This species was one of the most commonly encountered chitons in the present study, occurring in ~22% of the SCB samples containing chitons. All H. oldroydi examined in this study were collected in deep waters ranging from 50 to 191 m at sites located off of San Diego, Palos Verdes,

Santa Monica Bay and the northern Channel Islands. A total of 26 specimens of *H. oldroydi* have been examined so far, representing approximately 11% of the chitons collected. The maximum length of SCB specimens is 7.4 mm (mean = 4.2 mm), which is consistent with published records for this small species (see Ferreira, 1979b; Kaas & Van Belle, 1985a). *Hanleyella oldroydi* is commonly collected in samples with another lepidopleurid, *Leptochiton rugatus*, although the bathymetric range for the latter species includes the intertidal (see below). Other chitons collected at the same sites include *Leptochiton nexus*, *Lepidozona radians*, *L. mertensii*, *L. retiporosa*, *L. scrobiculata*, and possibly three undescribed species (*Lepidozona* spp. A and C, and *Leptochiton* sp.).

Leptochiton nexus Carpenter, 1864 (Plate 1, Figure 3)

Leptochiton nexus is known to occur along the West Coast from Cohen Island, Alaska to Punta Abreojos, Baja California, as well as in the Gulf of California at depths ranging from the intertidal to 144 m (Ferriera, 1979b; Kaas & Van Belle, 1985a). This chiton is reported here for the SCB from seven specimens collected at six sites located off of San Diego, Palos Verdes, Santa Monica Bay and the northern Channel Islands at depths of 18-82 m. The maximum length of the SCB specimens is 9.3 mm (mean = 5.9 mm), which is less than half the size that L. nexus typically reaches (see Ferreira, 1979b; Kaas & Van Belle, 1985a). Other chitons collected with L. nexus in the present study include Hanleyella oldroydi, Leptochiton rugatus, and Lepidozona retiporosa.

Leptochiton rugatus (Carpenter in Pilsbry, 1892) (Plate 1, Figure 4)

Certain recent authors (Ferreira, 1979b; Kaas & Van Belle, 1985a) have considered *Leptochiton rugatus* (Carpenter *in* Pilsbry, 1892) to be widely distributed

Table 2. Summary of chitons collected by benthic monitoring programs in the Southern California Bight (SCB) from 1988-2009.

Species	Number of Specimens	Number of Samples (Sites)	Body Length	Depth Range of SCB Sites
Leptochitonidae				
Hanleyella oldroydi	26	20 (13)	1 - 7.4 mm	50 - 191 m
Leptochiton nexus	7	6 (6)	3.5 - 9.3 mm	18 - 82 m
Leptochiton rugatus	60	33 (23)	1.2 - 8.5 mm	14 - 305 m
Leptochiton sp.	1	1	3 mm	116 m
Ischnochitonidae				
Callistochiton palmulatus	2	2 (2)	7 - 13 mm	80 - 85 m
Lepidozona golischi	3	2 (2)	20.5 - 23 mm	98 - 101 m
Lepidozona mertensii	3	3 (3)	13 - 15 mm	56 - 85 m
Lepidozona radians	7	6 (6)	3.8 - 10 mm	9 - 150 m
Lepidozona retiporosa	46	22 (19)	2.5 - 19 mm	55 - 305 m
Lepidozona scrobiculata	24	18 (15)	5.8 - 24 mm	14 - 101 m
Lepidozona sp. A	1	1	12.1 mm	101 m
Lepidozona sp. B	1	1	13 mm	305 m
Lepidozona sp. C	1	1	19.5 mm	90 m
Mopaliidae				
Dendrochiton gothicus	41	5 (1)	1 - 5.5 mm	16 - 18 m
Dendrochiton thamnoporus	9	5 (5)	1.6 - 9.3 mm	15 - 38 m
Mopalia imporcata	3	3 (3)	3.5 - 15 mm	38 - 69 m
Mopalia lowei	1	1	5 mm	17 m
Mopalia phorminx	2	2 (2)	20 - 24 mm	100 - 130 m
Placiphorella mirabilis	4	2 (2)	17 - 43 mm	43 - 104 m
Tonicella venusta	1	1	~10 mm	15 m

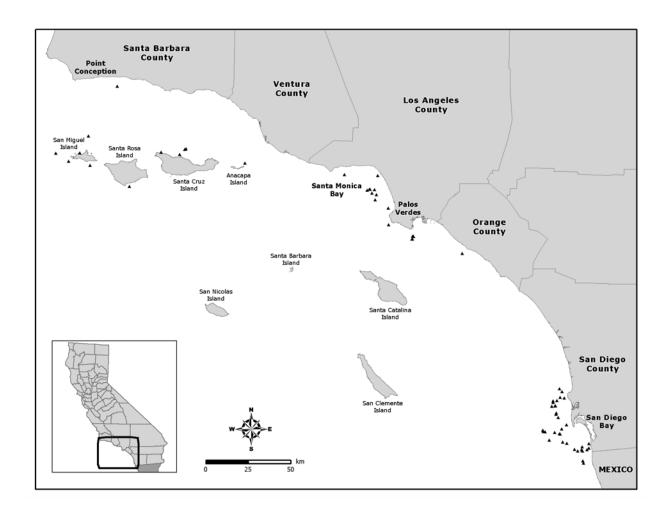


Figure 1. Stations (*) where chitons have been collected by benthic monitoring programs in the Southern California Bight (n = 66; see Appendix A). A few symbols overlap for sites located close together; 3 stations of unknown coordinates not shown, including 1 site off Point conception (150 m) and 2 sites off Palos Verdes (100 and 130 m).

throughout the North Pacific, occurring in the Sea of Japan, the Okhotsk Sea, the Bering Sea, along the West Coast from Alaska to Magdalena Bay, Baja California, and in the Gulf of California at depths ranging from the intertidal to 458 m. Other authors (e.g., Saito, 2000) regard the northwestern Pacific Leptochiton assimilis (Thiele, 1909) as distinct. Recent molecular studies have revealed even further distinctions (D. J. Eernisse and R. P. Kelly, unpublished), but based on its nearby type locality, those in at least the intertidal to shallow subtidal of California are still regarded as L. rugatus, whereas the identity of those from deeper water is still somewhat uncertain. This deeper water form of L. rugatus is the most common and abundant chiton encountered in the present study, occurring in ~36% of all samples. Specimens of this chiton have been collected at depths ranging from 14 to 305 m throughout the SCB, including sites located off of San Diego, Palos Verdes, Santa Monica Bay, Point Conception and the northern Channel Islands. A total of 60 specimens have been examined so far, which represents about 25% of the chitons collected in the region. SCB benthic specimens of L. rugatus in these deeper waters are relatively small with a maximum length of 8.5 mm (mean = 3.8 mm), while the maximum recorded size for the species is around 16 mm (see Ferreira, 1979b; Kaas & Van Belle, 1985a). Leptochiton rugatus has been collected with a number of other SCB chitons, including especially Hanleyella oldroydi and Lepidozona retiporosa. Other chitons that co-occurred at sites with Leptochiton rugatus were L. nexus and possibly another undescribed species of Leptochiton, as well as at least three members of Lepidozona: L. radians, L. scrobiculata, and L. sp. B.

Leptochiton sp.

We agree with R. N. Clark (personal communication) that a single specimen of *Leptochiton* could be distinct from *L. rugatus*. However, the specimen is small (3 mm length) and further work is needed to verify whether this chiton actually represents a nominal or new species or is merely a somewhat odd juvenile of *L. rugatus*. This specimen was collected at a depth of 116 m at a site located north of Point Loma, San Diego where *L. rugatus* and *Hanleyella oldroydi* also occur.

Family Ischnochitonidae Dall, 1889

Callistochiton palmulatus Carpenter MS, Dall, 1879 (Plate 2, Figure 5)

Callistochiton palmulatus is reported to occur along the West Coast from Mendocino County, northern California to San Pablo Point, Baja California at depths ranging from the intertidal to 82 m (Pilsbry, 1892-93; Ferriera, 1979a; Kaas & Van Belle, 1994; Eernisse, 1998). This chiton is reported here from two specimens collected at separate sites off San Diego at depths of 80-85 m, which represents a slight increase in the bathymetric range for this species. This chiton has also been observed as perhaps the most common chiton collected from rock dredges off San Pedro (DJE, personal observation), where it is often found inside empty mudstone burrows left behind by burrowing bivalves (e.g., Adula spp.). The maximum length of the SCB specimens is 13 mm (mean = 10 mm), which is consistent with published size records for this species (see Ferreira, 1979a; Kaas & Van Belle, 1994). Both specimens of C. palmulatus reported off San Diego were collected along with Lepidozona mertensii.

Lepidozona golischi (Berry, 1919) (Plate 2, Figures 6-7)

Lepidozona golischi was originally described by Berry (1919a) as a member of Ischnochiton based on a specimen collected at a depth of 100 fathoms (~183 m) off of Santa Monica, California. Ferreira (1978) subsequently synonymized L. golischi with Lepidozona scabricostata (Carpenter, 1864) in his review of the temperate eastern Pacific Lepidozona, and this species has since been reported to occur from the intertidal to depths of 1460 m along the West Coast from the Gulf of Alaska to Sebastian Vizcaino Bay, Baja California (see Ferreira, 1978; Baxter, 1983; Kaas & Van Belle, 1987; Clark, 1991; Eernisse, 1998).

Three chitons that fit this general morphology were collected in the present study at two sites off San Diego at depths of 98-101 m. The maximum length of these specimens is 23 mm (mean = 22 mm). Although we at first identified these chitons as L. scabricostata, comparison with the approximately 7 mm long holotype of that species (USNM 16268; see Figure 6a herein) revealed significant differences. As also noted by Berry (1917) and Ferreira (1978), the central regions of the L. scabricostata holotype's intermediate valves, in particular, are very similar to those of L. willetti (not reported in this study), even though their girdle scales differ substantially. The central areas of these two species are alike in their lattice-like sculpturing with cross-hatching. In between the left and right central areas, the jugal region differs, with longitudinal ribbing extending across the jugum in L. willetti, whereas the L. scabricostata holotype has almost quincunxially arranged granules on its jugum without longitudinal ribbing. Unlike Ferreira (1978), we also found the central regions of the L. scabricostata holotype to differ substantially from the lectotype of *Ischnochiton (L.)* golischi (hereafter as L. golischi) at the Santa Barbara Museum of Natural History (SBMNH 34395; see Figure 6b herein), with the longitudinal ribs of L. golischi extending across the jugal region similar to L. willetti. Unlike either L. willetti or L. scabricostata, the spaces between the finely beaded longitudinal ribs of the L. golischi lectotype lack strong cross hatching and instead have only irregularly scattered granular pustules. Like L. willetti, or even more like L. retiporosa (see below), the head valve and the lateral areas of the intermediate valves of the L. golischi lectotype have radiating rows of small, raised and rounded (bead-like) tubercles. In contrast, such bead-like tubercles appear lacking in L. scabricostata, although this can only be assumed for the missing end valves of the holotype. The lateral areas of this specimen, however, are quite different from L. golischi with small irregular pustules developing along the posterior edges that are more similar to that seen in L. scrobiculata (see below). Comparison of the three San Diego specimens of L. golischi collected as part of this study (e.g., Figure 7) with the L. golischi lectotype from the SBMNH (Figure 6b) and specimens identified as L. scabricostata for the Santa Maria Basin area at depths between 75-123 m (see Figures 3.2C-F in Eernisse, 1998) confirmed these differences and that these chitons are all the same species. Consequently, we herein concur with the treatment of Clark (2008: 80-81) in resurrecting L. golischi as a distinct species from L. scabricostata (Carpenter, 1864). Additional comparisons with specimens identified as L. scabricostata collected off San Diego at depths between 110-1281 m and housed in the Scripps Institution of Oceanography Benthic Invertebrate Collection (SIO Cat. Nos. M1208 and M1389) reveal these chitons to be L. golischi as well. Overall, this gives a confirmed depth range for L. golischi of 75-1281 m based on the SBMNH type material and specimens examined during this study or that of Eernisse (1998). Other chitons that co-occured with L. golischi in this study were Lepidozona retiporosa, L. scrobiculata, and Lepidozona sp. A.

As mentioned above, L. golsichi also bears similarities to another common species of Lepidozona in the SCB, L. retiporosa, especially in terms of its sparsely set, minute round tubercles on the end valves and lateral areas of the intermediate valves. However, L. golischi differs markedly in the sculpturing of the central areas,

especially in its possession of well-separated longitudinal riblets that are unlike anything seen in *L. retiporosa*. The above distinctions mostly agree with Clark (2008). The one discrepancy, however, is that Clark mentions *L. golischi* as being sculptured with "relatively large, often scattered pustules...," which seems quite different from the minute round or bead-like tubercles noted herein for this species.

Finally, besides finding clear differences between the primary type material of L. golischi and L. scabricostata, we have further considered whether L. scabricostata is distinct from other nominal species of Lepidozona discussed in this paper, given that the type specimen of this species was collected at comparable (but slightly shallower) depths off Santa Catalina Island. Our suspicion is that the small holotype of L. scabricostata (Figure 6a) is merely a juvenile specimen of L. scrobiculata, one of the most commonly dredged chitons in the SCB. It is our experience that juvenile specimens of L. scrobiculata resemble this holotype, especially in terms of the small irregular pustules that appear to be developing along the posterior edges of the intermediate valves. If true, Lepidopleurus scabricostus Carpenter, 1864, would then become a junior synonym of Chiton scrobiculatus von Middendorff, 1847. However, we stop short of proposing such a synonymy here, pending more detailed morphological comparisons of the holotype of L. scabricostata with confirmed L. scrobiculata juveniles.

Lepidozona mertensii (von Middendorff, 1847) (Plate 3, Figure 8)

Lepidozona mertensii occurs along the West Coast from Auke Bay, Alaska to Sacramento Reef, Baja California from the intertidal to depths of 100 m (Ferreira, 1978; Kaas & Van Belle, 1987). Reports from northern Japan waters (Taki, 1938) are doubtful and need to be confirmed. This chiton is reported here for the SCB from three specimens collected off of San Diego and Santa Monica Bay at depths between 56 and 85 m. The maximum length of the two SCB specimens that could be measured is 15 mm (mean = 14 mm), while the third individual was broken and disarticulated. This overall body size is relatively small for this species, which typically reaches lengths ~40 mm and may exceed 50 mm in some individuals (see Ferreira, 1978; Kaas & Van Belle, 1987). Lepidozona mertensii has been found to co-occur with Hanleyella oldroydi, Lepidozona retiporosa, and Callistochiton palmulatus in the present study.

Lepidozona radians (Carpenter in Pilsbry, 1892) (Plate 3, Figure 9)

Lepidozona interstincta (Gould, 1852) (with L. radians considered a junior synonym) has been previously reported to occur in the Aleutian Islands and along the West Coast from Prince William Sound, Alaska to Catalina Island, California from the intertidal to depths of 72 m (Kaas & Van Belle, 1990). However, Eernisse et al. (2007) restored the more commonly used name for California specimens, Lepidozona radians (Carpenter in Pilsbry, 1892) (formerly Ischnochiton radians), as distinct from the more northern L. interstincta. These two species are very similar except for range differences, coloration, and consistent DNA sequence differences (DJE, unpublished data). Lepidozona interstincta, which is uniformly tan in color, is probably the only species present in Alaska and extends south to at least the subtidal of the San Juan Islands, Washington, whereas the more variably colored L. radians extends north to at least the intertidal of Port Hardy at the northern end of Vancouver Island, and south to the intertidal of some cold-water upwelling sites south of Ensenada, Baja California, México, including new southern range extension records near Colonet (DJE, personal observation). Lepidozona radians is not generally found in the intertidal of southern California but is known from seven specimens in the present study collected at depths of 9-150 m ranging from northern Baja California to Point Conception and the northern Channel Islands. These records extend the maximum depth range of this species from 72 to 150 m and would be new southernmost records except for the previously mentioned Baja California specimens. The chitons reported here represent two primary color morphs. Specimens from off northern Baja and San Diego were mottled with olive-green and/or browns (e.g., Figure 7a), while specimens from off Point Conception and Santa Cruz Island were mostly white (e.g., Figure 7b). The maximum length of the SCB specimens is 10 mm (mean = 7 mm), which is rather small compared to the 28 mm in length this species or the similar L. interstincta may reach (see Kaas & Van Belle, 1990). Other chitons that co-occur with L. radians in SCB waters include Hanleyella oldroydi, Leptochiton rugatus and Lepidozona scrobiculata.

Lepidozona retiporosa (Carpenter, 1864) (Plate 4, Figure 10)

Lepidozona retiporosa is reported to occur along the West Coast from Kosciusko Island, Alaska to the

southern tip of Baja California from the intertidal to depths of 1463 m (Kues, 1974; Ferreira, 1978; Baxter, 1983; Kaas & Van Belle, 1987; Eernisse, 1998). This species represents one of the most common chitons and the second most abundant species in the present study, occurring in ~24\% of the samples and comprising ~19% of all individuals. A total of 46 L. retiporosa were collected at depths ranging from 55 to 305 m at sites located off of San Diego, Palos Verdes, Santa Monica Bay and the northern Channel Islands. Many SCB specimens of L. retiporosa are relatively large with a maximum length of 19 mm (mean = 11 mm), while the maximum size previously known for this species is 17 mm (see Ferreira, 1978; Kaas & Van Belle, 1987). Lepidozona retiporosa co-occurs with a number of other SCB chitons, including Hanleyella oldroydi, Leptochiton nexus, L. rugatus, Lepidozona golischi, L. mertensii, L. scrobiculata, Lepidozona spp. A, B and C, and Mopalia phorminx.

Lepidozona scrobiculata (von Middendorff, 1847) (Plate 4, Figure 11)

Lepidozona scrobiculata is reported from along the West Coast from Sonoma County, California to Thurloe Head on the outer coast of Baja California, and its vertical distribution extends from the intertidal to depths of 200 m (Ferreira, 1978; Kaas & Van Belle, 1987; Clark, 2004). The name, L. scrobiculata, which Clark (2004) demonstrated was the senior synonym of the name used for over 90 years, L. sinudentata (Carpenter in Pilsbry, 1892), refers to a highly variable species that is one of the most commonly encountered chitons in the present study. Specimens of L. scrobiculata occurred in ~20% of the SCB samples, which were collected at depths from 14 to 101 m located off of northern Baja California, San Diego, Palos Verdes, Santa Monica Bay, and the northern Channel Islands. A total of 24 specimens of L. scrobiculata were examined, which represents about 10% of the chitons collected. The maximum length of these specimens is 24 mm (mean = 13.5 mm), which is nearly as large as the maximum size reported for this species (see Ferreira, 1978; Kaas & Van Belle, 1987). Lepidozona scrobiculata occurs on a variety of substrates (e.g., rocks, metal, plastic and glass debris) collected by either benthic grabs or in trawl samples. One specimen from off northern Baja was found living adjacent to the operculum on the large turban snail Megastraea turbanica (Dall, 1910). Many species of southern California chitons co-occur with L. scrobiculata, including Hanleyella oldroydi, Leptochiton rugatus, Lepidozona golischi, L. radians, L. retiporosa, Lepidozona sp. A, Dendrochiton gothicus, D. thamnoporus, Mopalia lowei, and Placiphorella mirabilis.

Lepidozona sp. A (Plate 5, Figure 12)

A presently unidentified 12.1 mm long specimen of Lepidozona, referred to herein as Lepidozona sp. A, resembles but differs from the more southerly L. guadalupensis Ferreira, 1978 (known from Guadalupe Island, Baja California) as well as L. mertensii in terms of tegmental sculpturing, an opinion that is shared by R. N. Clark (personal communication). Lepidozona sp. A can be distinguished from these two species by the morphology of its girdle scales, which are only slightly convex (relatively flat) with each scale bearing about eight distinct longitudinal striations or ridges (see Figure 12e). In contrast, the scales of both L. guadalupensis (see Figures 32-33 in Ferreira, 1978) and L. mertensii (Figure 8e herein and Figures 20-21 in Ferreira, 1978; see also Kaas & Van Belle, 1987) are strongly convex or bulbous appearing, often mammillated, and at best may appear only weakly striated under normal magnification. Furthermore, the impression of striation in L. guadalupensis scales is due to rows of minute pustules present on their outer surface (see Ferreira, 1978), which appears unlike anything observed in Lepidozona sp. A. This chiton, also appears somewhat similar to another provisional species reported in this study, Lepidozona sp. B (see below), in terms of the distinctly cross-hatched and strongly pitted central areas, but may be distinguished from this and other members of the genus by the additional combination of characters given in the key. Lepidozona sp. A was collected southwest of Point Loma, San Diego at a depth of 101 m. Several other species of Lepidozona were collected with this chiton, including L. golischi, L. retiporosa, and L. scrobiculata.

Lepidozona sp. B (Plate 5, Figure 13)

A second unidentified specimen of *Lepidozona* measuring 13 mm in length was collected at a depth of 305 m at a site located west of Palos Verdes. This chiton appears identical with specimens of another unidentified *Lepidozona* collected at a depth of 425 m from the Santa Lucia Bank off of San Luis Obispo County north of the SCB (R. N. Clark, personal communication). This species, referred to here as *Lepidozona* sp. B, appears unique compared to other known West Coast members

of the genus, from which it can be distinguished by the combination of characters given in the key. Although this chiton bears some similarity to Lepidozona sp. A in the tegmental sculpturing of the central areas (see above), these two provisional species can be easily distinguished from each other by the morphology of their tubercles, which are round and flat or only slightly raised in Lepidozona sp. B compared to elongated or digitate in Lepidozona sp. A. Other species collected with Lepidozona sp. B were Leptochiton rugatus and Lepidozona retiporosa.

Lepidozona sp. C (Plate 6, Figure 14)

A third unidentified specimen of Lepidozona measuring 19.5 mm in length was collected at a depth of 90 m at a site located off San Diego. This chiton, referred to here as Lepidozona sp. C, is similar to L. mertensii (see above) and L. willetti (not reported in this study) in terms of the morphology of the girdle scales, which are strongly convex and crowned with a ribbed nipple unless broken off. However, the flat button-like tubercles of Lepidozona sp. C, which are especially prominent on the end valves, are clearly distinct from the large, globular to digitate tubercles of L. mertensii or the small, bead-like tubercles of L. willetti. Lepidozona sp. C also differs from L. willetti in lacking distinct narrow sulci that separate the radial rows of tubercles on the end valves and lateral areas of the intermediate valves. This species also appears similar to another undescribed species of Lepidozona reported for depths below 10 m ranging from the Cortez Bank, southern California to Sacramento Reef, Baja California Norte (R. N. Clark, personal communication). Other SCB chitons collected with Lepidozona sp. C include Hanleyella oldroydi and Lepidozona retiporosa.

Family Mopaliidae Dall, 1889

Dendrochiton gothicus (Carpenter, 1864) (Plate 6, Figure 15)

Dendrochiton gothicus is known to occur along the western coast and offshore islands of North America from Santa Cruz Island, southern California to Isla Asunción, Baja California from the intertidal to depths of 230 m (Ferreira, 1982; Kaas & Van Belle, 1985b). Although often found in deep waters, D. gothicus is reported here from only a single monitoring station (5 samples) in Santa Monica Bay at a depth of 16-18 m. A total of 41 specimens of D. gothicus were present in

these samples, however, which accounts for ~17% of all chitons examined in this study. The maximum length of the SCB specimens is 5.5 mm (mean = 3.4 mm), which is about half the size often reached by this small species (see Ferreira, 1982; Kaas & Van Belle, 1985b as Lepidochitona gothica). In rock dredges off San Pedro, this species has normally been found attached to coralline algae including juvenile specimens as small as about 1 mm in length (DJE, unpublished observation). Other chitons that co-occur with D. gothicus include Leptochiton nexus, Lepidozona scrobiculata, Dendrochiton thamnoporus, and Mopalia lowei.

Dendrochiton thamnoporus (Berry, 1911) (Plate 6, Figure 16)

Dendrochiton thamnoporus has been previously reported to occur from the intertidal to depths of 29 m along the western coast and offshore islands of North America from Bodega Bay, California to Punta Abreojos, Baja California (Ferreira, 1982; Kaas & Van Belle, 1985b as Lepidochitona (Dendrochiton) thamnopora). This species is reported from nine specimens in the present study with a maximum length of 9.3 mm (mean = 5.6 mm), which is consistent with published records for this small species (see Ferreira, 1982; Kaas & Van Belle, 1985b). These chitons were collected at depths of 15-38 m, which represents a slight extension of the depth range for this species, including one site off northern Baja California at a depth of 29 m, two sites off San Diego at a depths of 27-38 m, one site in Santa Monica Bay at a depth of 17 m, and one site just off San Miguel Island in the northern Channel Islands at a depth of 15 m. The specimen of D. thamnoporus from northern Baja was found living on the sides of Megastraea turbanica at a site where Lepidozona scrobiculata was also collected from another individual of this large turban snail. The specimen collected near San Miguel Island was found along with another chiton, Tonicella venusta, living on a rock covered with a flat, encrusting red coralline alga similar to Lithothamnion (D. B. Cadien, personal communication). Other SCB chitons that occur at the same sites with D. thamnoporus include Leptochiton nexus, Dendrochiton gothicus, Mopalia imporcata, and M. lowei.

Mopalia imporcata Carpenter, 1864 (Plate 7, Figure 17)

Mopalia imporcata is reported to occur along the West Coast from Kachemak Bay, Alaska to Punta Santo

Tomás, Baja California at depths ranging from the intertidal to 120 m (Clark, 1991; Kaas & Van Belle, 1994). This chiton is reported here from three individuals, including a tiny juvenile collected at a depth of 46 m off of Santa Rosa Island, northwestern Channel Islands, and two adults collected off San Diego and Santa Monica Bay at depths of 38 and 69 m, respectively. These specimens measured 3.5, 13.5 and ~15 mm in length, respectively, while the maximum reported size for this species is 23 mm (see Kaas & Van Belle, 1994). Another species of chiton collected with *M. imporcata* off San Diego was *Dendrochiton thamnoporus*.

Mopalia lowei Pilsbry, 1918 (Plate 7, Figure 18)

Mopalia lowei is known to occur along the entire coast of California at depths ranging from the intertidal to shallow subtidal (Kaas & Van Belle, 1994). This chiton is reported here from a single specimen collected in Santa Monica Bay at a depth of 17 m. The specimen was a juvenile with a body length of 5 mm compared to a maximum length of 30 mm reported for this species (see Kaas & Van Belle, 1994). Other SCB chitons that co-occur with M. lowei include Lepidozona scrobiculata and Dendrochiton gothicus.

Mopalia phorminx Berry, 1919 (Plate 7, Figure 19)

Mopalia phorminx is considered a rather uncommon chiton with a reported distribution along the West Coast ranging from Prince William Sound, Alaska to San Pedro, California at depths ranging from 18 to 183 m (Clark, 1991; Kaas & Van Belle, 1994). This chiton is reported here from two specimens collected at separate sites off Palos Verdes at depths of 100 and 130 m, although the exact locations of these sites are currently unknown (D. B. Cadien, personal communication). The maximum length of the SCB specimens is 24 mm (mean = 22 mm), which is relatively large for this species (see Kaas & Van Belle, 1994). This species co-occurs with Lepidozona retiporosa.

Placiphorella mirabilis Clark, 1994 (Plate 8, Figure 20)

Placiphorella mirabilis occurs from Santa Barbara, southern California to Isla Cedros, Baja California at depths of 28-155 m (Clark, 1994; Kaas & Van Belle, 1994, as Placiphorella species 1). This species is known

from a total of four specimens in the present study that were collected during trawls conducted as part of the Southern California Bight Pilot Project in 1994. These chitons occurred at two different sites off San Diego, which ranged in depth from 43 to 104 m. The maximum length of the SCB specimens of *P. mirabilis* is 43 mm (mean = 24.5 mm), which is rather large compared to previous records for this species (see Clark, 1994). Another chiton found with *P. mirabilis* was *Lepidozona scrobiculata*.

Tonicella venusta Clark, 1999 (Plate 8, Figure 21)

Tonicella venusta occurs along the West Coast from south-central Alaska to Isla Cedros, Baja California from the intertidal to depths of 140 m (Clark, 1999). This chiton is reported here from a single specimen collected at a depth of 15 m just off of San Miguel Island, the westernmost of the northern Channel Islands. It should be noted that this island has a chiton fauna that is more normally typical of central California, not southern California. The chiton was curled with an estimated length of ~ 10 mm, which is consistent with published size records for this species (see Clark, 1999). This specimen of T. venusta was found living with Dendrochiton thamnoporus on a rock covered with a flat, encrusting red coralline alga (~ Lithothamnion) that was brought up in the jaws of a benthic grab (D. B. Cadien, personal communication).

Discussion

The present study brings to 16 the number of described chiton species known to occur along the continental shelf and upper slope of the Southern California Bight (SCB) in waters mostly deeper than 30 m based on collections provided by benthic monitoring programs in the region, plus three provisional species as well as a fourth possibly undescribed species (see Tables 1 and 2). Of the two extant chiton lineages, Lepidopleurida is represented only by Leptochitonidae (3 species), while Chitonida is represented by Chitonina: Ischnochitonidae (6 described and 3 provisional species) and Acanthochitonina: Mopaliidae (7 species). Seventeen other species are also likely to occur based on published bathymetric and geographic distributions (see Table 1 and below), which brings the region's estimated chiton fauna for these deeper waters to about 36 species. In contrast, Eernisse (1998) reported only six species in material collected in a survey of relatively deep waters (50-250 m) of the Santa Maria Basin and Western Santa

Barbara Channel (all also sampled here), but he cautioned that these were limited samples with at least another 13 species likely to occur in the region (i.e., 19 species total), probably living in rockier bottoms than generally sampled in this study.

It is notable that although the total number of chiton species is relatively high in the SCB benthos, only three of about 12 total extant taxa typically ranked at a family level worldwide are present and the diversity of genera within these three families is not impressive. The genera that are most diverse are also the most diverse in the northern Pacific. This is similar to chitons living in shallow waters along the West Coast, where higher-level taxonomic diversity is low but certain genera (e.g., Cyanoplax, Lepidozona, Mopalia, Tonicella) are either exclusively northern Pacific or else are by far most diverse there. Our review thus supports the general pattern that both the shallow and moderately deep fauna of the northern Pacific has both a high degree of endemism, with relatively few higher taxa present, but those taxa that are present are impressively species-rich.

The general lack of overlap between the chiton fauna above or below about 30 m depth has implications for the extent of population connectivity of cooler water "northern" species that so far have not been reported in shallow water off southern California. These have been found in shallow water from especially the coolest sides of the northern and western Channel Islands, and also from the intertidal of known upwelling sites south of Punta Banda, northern Baja California, in the southernmost SCB. Are these apparently disjunct populations actually connected to central California through individuals living at depths > 30 m off mainland southern California? Our results suggest not. Assuming that these species have not merely been overlooked in shallower water along southern California shores, we propose that it is more likely that population connectivity, if it occurs at all, must be the result of relatively long-distance dispersion of larvae from central California. Given the predominantly warm nature of any return currents to central California via the Davidson countercurrent, and the relatively rare occurrence of such southern "refugia," it could be much less likely that planktonic larvae from southern disjunct "cool water" populations could be expected to recruit back to central California. The existence of such "peripheral isolate" shallow water southern populations could reflect ongoing processes of genetic isolation that could be producing incipient species. This opportunity for speciation, combined with climate-related latitudinal shifts over geological time, could help explain the high diversity of certain species-rich genera in the shallow waters of the cool temperate West Coast. Most previous emphasis in the literature has been on the parallel situation of northern refuge populations of warm temperate species in the anomalously warm parts of central California, such as Monterey Bay. This latter well-documented pattern of northern refugia is probably most important for taxa extending north from the warmer latitudes, whereas southern refugia are probably more important to those taxa whose primary diversification has been in the cool northern Pacific (e.g., Kelly & Eernisse, 2008).

Two of the four most widely distributed and abundant chitons encountered in this study are lepidopleurids of the family Leptochitonidae; each occurred in at least 22% of the samples. These common species include Leptochiton rugatus (Figure 4) and Hanleyella oldroydi (Figure 2), which together comprised more than 35% of the chitons examined. As mentioned previously, a new study (Eernisse & Kelly, unpublished) has provided DNA-based evidence that what we have referred to as L. rugatus is actually an undescribed deep-water species, which is part of a complex of northern Pacific species related to the "true" L. rugatus of shallow waters. A second Leptochiton species, L. nexus (Figure 3), is reported from several specimens, while a third and possibly new species of Leptochiton is known from a single small individual. At least two other species of Leptochiton that are presently known from only depths of 160 m or below, L. americanus and L. cf. belknapi, could also occur along the SCB continental shelf and slope (see Ferreira, 1979b; Wu & Okutani, 1984; Kaas & Van Belle, 1985a, 1987; Schwabe, 2008; also R. N. Clark, personal communication). Multiple specimens of another lepidopleurid, all identified as Oldroydia percrassa, have been regularly collected in rock dredge samples taken off southern California (DJE, personal observation). Their identities need to be reevaluated in light of Sirenko & Clark's (2008) recent revival of the similar Deshayesiella spicata (Berry, 1919) from off San Diego and elsewhere along the West Coast (see below and also Kaas & Van Belle, 1985a).

Chitonina: Ischnochitonidae is represented by Lepidozona and Callistochiton. Lepidozona is the most diverse of the SCB chiton genera that occur at depths below 30 m, being represented here by five described species, including L. golischi, L. mertensii, L. radians, L. retiporosa, and L. scrobiculata (Figures 6-11). Of these, L. retiporosa and L. scrobiculata are the most common species, with each occurring in at least 20% of the samples and together accounting for about 29% of the chitons examined. Additionally, three likely new species of this genus, herein designated Lepidozona

spp. A, B and C, are reported (Figures 12-14). The genus Callistochiton is represented by a single species, C. palmulatus (Figure 5), which is known from two records in the present study. However, this species is probably much more common in deeper SCB waters than indicated here, having frequently been observed to live in vacant mussel bore holes in soft mudstone collected off San Pedro, Los Angeles County (DJE, observation). Two other species of Callistochiton, C. crassicostatus and C. decoratus, may also occur in deep water habitats of the region (see Ferreira, 1979a; Kaas & Van Belle, 1994; also see below). Endnote Additional genera and species of Chitonina that may occur in the SCB at the depths sampled in this study are Chaetopleura gemma, Stenoplax corrugata (see below), and Stenosemus stearnsii (see Ferreira, 1983; Kaas & Van Belle, 1987, 1990).

Acanthochitonina: Mopaliidae is represented by four genera with seven species. These include Dendrochiton gothicus and D. thamnoporus (Figures 15-16), Mopalia imporcata, M. lowei and M. phorminx (Figures 17-19), Placiphorella mirabilis (Figure 20), and Tonicella venusta (Figure 21). Each of these species occurred in no more than five samples in this study and, with the exception of D. gothicus, was represented by at most a few individuals. Additional Acanthochitonina species likely to occur in relatively deep waters of the region include Acanthochitona avicula within Acanthochitonidae, Lepidochitona beanii within Lepidochitonidae, and Mopalia acuta, Dendrochiton flectens, D. semiliratus and Placiphorella pacifica within Mopaliidae (e.g., Ferreira, 1982; Kaas & Van Belle, 1985b, 1994; Eernisse, 1986; Watters, 1990; Clark, 1994). Another species within Mopaliidae, Katharina tunicata, has also long been reported to range as far south as Santa Catalina Island and the Coronado Islands, and to occasionally reach depths down to 40 m (e.g., Pilsbry, 1893; Oldroyd, 1927; Ricketts et al., 1985; Kaas & Van Belle, 1994). We do not include K. tunicata as part of the SCB benthic fauna discussed herein as we consider this normally intertidal chiton unlikely to occur in any subtidal samples from > 30 m depth. Additionally, aside from its presence in fossil deposits near San Pedro (see Berry, 1922), we have been unable to verify any records of the species south of San Luis Obispo County in central California.

Two additional chitons have been recorded previously from monitoring activities in the region, but are considered dubious records and are not included here as part of the SCB fauna. These include the lepidopleurid, *Hanleya hanleyi*, and an unidentified species of *Ischnochiton* (i.e., *Ischnochiton* sp. in

SCAMIT, 1994, 1996).

The H. hanleyi record was based on a single chiton collected off Point Conception in 1977 by the Southern California Coastal Water Research Project (SCCWRP). Unfortunately, the specimen was disposed of long ago (D. Tsukada, personal communication), and therefore the identification could not be verified. However, we agree with Ferreira (1979b) that Hanleya is not present in Pacific waters, or at least not in the eastern Pacific. Ferreira attributed previous eastern Pacific references to H. hanleyi by Oldroyd (1927), Smith (1947a, 1947b), Smith & Gordon (1948), and Jakovleva (1952) as probable misidentifications of juvenile Oldroydia percrassa (Dall, 1894). We agree that this is a good possibility, but it might alternatively be the nominal species that Sirenko & Clark (2008) have recently revived, Deshayesiella spicata (Berry, 1919). These authors regard D. spicata to be highly similar to O. percrassa but with a less conspicuously elevated jugal ridge and less projecting jugal articulamentum (the latter seen only in disarticulated valves). Deshayesiella spicata was first proposed as *Hanleya spicata* by Berry (1919b) and we have included it in our key, directly quoting their (Sirenko & Clark, 2008) primary distinctions between these nominal species. The contrast is complicated by the small size (4.5 mm length) of the holotype of D. spicata and the fact that this holotype has not yet been contrasted with typical O. percrassa of a similar size. It remains to be seen whether future studies will confirm these as distinct species or find instead that the differences reflect intraspecific variation, perhaps due to microhabitat differences experienced by the chitons. Larger "spicata" specimens similar to those described by Sirenko & Clark (2008) have been observed by one of us (DJE), taken by rock dredges off San Pedro in Los Angeles County, whereas several typical specimens of O. percrassa have been observed from slightly shallower depths off Point Loma in San Diego County (see below) and from the subtidal of Monterey County, central California (A. Draeger, personal communication). A third possibility is that the "Hanleya hanleyi" animal was a misidentification of Hanleyella oldroydi, which is relatively common in SCB samples, and may bear a superficial resemblance to Hanleya to non-chiton workers in terms of valve and girdle morphology.

It is unknown which species or even which genus the unidentified "Ischnochiton" may represent. Although one species of Stenosemus (considered by some a subgenus of Ischnochiton), S. stearnsii, could range into the shelf and upper slope depths sampled off southern California as noted above, this species is so far known

from only much deeper waters (> 400 m) and has not been confirmed by benthic monitoring programs in the region. It is more likely that the specimen represented a misidentification of Lepidozona radians or L. retiporosa, which are each known from the present study. Both species have previously been placed within *Ischnochiton*, probably because neither has the pronounced dorsal sculpturing apparent in other members of Lepidozona, and their assignment to Lepidozona partly depends on valve features only visible after valves are disarticulated (e.g., "jugal plate separated from apophyses by small notches" in Kaas & Van Belle, 1987). Another, somewhat doubtful, possibility is that the specimen could have been Ischnochiton newcombi Carpenter in Pilsbry, 1892 (type locality "California, Sta. Catalina Island"), which is only known from the holotype (see Kaas & Van Belle, 1990).

Finally, it is remarkable that southern California still lacks a complete treatment of chitons for shallower depths than those covered here. While intertidal chitons are relatively well known, very little is known about subtidal chitons accessible by SCUBA. Three examples were brought to light by the recent examination of collections made by the late David Mulliner while diving about one mile off the coast of Point Loma, San Diego, each species which is also likely to occur in deeper waters of the region (see Table 1). The first is a lot of five specimens of typical Oldroydia percrassa (Plate 9, Figure 22), which were collected at depths of 15-18 m in October 1972. We fully expect that this species will eventually be collected at depths that were the focus of this study. Likewise, two lots of Callistochiton decoratus (Figure 23), representing 15 specimens also collected from 15-18 m in 1972 and 1975, reveal that this species is relatively common at those depths, and it seems likely it may also occur in deeper waters of the region. Finally, a single individual of the rare Stenoplax corrugata (Figure 24), which was the first specimen either of us had ever seen, was collected at 18-20 m in February 1973 and originally identified as "Stenoplax sp." After we had studied this specimen, DJE collected a second S. corrugata specimen off San Pedro using a rock dredge (February 29, 2008; length ~35 mm; 23-29 m on a rock). Again, it is likely that this species occurs at the depths treated herein, but has been missed because of its rarity or because it is restricted to a specific unsampled rocky bottom habitat. It is our hope that we can next undertake a companion contribution on the intertidal and shallow subtidal chitons of southern California and northern Baja California, but we will need the similar cooperation of those dedicated to discovering the habitat and ecology of chitons accessible by diving.

Endnote

As part of this study we also investigated a suggestion made by Coan (1985) and adopted in Turgeon et al. (1998) to recognize little-known descriptions provided by Josiah Keep in 1887 for two species of Callistochiton that occur in southern California waters. If valid this would a) affect the authority for C. decoratus giving priority to Keep (1887) instead of Carpenter MS, Pilsbry, 1893, and b) make C. crassicostatus Pilsbry, 1893, a junior synonym of C. fimbriatus Keep, 1887. The additional description of C. palmulatus Carpenter MS in Keep (1887) would not have similar priority because this name was validated earlier as C. palmulatus Carpenter MS, Dall, 1879, a name for which Ferreira (1979a) has designated a neotype. Below is a summary of our findings.

Briefly, Keep (1887) provided short descriptions of C. decoratus, C. palmulatus, and C. fimbriatus, in this order and all attributed to Carpenter's manuscript. No figures were provided in support of these descriptions and, unfortunately, no specimens identified as C. decoratus or C. fimbriatus exist in all that apparently remains of the Keep Collection, which is now housed at Tohoku University (Sendai, Japan). There is one Callistochiton included in the collection, a complete set of disarticulated valves, identified on the outside of the vial as "Callistochiton palmulatus Cpr Monterey" (H. Saito and J. Nemoto, personal communication). Further complicating matters, our study of the images of these valves provided courtesy of J. Nemoto have revealed that they correspond instead to C. crassicostatus.

Based on our review of the available information, we feel that Keep's descriptions of C. decoratus and C. fimbriatus are inadequate to distinguish these taxa from each other or any other species of Callistochiton. Additionally, given the sparse and inadequate descriptions of these species in Keep (1887), the lack of identified specimens of either C. decoratus or C. fimbriatus in the Keep Collection, and the misidentification of Keep's C. palmulatus material, we do not believe it is possible to reliably determine which species of Callistochiton Keep was referring to in each of his descriptions. Thus, we consider Keep's designations of these two species in 1887 to be nomina dubia, and herein retain Callistochiton crassicostatus Pilsbry, 1893, and Callistochiton decoratus Carpenter MS, Pilsbry, 1893, as the oldest available names and authorities for these chitons (see Table 1).

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SPECIES PLATES (Figures 2-24)

and

APPENDIX A

PLATE 1 (Figures 2-4)

Figure 2. Hanleyella oldroydi (Bartsch MS, Dall, 1919). (a) Dorsal view of specimen, 4 mm length, collected west of Mission Bay, San Diego County, California at a depth of 88 m; (b) Lateral view of live specimen, ~5 mm length, collected southwest of Point Loma, San Diego County, California at a depth of 90 m.

Figure 3. Leptochiton nexus Carpenter, 1864. Dorsal view of 9.3 mm long specimen collected just south of San Miguel Island, northern Channel Islands, California at a depth of 71 m.

Figure 4. Leptochiton rugatus (Carpenter in Pilsbry, 1892). Specimen, 5.4 mm length, collected southwest of La Jolla, San Diego County, California at a depth of 117 m: (a) Dorsal view of whole animal; (b) Lateral view of whole animal.

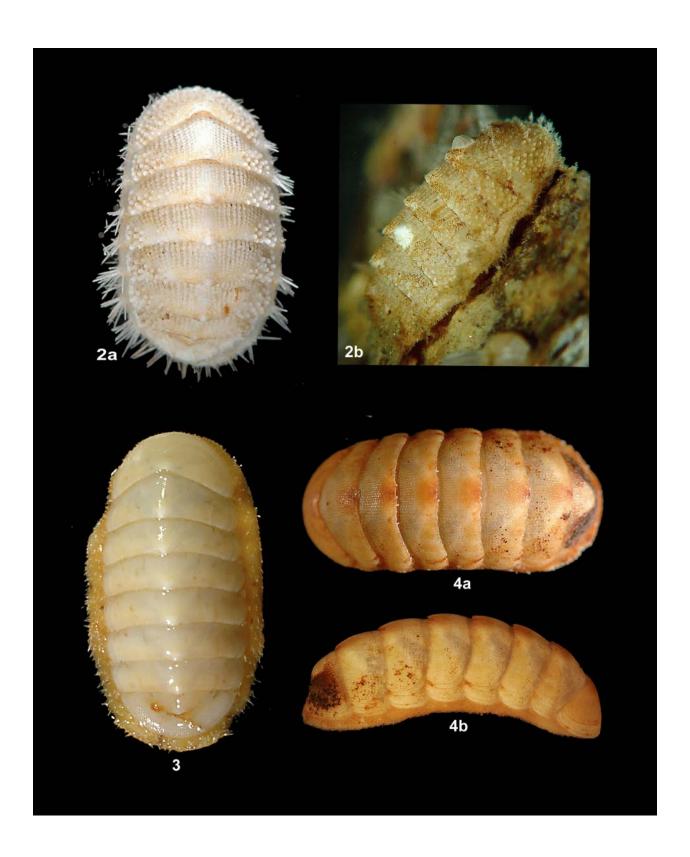


PLATE 2 (Figures 5-7)

Figure 5. Callistochiton palmulatus Carpenter MS, Dall, 1879. Dorsal-lateral view of 13 mm long specimen with typical bulging, fist-shaped tail valve, collected southwest of La Jolla, San Diego County, California at a depth of 85 m.

Figure 6. Type specimens of *Lepidozona scabricostata* (Carpenter, 1964) and *Ischnochiton (Lepidozona) golischi* Berry, 1919. (a) Dorsal view of holotype of *L. scabricostata* (USNM 16268; image courtesy of A. Draeger); (b) Dorsal view of lectotype of *I. (L.) golischi* (SBMNH 34395; image courtesy of P. Valentich-Scott and P. Sadeghian); (c) Enlarged view of lateral and central areas of *I. (L.) golischi* lectotype.

Figure 7. Lepidozona golischi (Berry, 1919). Specimen, 22.5 mm length, collected west of Imperial Beach, San Diego County, California at a depth of 98 m: (a) Dorsal view of whole animal; (b) Head valve region; (c) Tail valve region; (d) Lateral areas of intermediate valves; (e) Girdle scales.

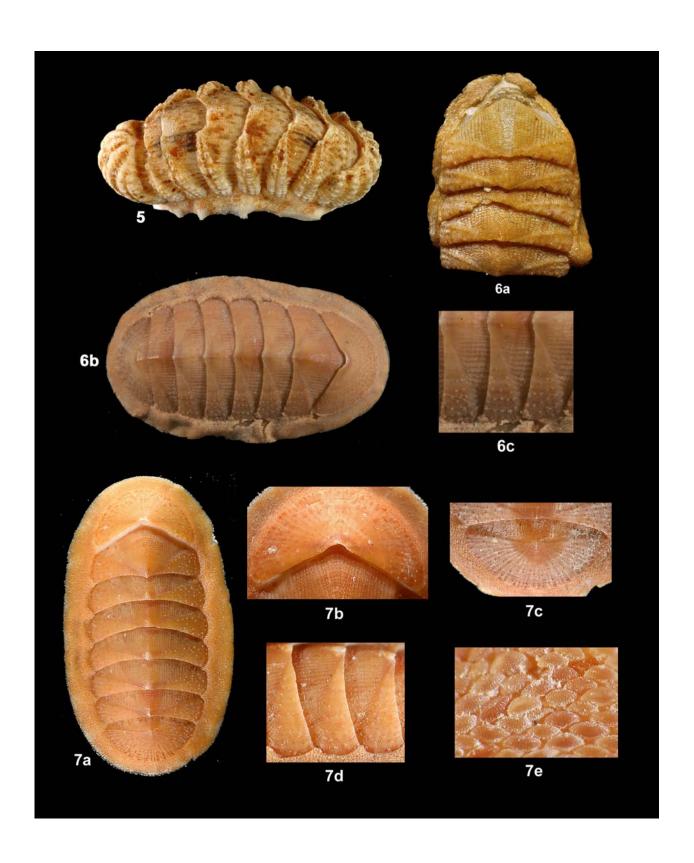


PLATE 3 (Figures 8-9)

Figure 8. Lepidozona mertensii (von Middendorff, 1847). Specimen, 15 mm length, collected west of Imperial Beach, San Diego County, California at a depth of 80 m: (a) Dorsal view of whole animal; (b) Head valve region; (c) Tail valve region; (d) Lateral areas of intermediate valves; (e) Girdle scales.

Figure 9. Lepidozona radians (Carpenter in Pilsbry, 1892). (a) Dorsal view of olive green and brown specimen, 6.9 mm length, collected west of the Tijuana River, San Diego County, California at a depth of 14 m; (b) Girdle scales of previous chiton; (c) Dorsal view of white specimen, 7.4 mm length, collected off Santa Cruz Island, northern Channel Islands, California.

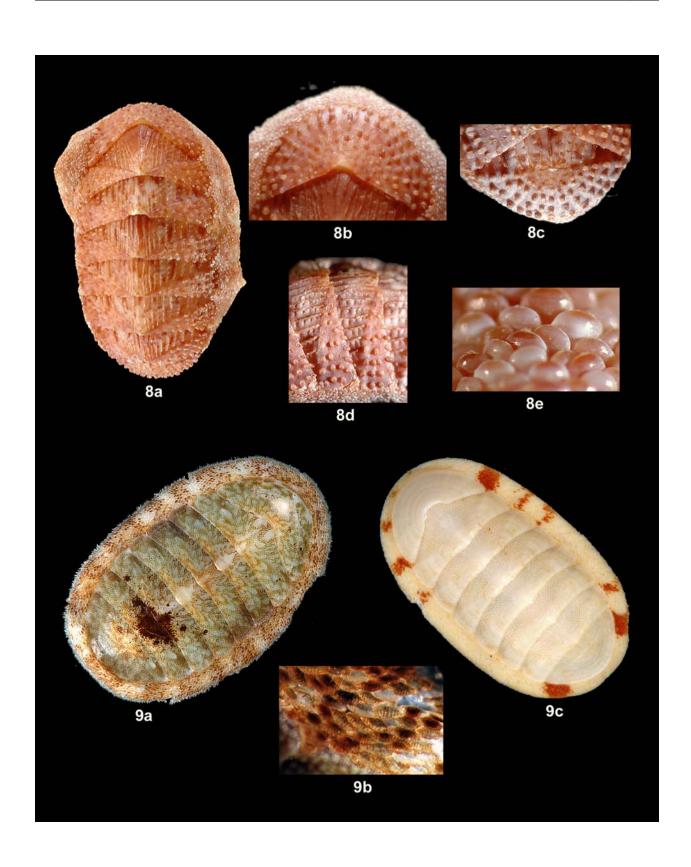


PLATE 4 (Figures 10-11)

Figure 10. Lepidozona retiporosa (Carpenter, 1864). Specimen, 17 mm length, collected west of Imperial Beach, San Diego County, California at a depth of 98 m: (a) Dorsal view of whole animal; (b) Head valve region; (c) Tail valve region; (d) Lateral areas of intermediate valves; (e) Girdle scales.

Figure 11. Lepidozona scrobiculata (von Middendorff, 1847). Specimen, 15.8 mm length, collected west of the Tijuana River, San Diego County, California at a depth of 28 m: (a) Dorsal view of whole animal; (b) Head valve region; (c) Tail valve region; (d) Lateral areas of intermediate valves; (e) Girdle scales.

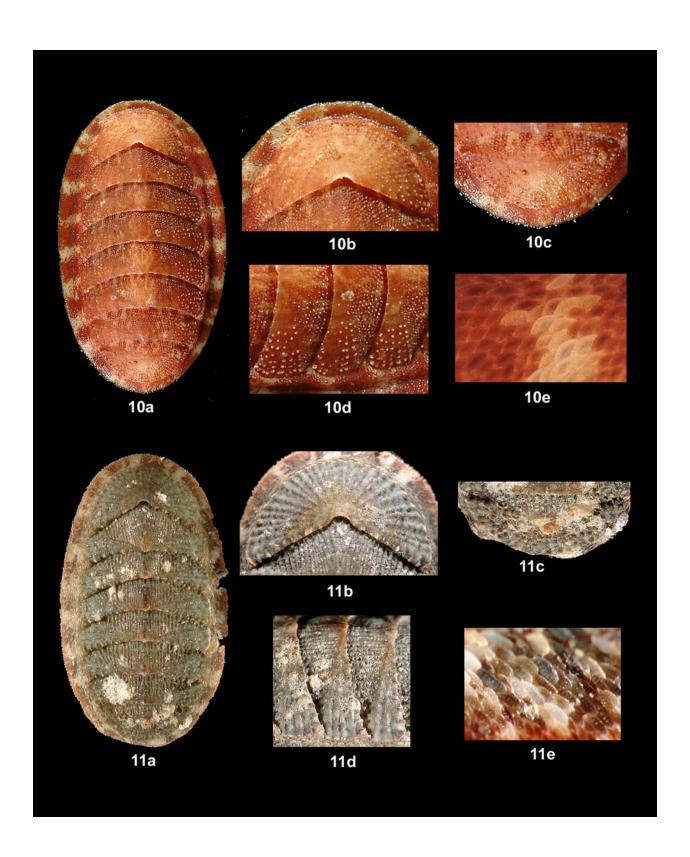


PLATE 5 (Figures 12-13)

Figure 12. Lepidozona sp. A. Specimen, 12.1 mm length, collected southwest of Point Loma, San Diego County, California at a depth of 101 m: (a) Dorsal view of whole animal; (b) Head valve region; (c) Tail valve region; (d) Lateral areas of intermediate valves; (e) Girdle scales.

Figure 13. Lepidozona sp. B. Specimen, 13 mm length, collected off Palos Verdes, Los Angeles County, California at a depth of 305 m: (a) Dorsal view of whole animal; (b) Head valve region; (c) Tail valve region; (d) Lateral areas of intermediate valves; (e) Girdle scales.

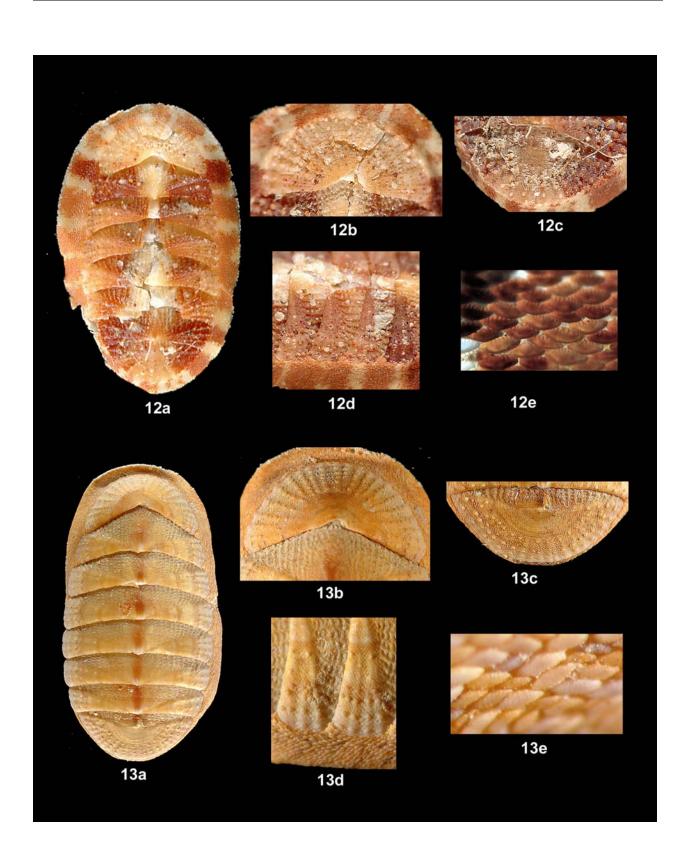


PLATE 6 (Figures 14-16)

Figure 14. *Lepidozona* sp. C. Specimen, 19.5 mm length, collected southwest of Point Loma, San Diego County, California at a depth of 90 m: (a) Dorsal view of whole animal; (b) Head valve region; (c) Tail valve region; (d) Lateral areas of intermediate valves; (e) Girdle scales.

Figure 15. Dendrochiton gothicus (Carpenter, 1864). Dorsal view of 5.2 mm long specimen collected in Santa Monica Bay, Orange County, California at a depth of 17 m.

Figure 16. Dendrochiton thamnoporus (Berry, 1911). (a) Dorsal view of 6 mm long specimen collected west of La Jolla, San Diego County, California at a depth of 27 m; (b) Dorsal view of 7.3 mm long specimen collected southwest of the Tijuana River, San Diego County, California at a depth of 38 m.

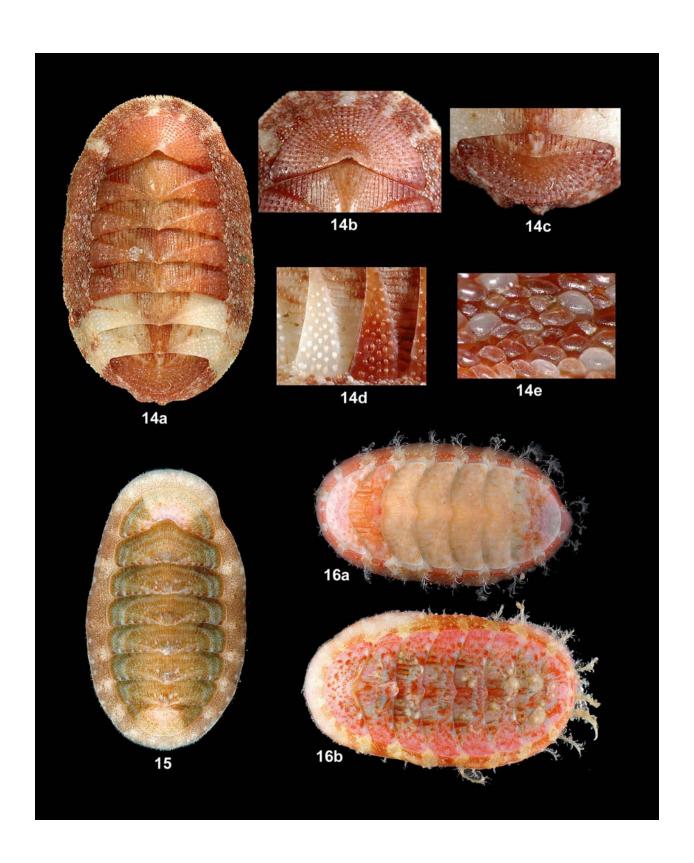


PLATE 7 (Figures 17-19)

Figure 17. Mopalia imporcata Carpenter, 1864. (a) Dorsal view of juvenile chiton, 3.5 mm length, collected just south of Santa Rosa Island, northern Channel Islands, California at a depth of 46 m; (b, c) Close-ups of girdle bristles of juvenile chiton; (d) Anterior end of 15 mm long adult chiton collected in Santa Monica Bay at a depth of \sim 69 m; (e) Close-up of girdle bristle of adult chiton.

Figure 18. *Mopalia lowei* Pilsbry, 1918. Juvenile chiton, 5 mm length, collected in Santa Monica Bay, Orange County, California at a depth of 17 m; (a) Dorsal view of whole animal; (b) Close-up of girdle bristles.

Figure 19. Mopalia phorminx Berry, 1919. Specimen, 20 mm length, collected off Palos Verdes, Los Angeles County, California at a depth of 100 m: (a) Dorsal view of whole animal: (b) Close-up of girdle bristles.

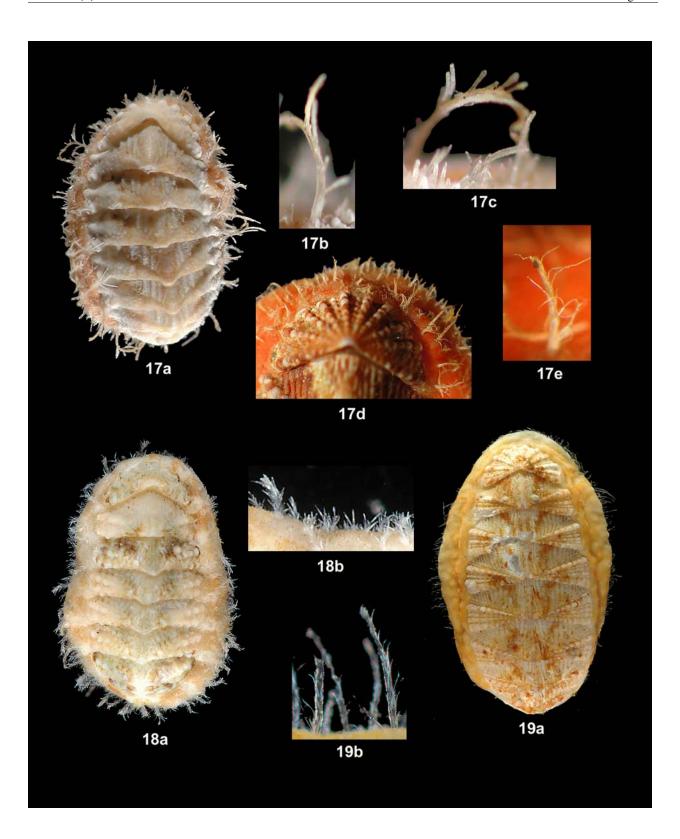


PLATE 8 (Figures 20-21)

Figure 20. Placiphorella mirabilis Clark, 1994. Specimens collected southwest of La Jolla, San Diego County, California at a depth of 104 m: (a) Dorsal view of ~ 17 mm preserved "green" specimen; (b) Dorsal view of ~ 18 mm preserved "red" specimen; (c) Dorsal view of live specimen, ~ 25 mm length, showing typical girdle pigmentation.

Figure 21. *Tonicella venusta* Clark, 1999. Curled specimen, ~ 10 mm length, collected just off the eastern side of San Miguel Island, northern Channel Islands, California at a depth of 15 m: (a) Dorsal view of whole animal showing valves I-VI; (b) Enlarged view of valves III-VI.

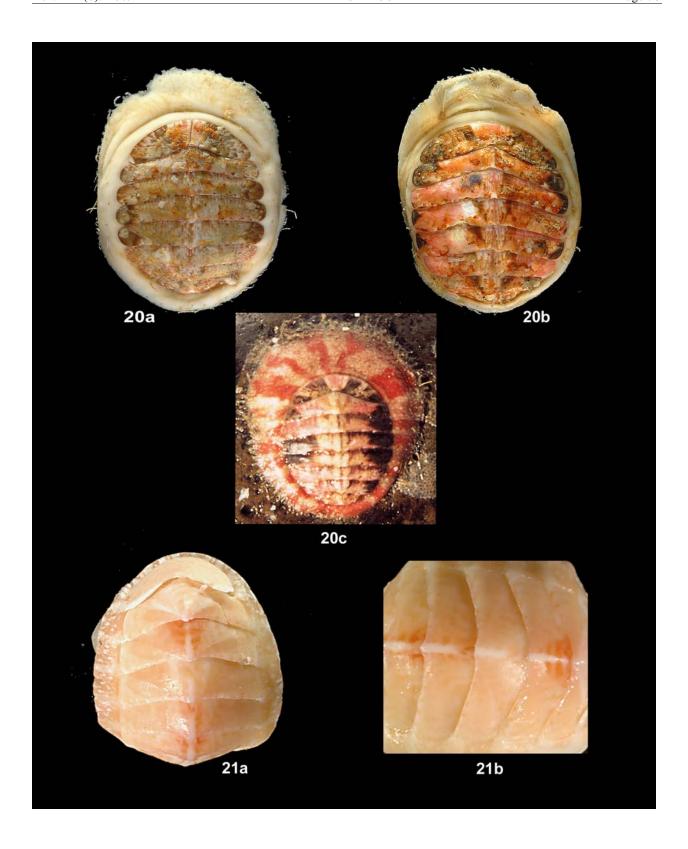
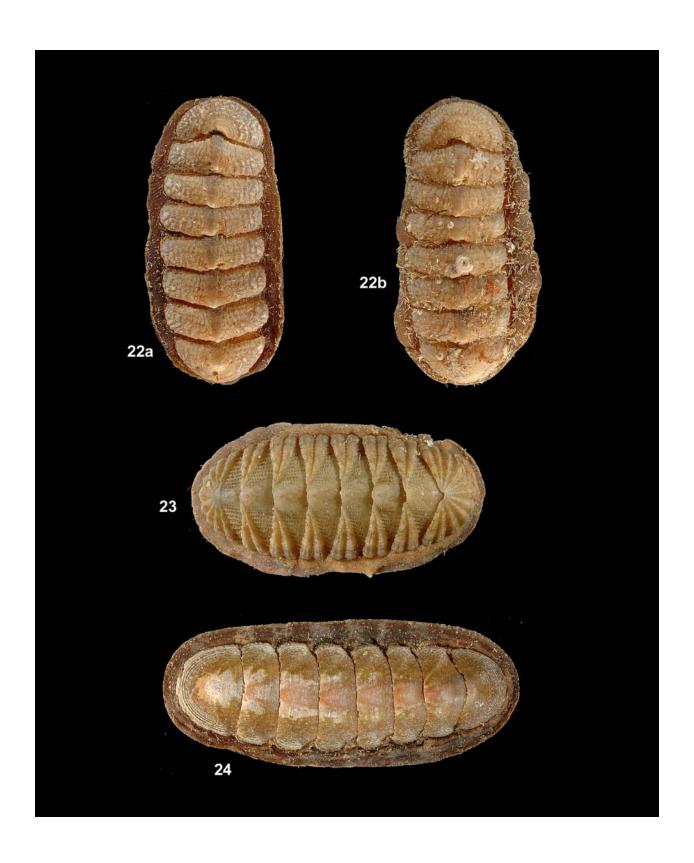


PLATE 9 (Figures 22-24)

Figure 22. Oldroydia percrassa (Dall, 1894). Specimens collected by D. Mulliner, scuba diving, 1 mile offshore of Point Loma, San Diego County, California, depth of 50-60 ft, Oct. 1972, (UMMZ Cat. No. 252687): (a) Dorsal view of 22 mm specimen; (b) Dorsal view of 21 mm specimen with girdle spines intact (not broken off).

Figure 23. Callistochiton decoratus Carpenter MS, Pilsbry, 1893. Dorsal view of specimen, 20 mm length, collected by D. Mulliner, scuba diving, 1 mile offshore of Point Loma, San Diego County, California, depth of 50-60 ft, Oct. 1972, (UMMZ Cat No. 252668).

Figure 24. Stenoplax corrugata (Carpenter in Pilsbry, 1892). Dorsal view of specimen, 24.5 mm length, collected by D. Mulliner, scuba diving, 1 mile offshore of Point Loma, San Diego County, California, depth of 60-65 ft, Feb. 1973, (UMMZ Cat. No. 252650).



Appendix A. List of stations from North to South where chitons have been collected in the Southern California Bight (SCB) by regular or regional benthic monitoring programs (see Figure 1). Species collected at each site from single or multiple samples are indicated (N = number of chiton samples/station). Monitoring programs principally responsible for sampling each station are City of San Diego (CSD), Orange County Sanitation District (OCSD), City of Los Angeles (CLA), Los Angeles County Sanitation Districts (LACSD), 1994 SCB Pilot Project (SCBPP), and 1998, 2003 and 2008 SCB Regional Monitoring Programs (Bight'98, Bight'03, Bight'08). Main regions within the SCB where chitons were collected include northern Baja California (BC), San Diego (SD), Orange County (OC), Palos Verdes (PV), Santa Monica Bay (SMB), Point Conception (PC), and the northern Channel Islands (CI), the latter including sites off San Miguel Island (SMI), Santa Rosa Island (SRI), Santa Cruz Island (SCI), and Anacapa Island (AI). * = coordinates unknown (stations not shown in Figure 1).

Station	N	Depth (m)	Latitude (°N)	Longitude (°W)	Monitoring Program	Region	Species Present
103	1	93	34.421	120.184	SCBPP	PC	H. oldroydi
PC-1	1	150	*	*	LACSD	PC	L. rugatus, L. radians
2480	1	106	34.150	120.355	Bight'98	CI(SMI)	L. rugatus
2477	1	15	34.058	120.405	Bight'98	CI(SMI)	D. thamnoporus, T. venusta
4255	1	207	34.052	120.558	Bight'03	CI(SMI)	L. rugatus
2491	1	95	34.011	120.475	Bight'98	CI(SMI)	L. rugatus
4159	1	71	33.995	120.337	Bight'03	CI(SMI)	L. nexus, L. rugatus
4417	1	46	33.890	120.082	Bight'03	CI(SRI)	M. imporcata
2538	1	120	34.101	119.729	Bight'98	CI(SCI)	L. radians
2518	1	112	34.097	119.737	Bight'98	CI(SCI)	L. rugatus, L. retiporosa
2493	1	44	34.079	119.888	Bight'98	CI(SCI)	L. scrobiculata
2479	1	84	34.069	119.770	Bight'98	CI(SCI)	L. rugatus
4029	1	75	34.034	119.352	Bight'03	CI(AI)	H. oldroydi, L. nexus, L. rugatus, L. retiporosa, Lepidozona sp.
E1	1	150	33.988	118.714	CLA	SMB	L. rugatus
A1	6	15-18	33.986	118.502	CLA	SMB	L. nexus, L. scrobiculata, D. gothicus, D. thamnoporus, M. lowei
NB1	1	70	33.913	118.555	CLA	SMB	L. nexus, L. rugatus
Z2	2	60	33.912	118.521	CLA	SMB	L. retiporosa, L. scrobiculata
D1	1	74	33.912	118.550	CLA	SMB	L. retiporosa

Station	N	Depth (m)	Latitude (°N)	Longitude (°W)	Monitoring Program	Region	Species Present
FA13	1	82	33.907	118.568	CLA	SMB	L. nexus
Short Bank	2	56	33.893	118.538	CLA	SMB	H. oldroydi, L. mertensii, L. retiporosa
FA10	1	54	33.885	118.508	CLA	SMB	L. rugatus
7415	1	69	33.856	118.516	Bight'08	SMB	M. imporcata
T0-60	1	~ 60	33.814	118.431	LACSD	PV	L. retiporosa
T1-1000	1	305	33.726	118.427	LACSD	PV	L. rugatus, L. retiporosa, Lepidozona sp. B
V50	1	50	33.667	118.269	LACSD	PV	H. oldroydi
V80/V50	1	48-90	33.667	118.273	LACSD	PV	L. scrobiculata
E40	1	40	33.666	118.268	LACSD	PV	L. rugatus
E60	1	60	33.655	118.274	LACSD	PV	L. nexus
E-80	1	82	33.652	118.276	LACSD	PV	L. retiporosa
TA-100	1	100	*	*	LACSD	PV	M. phorminx
TA-130	1	130	*	*	LACSD	PV	L. retiporosa, M. phorminx
Т3	1	55	33.581	117.956	ocs	OC	L. retiporosa
2015	1	109	32.868	117.332	CSD	SD	L. rugatus
2137	1	48	32.852	117.314	CSD	SD	L. rugatus
B5	1	62	32.821	117.327	CSD	SD	H, oldroydi, L. retiporosa
2655	1	27	32.818	117.301	CSD	SD	D. thamnoporus, L. scrobiculata
1767	1	85	32.805	117.347	SCBPP	SD	C. palmulatus, L. mertensii
2145	1	117	32.803	117.370	CSD	SD	L. rugatus
1774	1	104	32.793	117.370	SCBPP	SD	P. mirabilis
B11	8	88	32.776	117.356	CSD	SD	H. oldroydi, L. rugatus, L.retiporosa
2023	3	89-91	32.775	117.358	CSD	SD	H. oldroydi, L. rugatus, L. radians
B13	4	116	32.773	117.377	CSD	SD	H. oldroydi, L. rugatus, Leptochiton sp.
SD14	1	100	32.738	117.349	CSD	SD	L. retiporosa

Station	N	Depth (m)	Latitude (°N)	Longitude (°W)	Monitoring Program	Region	Species Present
2663	1	130	32.731	117.352	CSD	SD	L. rugatus
SD13	1	101	32.714	117.338	CSD	SD	L. golischi, L. scrobiculata
A16	1	61	32.676	117.284	CSD	SD	H. oldroydi
SD9	3	88-92	32.654	117.314	CSD	SD	L. retiporosa, L. scrobiculata
2125	1	157	32.645	117.433	CSD	SD	L. rugatus, L. retiorosa
2035	1	149	32.639	117.431	CSD	SD	L. retiporosa
7029	1	150	32.636	117.417	Bight'08	SD	L. rugatus
2189	1	191	32.635	117.357	CSD	SD	H. oldroydi
2190	1	99	32.628	117.328	CSD	SD	H. oldroydi
SD8	3	90-99	32.626	117.323	CSD	SD	H. oldroydi, L. retiporosa, Lepidozona sp. C
4388	1	141	32.593	117.391	Bight'03	SD	H. oldroydi, L. retiporosa
SD7	1	98-101	32.584	117.307	CSD	SD	L. golischi, L. retiporosa, L. scrobiculata, Lepidozona sp. A
2336	1	9	32.577	117.143	Bight'98	SD	L. radians
2095	1	80	32.577	117.281	CSD	SD	C. palmulatus, L. mertensi
SD19	1	28	32.558	117.185	CSD	SD	L. scrobiculata
2334	1	14	32.552	117.143	Bight'98	SD	L. rugatus, L. radians, L. scrobiculata
2001	1	43	32.546	117.232	SCBPP	SD	L. scrobiculata, P. mirabilis
2335	1	18	32.545	117.155	Bight'98	SD	L. scrobiculata
SD18	1	30	32.543	117.189	CSD	SD	L. scrobiculata
I16	1	23	32.538	117.183	CSD	SD	L. scrobiculata
I13	1	38	32.538	117.212	CSD	SD	D. thamnoporus, M. imporcata
SM152	1	31	32.485	117.179	CSD	BC	L. radians
SD15	1	29	32.473	117.175	CSD	ВС	L. scrobiculata, D. thamnoporus

ERRATA *

Stebbins, T. D., and D. J. Eernisse. 2009. Chitons (Mollusca: Polyplacophora) known from benthic monitoring programs in the Southern California Bight. *The Festivus*, (Special Issue) 41(6): 53-100

- 1. **Cover photo caption (facing page 53):** The chiton depicted in the cover photo is *Lepidozona* sp. C (not *Lepidozona* sp. A). The correct legend should be:
 - Live specimen of *Lepidozona* sp. C occurring on a piece of metal debris collected off San Diego, southern California at a depth of 90 m. Photo provided courtesy of R. Rowe.
- 2. **Page 56:** The symbol † next to "Sources" at the top right of Table 1 on this page should be changed to a ‡ to match the footnote at the bottom of the page (i.e., Sources ‡).
- 3. **Page 58:** In the footnote at the bottom of the page, *Leptochiton* cf. *belknapi* should be spelled with a period after the "cf" instead of a comma.
- 4. **Page 80:** In the caption for Figure 2, the sample depth listed for the chiton depicted in Figure 2a should be 88 m instead of 18 m. The correct legend should be:
 - Figure 2. *Hanleyella oldroydi* (Bartsch MS, Dall, 1919). (a) Dorsal view of specimen, 4 mm length, collected west of Mission Bay, San Diego County, California at a depth of 88 m; (b) Lateral view of live specimen, ~5 mm length, collected southwest of Point Loma, San Diego County, California at a depth of 90 m.

* The above errata to the original hardcopy version of this paper that was published on June 11, 2009 will be published in a forthcoming issue of *The Festivus*. However, these errors have already been corrected in this PDF version of the paper. [TDS, June 2009]