

Calliostoma and *Akoya* of the Californian Marine Province (Gastropoda: Calliostomatidae)

Paul M. Tuskes & Ann McGowan-Tuskes
3808 Sioux Ave., San Diego, California, 92117
tuskes@aol.com

ABSTRACT Fifteen species of Calliostomatidae are known to occur in the Californian marine province. Biological observations *in situ* on shallow water species indicates they are primarily carnivores, feeding on sessile organisms such as sponge, bryozoan, hydrozoa, diatoms and various Cnidaria. Adult variation, distribution, depth, and habitat are discussed and a summary of distribution records are provided for unique species. Analysis of shell morphology indicates *Akoya titanium* is a synonymy of *A. platinum*. A review of museum material also suggests that *C. splendens* appears to be correctly placed as a synonym of *C. supragranosm*. A new species of *Calliostoma* from the most southern portion of the Californian marine province is described and illustrated.

KEY WORDS *Calliostoma*, *Akoya*, *Callisotoma guerreroensis*, Calliostomatidae, Californian Marine Province, diet, distribution.

INTRODUCTION

The Calliostomatidae constitutes a unique group of snails which had long been placed in the family Trochidae (Rafinesque, 1815). Although the family Calliostomatidae are quite diverse, only two genera are known from the Californian Marine Province (MP), *Akoya* (Habe, 1961) and *Calliostoma* (Swainson, 1840). Both have a closed umbilicus and tend to be pyramidal in shape with thin spiral ridges called threads (lirae) that may be smooth or beaded; larger threads are called cords. The shell of *Calliostoma annulatum* (Lightfoot, 1786) has beaded threads and cords (Figure 1), while the cords of *Calliostoma canaliculatum* (Lightfoot, 1786) are not beaded giving the texture of the shell a different feel and appearance (Figure 2).

Within the Californian MP, there are at least 15 species of Calliostomatidae, approximately two-thirds of which are shared with the Oregonian MP to the north, and one-third with the Panamic MP to the south. *Calliostoma turbinum* (Dall,

1896) is the only species thought to be endemic to the Californian MP. Because many of the same species occur in multiple marine provinces, relevant observations from both the Oregonian and Panamic MP are included as appropriate.

The Californian MP extends from Point Conception, Santa Barbara County, California south to the area of Bahia Asuncion, Baja California Sur, Mexico. The cool waters of the Oregonian MP lay mostly north of Point Conception. The transition zone between the Oregonian and Californian MP is relatively narrow while, the transition zone between the Californian and Panamic MP is very broad.

North of Point Conception, the authors have found *C. canaliculatum*, *C. ligatum* (Gould, 1849), *C. gloriosum* (Dall, 1871), *C. gemmulatum* (Carpenter, 1864), and *C. tricolor* (Gabb, 1865), in rocky intertidal habitat during minus tides; occasionally *C. annulatum* is also found there. In southern California, summer surface water temperatures are 74° to 80° F, as a

result, these and other cool water *Calliostoma* from the Oregonian MP are typically found only subtidally, and often below the thermocline. Approximately 25% of the Calliostomatidae species in the Californian MP are most frequently found at depths greater than 90 m.

Abbreviations

(ANSP)	Academy of Natural Sciences, Philadelphia, PA
(SIO)	Benthic Invertebrate collection, Scripps Institute of Oceanography, CA
(CM)	Carnegie Museum, Pittsburg, PA
(CSDOMP)	City of San Diego Ocean Monitoring Program, CA
(LACM)	Natural History Museum of Los Angeles County, CA
(SBMNH)	Santa Barbara Museum of Natural History, CA
(SDMNH)	San Diego Museum of Natural History, CA
(USNM)	United States National Museum, Smithsonian, Washington D.C.
(BCS)	Baja California Sur, Mexico
(MP)	Marine Province
(PNW)	Post Nuclear Whorl
RV	Research Vessel

METHODS

In addition to visiting the above museums, private collections in southern California were examined.

To address the identity of the three large white deep water *Akoya*, the holotypes of *Akoya platinum* (Dall, 1890), *A. titanium* (McLean, 1984) and *A. bernardi* (McLean, 1984) were examined and the descriptions reviewed. A table was made of characters used to score each shell: (1) peripheral cord (weak vs. strong), (2) threaded above the peripheral cord on final whorl (no, weak, strong), (3) threads above the

peripheral cord beaded (no, weak, strong), (4) post nuclear whorl 1 (PNW) with crenulation (yes, no), (5) shoulder immediately below suture tabulated (no, weak, strongly) and, (6) shoulder cord of body whorl beaded (no, weak, strongly). Shell shape, texture and luster were found to be inconsistent characters and therefore were not utilized as characteristics for determining identity. Each shell was evaluated for these six characteristics and the data entered into a spread sheet.

Once evaluated the shell was scored based on its similarity to the type series of each taxa. For example, if the specific character was strongly defined on the type, but absent on the shell examined the score was zero, if weakly developed it received a half point, and if similar to the type it received 1 point. Shells with characters close to the type could score 4.5-6 points (representing an overall character similarity of 75 - 100%), while dissimilar shells would score lower. Characters were evenly weighted. The data was then sorted in any number of ways to examine character associations, and the similarity of each shell to the types. Shells were considered to be intermediate if none of the 3 scoring opportunities met or exceeded 75% similarity.

DIET AND REPRODUCTION

The diet of only a few west coast calliostomids has been confirmed by field observation and gut analysis. *Calliostoma* are omnivorous with a strong preference for sessile invertebrates and a few species may consume kelp. The diet undoubtedly varies by location and opportunity. In Washington, Perron (1975) found that the gut of *C. annulatum* contained sponge spicules and both *C. annulatum* and *C. variegatum* (Carpenter, 1864) fed *in situ* on various species of hydroids, while *C. ligatum* fed mostly on diatoms. In captivity, he reported *C. ligatum*

also consumed hydroids while *C. annulatum* fed on sea pens, bryozoans, anemones, nudibranch eggs, and dead animal material. Harbo (2007) illustrated *C. variegatum* feeding on hydrocoral *Stylaster californicus* (Verrill, 1866). In Alaska, Stone, *et al.* (2014) photographed *Akoya platinum* (Dall, 1890) feeding on the gorgonian *Primnoa pacifica* (Kinoshita, 1907) at 200 m. Deep water species are probably both opportunistic predators and scavengers.

Three species are periodically associated with kelp fronds. In central California, Lowry, *et al.* (1974) reported *C. annulatum*, *C. canaliculatum* and *C. ligatum* were found predominately on the reproductive growth of the brown kelp *Cystoseira* sp. in the spring and summer, but during the fall *C. annulatum* and *C. canaliculatum* moved to *Macrocystis* sp. while *C. ligatum* moved to rock substrate. They also discussed the vertical movement of these species on kelp stipe. These observations have been interpreted by some that they were consuming the kelp but that is not stated in the paper. R.H. Morris *et al.* (1990) reported *C. annulatum* fed on the anemone *Corynactis californica* (Carlgren, 1936), which occur on hard substrate, and both *C. annulatum* and *C. ligatum* fed to some extent on the fronds of brown kelp such as *Macrocystis pryerifera* (L) and *Cystoseira* sp. Both of these *Calliostoma* have a digestive enzyme laminarinase, that assists with the breakdown of the main carbohydrate in kelp, Morris, *et al.* (1990).

In southern California, *C. annulatum* and *C. canaliculatum* have been observed grazing on microfauna that live on the kelp fronds. In Mission Bay, *C. gloriosum* was observed feeding on sponge, and *C. supragranosum* (Carpenter, 1864) fed on bryozoans. Keen (1975) noted that in captivity when natural food sources are not provided that *Calliostoma* may attack a wide variety of soft bodied

invertebrates that are dead or alive, and reported *Calliostoma* feeding on dead fish *in situ*. The varied diet has likely contributed to their success in a wide range of habitats and depths.

The reproductive biology of the North Eastern Pacific *Calliostoma* is virtually unknown. Hunt (1980) reported a female *C. ligatum* released approximately 3,000 small spherical green eggs during the course of just over 2 hours. Ten to 12 eggs were contained in each clear mucus sheath, which settled to the bottom of the container. Holyoak (1988) followed up on this observation with a detailed account of spawning and larval development. He reported a greater number of eggs contained in gelatinous strands, which were fertilized by sperm released into the same water column. In captivity, veligers emerged from eggs after 6 days (maintained at 10°C) and remained in the water column for 3-4 days, after day 4 larvae alternately crawl and swim before metamorphosing on day 12. Spawning occurred frequently in captivity and slight increases in water temperature may have been the trigger. For additional details on fertilization and development, review the work of Holyoak 1988. The reproductive biology of *Tegula funebris* (Adams, 1855) from California was described in detail by Moran (1997) and many aspects are similar to that described by Holyoak (1988) for *C. ligatum*.

DISCUSSION

Depth and distribution records are provided as general guidance. The Pacific coast of Baja California, Mexico has not been sampled as extensively as southern California. It is likely that many deep-water species, not yet reported, occur at appropriate depth and habitat in Baja California. Seasonal and long-term cyclical events, such as El Niño, cause notable fluctuations in oceanic conditions which may affect species abundance and short-term shifts

in distribution. Having reviewed material from Alaska to Central America, other than size, geographic variants have been minimal.

For each species the author, date, location of the holotype and type locality are provided if designated. With the exception of the new species described in this paper, notes regarding shell characteristics are provided for general guidance. Additional location and depth records are given for species that are seldomly found. The distribution and depth range of common species is included but multiple locations are not cited.

Comments regarding relative abundance of species in collections may not reflect the extent of natural populations. Many of the deeper water species appear numerous at 100 meters or more, but are uncommon to rare in collections because (1) the need for a sizable boat, (2) the equipment required to collect at that depth, (3) regulations and required permits to conduct such sampling, and (4) restricted access and collecting prohibitions in some countries.

One specimen of *C. antonii* (Koch in Philippe, 1843) in the USNM has San Diego, California data. No additional specimens from California or the length of Baja California Peninsula have been reported. The species is known from mid Central America, south to Peru (McLean, 1971), and therefore not included as a member of the Californian Marine Province.

Other recent publications regarding west coast Calliostomatidae include Berschauer & Clark (2018) who illustrate *Calliostoma* found in southern California and Tuskes (in press) who reviewed and illustrated all genera and species of Calliostomatidae from the Northeastern Pacific (Bering Sea to central Baja California, Mexico) and the dated but classic works of Oldroyd, 1927, and McLean, 1978.

SPECIES ACCOUNTS

Calliostoma Swainson, 1840

Type Species *Trochus conulus* (Linnaeus, 1758).

1. *Calliostoma annulatum* (Lightfoot, 1786)

[Figure 1]. Holotype and type locality not designated.

Shell height. 25-35 mm. The shell of this distinctive species is gold to yellow with a purple ring at the periphery and above the suture. The spiral threads are brown with yellow to gold beads and the whorls are slightly convex. Both the yellow and purple colors of the shell may fade over time. The animal is golden yellow with dark brown to black spots.

Calliostoma annulatum is more frequently observed in the northern Channel Islands off Santa Barbara. Further north, in the Oregonian MP, it may be found in rocky habitat during minus tides, and has been collected at 190 m. In the Californian MP, this species occurs subtidal on kelp and hard surfaces. On calm sunny days, this species is occasionally found on kelp fronds that have reached the surface of the water.

Range. East of Afognak Island, Gulf of Alaska, to the coast of Alaska (Clark 2018). Prior records were from Forrester Island and Bear Bay, Alaska south to Isla San Geronimo off the west coast of northern Baja California, Mexico. Scarce south of Santa Barbara, California.

Calliostoma bernardi McLean, 1984
see *Akoya platinum* # 15

2. *Calliostoma canaliculatum* (Lightfoot, 1786)

[Figure 2]. Holotype and type locality not designated.

Shell height. 23-35 mm, large specimens to 45 mm. This is the largest species in both the Oregonian and Californian marine provinces.

The shell is off-white to light brown with prominent smooth spiral cords and occasionally darker brown flammules. The whorls are relatively flat.

Although usually found in water less than 30 m deep, *C. canaliculatum* does occur to depths of 80-90 m. In central California, we have observed small adults of *C. canaliculatum* living in the rocky intertidal surf zone north of Shell Beach (San Luis Obispo County, CA). *Calliostoma canaliculatum* is found infrequently on the surface fronds of *Macrocystis porphyra* off San Diego and tend to be larger than those we have found intertidally in central California.

Range. Sitka, southern Alaska, south to Isla San Benito, Baja California, Mexico. Locally common north of Point Conception. Scarce in the Californian MP.

3. *Calliostoma eximium* (Reeve, 1842)
[Figures 3a-b]. Holotype: Museum
Cuming; Payanum, Panama Bay,
Panama, muddy sand, 10 fm. (18.3 m).

Shell height. 20-25 mm, large specimens to 32 mm, shell sturdy, gray to tan. The periphery of each whorl is vertical. As a result, when the next whorl is added, the area above the suture is nearly vertical, and then becomes distinctly concaved, giving the whorls a stepped appearance. Some individuals have numerous dark spots with occasional dark brown dashes on the threads forming broken lines, while others have bold flammules especially on the final whorl. The two specimens illustrated represent the expected variation in both color and shape.

Live specimens have been collected on sand, muddy sand, and rubble from the low intertidal zone to at least 75 m, but most are taken in less

than 37 m of water. When described, Reeve (1842) only cited Panama, much later Dall (1921) and Oldroyd (1927) listed Santa Catalina Island off southern California as the northern extent of the range. Subsequent authors have not listed it as a California species (Keep 1947, McLean 1971, Abbot 1974, Keen 1975). We found one specimen in the SDMNH of *C. eximium* mixed with a series of *C. gloriosum*. The file card that matched the number on the shell did not provide a date or collector and is for *C. tricolor* from La Jolla. Considering the discrepancies with the data, it is not treated as a valid record. The species is well documented in the most southern portion of the Californian MP.

Range. Isla Cedros, Baja, California, Laguna Scammons and Laguna San Ignacio, south to Bahia Magdalena, Baja Sur, Mexico and from Punta Penasco, Sonora in the upper Gulf of California south to Caelata La Cruz, Peru, with the last record from Shasky (1997). Uncommon.

4. *Calliostoma gemmulatum* Carpenter, 1864
[Figure 4]. Holotype: USNM 16261.
San Pedro, California.

Shell height. 13-17 mm, large specimens to 21 mm. The shell is gray to gray-brown with light brown to dark gray-green blotches. There are two prominent beaded cords one on the shoulder the other at the periphery. The peripheral cords are above the suture on past whorls, lesser cords are strongly beaded, while threads are variable.

Based on museum collections, in the past this species has been locally common in southern California. It is found subtidally to at least 25 m in rock habitat on the open coast and protected areas. Crabbed specimens in good condition may be found intertidally.

Range. The species occurs as far north as San Simeon (records from specimen at CM) in San Luis Obispo County, California and has been a dependable find during minus tides at Cayucos. There are numerous records for southern California and northern Baja with the most southern record currently known from Punta Pequena, San Juanico, Baja California Sur, Mexico. Uncommon in Californian MP.

5. *Calliostoma gloriosum* Dall, 1871
[Figures 5a-c]. Holotype: USNM 206134.
Monterey Bay, California.

Shell height. 22-35 mm, shell sturdy. The base color of the shell is either dull orange or tan, with one or two rows of darker brown blotches or flammules on the whorls, occasionally with a light tan line between the blotches. The extent of dark blotches and/or flammules are variable. Some dull orange shells from Morro Bay, California have a light rose cast and Johnathan Centoni has collected some that are more intensely colored in Monterey Bay, California.

In the Oregonian MP, the species has been collected intertidally/subtidally to 100 m and is locally common. In southern California, this species is associated with rock substrate at depths of 5 m in protected areas, to greater than 90 m (CSDOMP) off shore.

Range. San Francisco south through southern California and northern Baja California, to Isla San Benito, Baja, Mexico, and corresponding off shore islands to the north. Uncommon in Californian MP.

6. *Callisotoma guerreroensis*
Tuskes & Tuskes, 2019, new species
[Figures 6a-c]

Description. Shell sturdy, ground color light yellow-brown (straw). Protoconch off-white to

straw, 1-1.2 whorls. Postnuclear whorls (PNW) 1-4 straw colored; relatively flat, often lustrous copper; suture lightly impressed. **PNW 1-2** three beaded threads. **PNW 3** four beaded/non-beaded threads. Whorls nearly flat. **PNW 4-5** Shoulder five beaded threads, subsutural and shoulder threads prominent; four-five threads on lateral surface beaded/not beaded. **PNW 5**, shoulder lightly rounded and light brown flammules present. **PNW 6** Shoulder angulate with five beaded cords, beads alternating cream/straw; lateral surface nearly vertical, five - six straw cords, mostly non-beaded; some interspaced threads present; flammules present. **PNW 7** Shoulder angulate, at approximately 40 degrees with six beaded cords and lightly bead/nonbeaded thread between cord. Diagonal flammules raised/not raised with alternating brown/cream, markings; below last prominent cord of shoulder the angle abruptly changes to nearly vertical (80-90 degrees). Lateral surface, 8-9 threads, beaded/ mostly non-beaded with fine interspace threads; 2-3 peripheral cords above lower suture, alternating brown marking slightly rectangular/longer rectangular cream markings. **PNW 8** Shoulder angulate, at approximately 35-40 degrees with 8-9 beaded cords on shoulder and fine threads interspaced. Prominent diagonal flammules on shoulder alternate cream and brown, raised / not raised. The lateral surface descends at 86-90 degrees with 8-9 beaded cords, interspaced with smooth fine shallow straw threads; Peripheral band, with 4 cords, alternating brown square marking with larger cream rectangular bar, cords beaded, alternating cream/straw. Base with 24-27 low straw cords with/without very shallow beading, fine interspace threads present, varying number of basal cords with alternating cream and straw markings; cords proximal to columella broader. Columella white, columellar scar white, shallow and lustrous. Aperture slightly oval, outer lip cream, margin lightly crenate; inner shell lightly lustrous.

Diagnosis. *Calliostoma guerreroensis* has been confused with *C. gloriosum* (Figure 5a-c). Mature and subadults of *C. guerreroensis* have a unique profile; as the whorls have a well-defined angulate shoulder sloping at approximately 35°, to the lateral surface, which abruptly changes to 80-90° to the peripheral area; basal threads few to many with alternating cream and light brown spotted cords; post-nuclear whorls 1-4 often with metallic copper luster between the cords. *Calliostoma gloriosum* has somewhat uniformly curved body whorls, basal threads lack alternating colored spotting, and ground color does not overlap that of *C. guerreroensis*.

Paratype variation. The intensity of the peripheral band is variable and often not notable in juveniles. Ground color may be slightly darker among juveniles. Number of basal cords with alternating cream/light brown spots variable but always present. Shell colorations may be more intense and contrasting than the holotype. The slope of the shoulder and periphery are always notable especially after the 5th or 6th whorl, with only moderate variation in large subadults and the mature shell. Juvenile shells typically lack the distinct pattern of mature shells; subadults generally have the shape and markings of adults, but lack bulk. A 23 mm shell with 6.5 whorls, collected north of Guerrero Negro, BCS has a more contrast yellow-straw ground color and not quite as angular, but the threads, cords, shape and markings on the basal threads consistent with *C. guerreroensis*.

Holotype. LACM 3640. 1 mature specimen. Shell height/width 32.0 × 29.4 mm.

Type Locality. Baja California Sur, Mexico, 24°37.2'N, 112° 01.00'W. 5.45 mi. 230° from Punta Entrada, Bahia Magdalena. 24-27 m sand.

H/W 32.4 × 29.4 mm, R/V Velero IV, 3 May 1950.

Paratypes. 1 adult, 1 juvenile. Baja California, Mexico, 28°17.43'N - 14°32.32'W off Laguna Guerrero Negro, 20-30 fms. H/W 23.6 × 22.5 mm, Mary Ricaud 1965 SBMNH 616620; 3 juveniles, 1 subadult. Baja California, Mexico, 27°57'N, 115°08.5'W. Kellett channel S. of Isla Cedros, 37 m, pebbles/shale. H/W 15.3 × 15 mm, 12.5 × 12 mm, 8.3 × 8.0 mm 6.8 × 6.6 mm. R/V Searcher, 20 Oct. 1971. Dead collected. LACM 71-159.9; 2 subadults. Baja California Sur, Mexico, 27°52.0'N, 115°12.7'W, Twelve Fathom Reef off Isla Natividad, 22 m. H/W 14.9 × 13.3 mm, 14.5 × 14.0 mm. R/V Searcher, 21 Oct. 1971, McLean & LaFollette. LACM 71.165.10; 1 subadult. Baja California Sur, Mexico, 27°43.3'N, 115°00.05'W, Punta Rompiente, 15 m, under kelp. H/W 16.4 × 14.1 mm. R/V Searcher, 21 Oct. 1971, McLean & LaFollette. LACM 50.141.4; 11 juvenile specimens. Baja California Sur, Mexico, 27°17.6'N, 114°30.0'W, Bahia San Cristobal, 31m. H/W 2.9 × 3.0 mm to 9.5 × 9.1 mm. R/V Searcher, 24 Oct. 1971, McLean & LaFollette. LACM 71-173.4; 4 juvenile specimens. Baja California Sur, Mexico, 27°12.5'N - 114°28.8'W, Punta San Pablo. 21-30 m. H/W 13.8 × 13.4 mm, 13.3 × 12.6 mm, 11.0 × 10.0 mm, 10.9 × 10.0 mm. R/V Searcher, 25 Oct. 1971, McLean & LaFollette. LACM 71.178.19; 2 subadults. Baja California Sur, Mexico, 24°37.2'N, 112° 01.00'W. 5.45 mi. 230° from Punta Entrada, Bahia Magdalena. 24-27 m sand. H/W, 16.4 × 15.5 mm, 14.7 × 14.5 mm. R/V Velero IV, 3 May 1950. LACM 50-41.4.

Other material examined but not included in type series. 2 juvenile specimens. Baja California Sur, Mexico, 27°37.52'N, 114°50.62'W. 14-18 m. Under kelp off Cabo Thueloe. H/W 11.5 × 10.6 mm, 6.8 x broken base. R/V Searcher, 23 Oct. 1971. McLean &

LaFollette. LACM 71-170.16; 1 juvenile, Baja California, Mexico. 27°57'N, 115°08.5'W. Kellett channel S. of Isla Cedros, 37 m, pebbles/shale. H/W 6.8 × 6.6 mm. R/V Searcher, 20 Oct. 1971. Dead collected. LACM 71-159.9.

Etymology. Named after the closest community to where the first specimen was identified from, Guerrero Negro, Baja California Sur, Mexico (“BCS”).

Distribution. Currently known from the area of Isla Cedros, Baja California, south to Bahia Magdalena Bay, BCS, this distance spans approximately 800 km. The occurrence further south is expected but not known.

Remarks. The majority of the *C. guerreroensis* in museums are subadults or juveniles found at depths between 20-37 m and collected during two research trips, 1950 and 1971. Access to the Pacific coast of BCS is limited and the collection of shells by individuals is prohibited. Initial specimens were found mixed with *C. gloriosum* in museum collections.

7. *Calliostoma keenae* McLean, 1970
[Figure 7]. Holotype: LACM 1272.
Off Laguna Beach, California, 106-109 m.

Shell height. 12-15 mm. Shell drab green-brown to yellow-brown with a peripheral band that has alternating olive and white markings. Whorls convex with beading absent on upper whorls but present on lower whorls. Brown flammules may be present. Based on an earlier photo of the holotype, the peripheral band has lost much of the color.

Range. Southern California south to the Jaime Bank off Cabo San Lucas, BCS and Isla Clarion in the Revillagigedo group off western Mexico. The species has also been found within the Gulf

of California, Skoglund & Koch (1993) reported collecting specimens at Los Frailes, Isla Danzante both Baja Sur, and off Bahia de Los Angeles, Baja California. Other records include, 58 Fathom Bank, 12 miles of Laguna Beach, Orange County, California; San Diego, California at 58 m (CSDOMP); Isla Cedros 117-119 m, Baja California; Dewey Channel between Isla Natividad and Punta Eugena 44-46 m, San Jaime Bank 137 m, Baja California Sur; and Emerson (1995) reported the species from Isla Clarion at 35-110 m. The shallowest collection was a small specimen collected by Ron McPeak on a sea mount near Bahia Asuncion, BCS at 26-30 m (Hertz & Hertz, 1984). Rare.

8. *Calliostoma ligatum* Gould, 1849
[Figures 8a-c]. Holotype: USNM 5608.
Puget Sound, Washington.

Shell height. 24-30 mm. Shell color is light to dark brown with light brown to beige cords that lack beads (Figure 8a). Occasionally shells have brown flammules below the suture and are referred to as form *pictum* (Figure 8b) while other shells may have a blue band on the upper whorls, form *caeruleum* (Figure 8c) that tend to fade over time. Conditions that result in the outer shell being eroded away reveal a persistent bright iridescent blue layer of shell that is not visible in intact specimens.

Collections that have not been curated for many decades may still inventory this species as *C. costatum* Martyn, 1784. *C. ligatum* is seldom seen in southern California but is most likely to be found in the North-West Channel Islands which are impacted by the cool California Current, and in deeper water well below the thermocline. We have found the species commonly at Morro Bay (Oregonian MP) during minus tides on rock covered with debris,

sponge, algae, and bryozoans, but have never personally observed this species off San Diego.

Range. Cook Inlet, Kachemak Bay, Kenai Peninsula, Prince William Sound, Alaska south to Santa Barbara California, after which the species is uncommon. A dead specimen was found in San Diego, California (Bishop & Bishop, 1973). The southern most record is from Isla San Benito at a depth of 83-95 m, Baja California. Uncommon in the Californian MP.

9. *Calliostoma nepheloides* Dall, 1913
[Figures 9a-b]. Syntype: USNM 96637.
Panama Bay, Panama, 86 m.

Shell height. 15-23 mm. Whorls are flat with small, tightly spaced spiral threads that are beaded above and below the suture. There are two prominent peripheral cords, the upper most is beaded, the lower one is not. Most shells are olive-brown in coloration, some have darker flammules and the upper whorls can have a brown metallic luster.

Range. Punta Abreojos, west of Laguna San Ignacio, BCS, Mexico south to Panama (McLean, 1971). McLean (1971) gives a depth range of 73-120 m, which is consistent with other museum specimens we have examined. Houston (1980) stated the species is found intertidally; but this has not been confirmed by others, if correct this would be the first record from shallow water. Uncommon in the Californian MP.

10. *Calliostoma sanjaimense* McLean, 1970
[Figure 10]. Holotype: LACM 1269.
San Jaime Bank, Baja California
Sur, Mexico, 137 m.

Shell height. 10-15 mm. The whorls are flat sided, shell dark yellow. Threads and cords are

strongly beaded yellow-brown with a prominent peripheral band of alternating brown and white patches. When described by McLean (1970), it was known from only four specimens, all from the San Jaime Bank, west of Cabo San Lucas, BCS at 137 m. LaGrange (1992) collected a live specimen while dredging at 140-160 m on the Nine Mile Bank off San Diego. A specimen was collected at at depth 68 m in the Gulf of Panama.

Range: San Diego, California south to Panama. Rare.

11. *Calliostoma supragranosum* Carpenter, 1864
[Figures 11a-d]. Holotype: USNM 14925,
San Diego, California.

Shell height. 7-11 mm but older museum collections contain specimens from 8-19 mm. Shells are orange-brown, light brown to brown. Beaded threads are expected especially on the upper whorls and adjacent to the sutures. Some individuals lack notable beading. When present, the peripheral band consists of alternating light to darker brown markings that may vary in intensity.

Variation in shell color and pattern includes; brown with light blue trim on prominent threads and the presence of weak flammules. The uncommon blue shell may have a prominent peripheral band (Figure 11b). *Calliostoma supragranosum* is perhaps the most frequently encountered species in southern California. The species is usually under rocks and on overhangs in association with bryozoans, sponge, and colonial ascidian tunicates at depths of 2-50 m. Somewhat common below 20 m, but populations are localized.

Comparison *Calliostoma supragranosum* vs. *Calliostoma splendens*.

Calliostoma splendens (Carpenter, 1864) has been treated as a junior synonym of *C. supragranosum* for more than 50 years yet *C. splendens* still appears in popular literature and on some web-sites. Based on a small sample in our personal collection there appeared to be two distinct phenotypes, that is, until hundreds of museum specimens were examined and found that the number of threads beaded/not beaded is variable as is the presence/absence and intensity of contrasting peripheral markings. The confusion starts when Carpenter (1864) published the description of both *C. supragranosum* and *C. splendens*, and did not illustrate them or provide a diagnosis. The description of *C. splendens* is based on a juvenile of 4.8 mm and two paratypes in the range of 3 mm. As such they have been commonly sorted not by shell characteristics, but rather size and depth of collection. We visited the USNM to examine type specimens for both *C. supragranosum* USNM 14925 and *C. splendens* USNM 16278 and have illustrated them (Figures 11c and 11d).

The descriptions of both were written in Latin and in our opinion somewhat generalized. The holotypes of *C. supragranosum* and *C. splendens* were both described as brown, but over the past 150 plus years they have become light tan. Figures 11c and 11d show both holotypes to scale in relation to each other, otherwise the relative size of the threads and the distance between would be out of proportion. The holotype of *C. splendens* was dead collected and the lip partly missing.

A review of the later works of Olroyd 1927, Keep 1947, P.A. Morris 1966 and Abbott 1974, indicates there is little agreement as to habitat or characteristics that would separate *C.*

supragranosum from *C. splendens*; this includes size, shape, color, beading, peripheral banding and depth. Van Winkle Palmer (1958) published a compilation of many West Coast shells described by Carpenter, which included black and white illustrations.

Range. Monterey Bay to San Diego, California, south along the Baja coast and off shore islands such as Guadalupe (Chace, 1958) to at least Punta San Pablo just north of Bahia Asuncion, BCS, Mexico. Occasionally locally common.

12. *Calliostoma tricolor* Gabb, 1865

[Figures 12a-b].

Syntype: ANSP 38184.

San Pedro, California.

Shell height. 15-22 mm, shell fragile. A distinctive species with prominent beaded threads. The shell color is yellow-brown to light brown. Approximately every 3rd to 5th thread is colored with alternating clusters of dark brown and white beads forming distinctive bands (Figure 12a). The greater the frequency of these darker beaded threads, the darker the shell is in appearance (Figure 12b). In the Californian MP the species is found subtidally on rock or sand habitats. Specimens have been collected in grab samples at 100 m (CSDOMP) off San Diego, California.

Range. Santa Cruz, California south to Bahia Tortuga south of Punta Eugena, BCS. Locally common intertidally north of Point Conception. Uncommon in the Californian MP.

13. *Calliostoma turbinum* Dall, 1896

[Figures 13a-b].

Holotype: USNM 122578.

Santa Barbara Channel, Point Conception, California, 183 m.

Shell height. 15-22 mm. The shell structure is thin and delicate with a coppery iridescence. There are prominent peripheral cords. The first few threads below the suture are beaded, the remainder are typically not beaded or only minutely beaded.

The species has been taken while dredging at 140-160 m on the Nine Mile Bank off San Diego (LaGrange, 1992); at 109 m off Point Conception and Santa Catalina Island at 90-180 m. Although most specimens taken in grab samples off San Diego are at 90-100+ m, a few have been found as shallow as 27-30 m (CSDOMP). There is a small juvenile shell in the SDMNH from Isla Cedros collected at 15 m, but may have been transported into the shallower water by a hermit crab. The deepest specimen off California was from 914 m.

Range. Point Conception, Santa Barbara County, California, south to Isla San Benito at 126-144 m, Baja California Mexico. The species is taken with some frequency in deep water samples off San Diego. Rare.

14. *Calliostoma variegatum* Carpenter, 1864
[Figure 14]. Holotype: USNM 4201.
Puget Sound, Washington.

Shell height. 17-24 mm. The shell is soft yellow and the apex of a freshly collected shell may be yellow or purple; whorls are flat. Threads strongly beaded that are light brown to orange-brown separated by light yellow. A unique specimen with a white shell and purple apex was taken off San Diego, California and is in the collection of Chuck Reitz. With age, shells in collections often lose much of their color and become more subdued.

In the Oregonian MP off Vancouver, British Columbia, Canada this species is taken by SCUBA divers as shallow as 10 m and by

dredge to at least 146 m. In southern California it is a deep-water species collected by dredging at 70 m off Santa Catalina Island (McLean & Gosliner, 1996), Nine Mile Bank 140-160 m off San Diego (LaGrange, 1992), Cortez Bank 230 m, and 126-144 m off Isla San Bonita, Baja Ca., Mexico. Rare in the Californian MP.

Range. Gulf of Alaska East of Afognak Island, (Clark, 2018), south to Isla Cedros, Baja California (McLean & Gosliner, 1994). A rare deep-water species in the Californian MP.

Akoya Habe, 1961

Type species; *Calliostoma akoya*
Ikebe, 1942

The genus *Akoya* consists of moderate to deep water white shells, with beaded/not beaded spiral cords/threads in varying numbers. The presence of the periostracum may give the shell a gray appearance if not removed. Their habitat and appearance is closer to *Otukaia* Ikebe, 1943 than *Calliostoma*. *Calliostoma* from Alaska to the Pacific coast of Baja California Mexico, have shells with multiple colors, other than white. With improved analytical techniques we may better understand the relationship of similar appearing deep water white calliostomids. Do they represent convergence from multiple genera, or will they be found to form a tight clade?

15. *Akoya platinum* (Dall, 1890)
[Figures 15a-f]. Holotype: USNM 96558.
Station 2839 near Santa Barbara Island,
California, 756 m.

Calliostoma titanium McLean, 1984. Holotype:
LACM 1995. R/V Velero, 8.3 km SE of
Santa Catalina Island, California, 256-274 m.

Calliostoma bernardi McLean, 1984. Holotype:
LACM 1996. R/V Velero, off SE end of
Santa Catalina Island, California, 241-271 m.

Akoya platinum average height is 27.9 mm (N=34), most mature specimens range from 24-33 mm, large specimens to 37 mm; form *titanium* averages 28.6 mm (N=17), most mature shells ranged from 22-33 mm, large specimens 36 mm; form *bernardi*, average 28.7 mm (N=18), mature shells measured 24-33 mm, large specimens to 36.6 mm. The average and maximum height were all within 1 mm (Table 1). Shells white, peripheral cord prominent, numerous threads below peripheral cord to base, threads and cords above peripheral variable in number, size, and beading. Subsutural cord present/absent, subsutural area may be tabulate to varying degrees; columellar scar white, lip smooth, inner shell lustrous light green to pink.

Species and forms	Sample size	Average Height mm	Largest shell mm
<i>A. platinum</i>	34	27.9	37
form <i>titanium</i>	17	28.6	36
form <i>bernardi</i>	18	27.7	36.6
Non assigned	26	28.3	36.6

Table 1. Measurements of 95 mature shells in the *Akoya platinum* complex.

Calliostoma platinum is dredged at 100 to 700+ m or taken associated with deep-water bait traps. Although found on the traps they are not always associated with the bait. In Alaska they have been photographed via Remote Operated Vehicle in deep water feeding on gorgonian Stone, *et al.* (2014).

Range. Icy Bay, Gulf of Alaska (Clarke, 2018) south to San Diego and probably similar habitat

in Baja California, Mexico. Depth 180-700 m. Rare.

Discussion of *Akoya platinum* Complex.

McLean (1984) in his descriptions of *Akoya titanium* and *A. bernardi*, provided a diagnosis that included *A. platinum* and is summarized as follows: Whorls 3 - 4 of *A. titanium* similar to *A. platinum*, both lacking threads; *A. platinum* shell weak, *A. titanium* shell sturdy with subsutural tabulation and numerous fine cords (threads) on final whorl. “*Calliostoma bernardi* is closest to *C. titanium*” but smaller and has strong spiral cords on all whorls compared to *A. titanium*. Having recently examined the holotype of *A. platinum* at the USNM, the shell is only weak in the sense that nearly all of the lip is missing and there is a hole on the opposite side of the shell.

LaGrange acquired the first large series of shells from east end of Santa Catalina Island at 350 m. These shells were examined by McLean in 1984, who concluded that *C. titanium* and *C. bernardi* are conspecific. La Grange (1998) discussed these findings, illustrated specimens and designated *C. bernardi* a junior synonym of *C. titanium*. The holotypes of *A. titanium* and *A. bernardi* were both collected south east of Santa Catalina Island and the holotype of *A. platinum* was collected off Santa Barbara Island which is adjacent to Santa Catalina Island. We treat *A. titanium* as a synonym of *A. platinum*. Forms *titanium* and *bernardi* represent steps along a character cline.

As indicated in Table 1, the average height and maximum height are all within less than 1 mm. In our analysis, each of 95 mature shells were evaluated against six characters and were then compared to the type of all three taxa (Table 2). Of the 95 mature shells, 33.7 % were identified as *A. platinum*, 18% as form *titanium*, and 19% as form *bernardi*. The remaining 29.3% could

not be assigned to any of the three taxa based on a minimum of 75% similarity and were distributed as follows: intermediate characters between *A. platinum* and form *titanium* 9.5%, between form *titanium* and form *bernardi* 6.3%, between *A. platinum* and form *bernardi* 2%, and 11.5% were evenly distributed between all three (Illustration 1). Table 2 provides collective information regarding character distribution.

	<i>platinum</i> N = 32	<i>titanium</i> N = 17	<i>bernardi</i> N = 16	Intergrade N = 28
Peripheral cord #1				
S	29	2	10	
W	3	15	8	
N	0	0	0	
Threaded above peripheral cord on body whorl #2				
S	19	0	17	14
W	13	15	1	12
N	0	2	0	2
Threads beaded above peripheral cord #3				
S	0	0	15	8
W	0	12	3	8
N	32	3	0	12
Carinations on postnuclear whorl 1 #4				
S	24	5	17	15
W	0	0	0	0
N	8	12	1	13
Shoulder below suture of body whorl tabulated #5				
S	0	3	12	14
W	25	7	6	13
N	7	7	0	1
Shoulder cord beaded weak #6				
S	0	1	15	5
W	7	9	3	13
N	25	7	0	10

Table 2. Number of shells exhibiting specific characters.

In summary, all of the type specimens came from either Santa Barbara Island or Santa Catalina Island which are adjacent to each other. There does not appear to be a difference in average size or maximum height of the shells (Table 1). McLean recognized *bernardi* as a synonym of *titanium* (LaGrange, 1998). Our

sample of 95 mature shells documents to some extent the variability. Figures 15a-h illustrate some of the intermediate forms in this complex. The difference between *A. platinum* and form *titanium* is less than the difference between *titanium* and form *bernardi*. *Akoya platinum* is the least ornate and form *bernardi* the most, and are at opposite ends of a character continuum with *C. titanium* and the other 27.2% of the non-assigned shells between them.

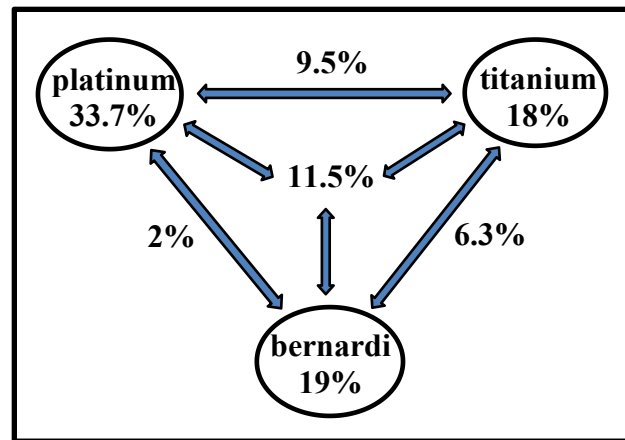


Illustration 1. *Akoya platinum* complex. Affinity of 95 shells. Based on the type specimens, 29% of the shells could not be assigned to a specific phenotype.

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LITERATURE CITED

- Abbott, R.T. 1974.** American Seashells. The Marine Mollusca of the Atlantic and Pacific Coasts of North America. Van Nostrand Reinhold Co. NY. 683 p.
- Berschauer, D.P. & R.N. Clark. 2018.** The Shells of Southern California. Published by San Diego Shell Club. 131 p.
- Bishop, J.M. & S.J. Bishop. 1973.** A Census of Marine Prosobranch Gastropods in San Diego, California. *The Veliger* 16(2):143-152.
- Carpenter, P.P. 1864.** Description of new Marine shells from the coast of California. Pt. 1 California Academy of Science Proceedings. Vol III, Jan-Dec. p. 155-159 pt. III p. 175-177.
- Chace, E.P. 1958.** The Marine Molluscan Fauna of Guadalupe Island, Mexico. San Diego Society of Natural History. XII (19):319-332.
- Clark, R.N. 2018.** New range data for five trochiform gastropods (Seguensiida & Trochida) from Alaska. *The Festivus* 50:114-116.
- Dall, W.H. 1921.** Marine Shellbearing Mollusks of the Northwest Coast of America from San Diego, California to the Polar Sea, mostly contained in the Collection of the United States national museum, with Illustrations of Hitherto Unfigured species. Washington, Government Printing Office. p. 176.
- Emerson, W.K. 1995.** A Zoogeographic Summary of the Marine Mollusks of the Revillagigedo Islands (Tropical Eastern Pacific Ocean). *The Festivus* 27(1):3-18.
- Harbo, R.M. 2007.** Shells & Shellfish of the Pacific Northwest. Harbour Publishing, Madeira Park, B.C., Canada. pp. 271.
- Hertz, J. & C. Hertz. 1984.** Survey of Mollusks at Punta Asuncion and Vicinity, Baja California, during November 10-14, 1981. *The Festivus* 16(10):98-112.
- Holyoak, A.R. 1988.** Spawning and Larval Development of the Trochid Gastroopod *Calliostoma ligatum* (Gould, 1849). *The Veliger* 30(4):369-371.
- Houston, R.S. 1980.** Mollusca. *In:* Richard C. Brusca (Ed.). Common Intertidal Invertebrates of the Gulf of California. The University of Arizona Press, Tucson, Arizona, 130-204.
- Hunt, D.E. 1980.** Observation on Spawning in *Calliostoma ligatum* (Gould, 1849). *The Veliger* 22(3) p 292.
- Keen, A.M. 1975.** On Some West American Species of *Calliostoma*. *The Veliger* 17(4):413-414.
- Keop, J. 1947.** West Coast Shells. Revised by Joshua L. Baily, Jr., 2nd printing. Stanford University Press, Stanford California. 350 p.
- LaGrange, J. 1992.** Dredging off Nine Mile Bank, San Diego, California. *The Festivus* 24(5):47-56.
- LaGrange, J. 1998.** California's Deep-Water Calliostomas. *The Festivus* 30(4):45-47.
- Lowry, L.F., A.J. McElroy & J.S. Pearse. 1974.** The distribution of six species of gastropods molluscs in a California Kelp Forest. *Biological Bulletin* 147:386-396.
- McLean, J.H. 1970.** Notes on the Deep Water Calliostomas of the Panamic Province with Descriptions of Six New Species. *The Veliger* 12(4):421-426.
- McLean, J.H. 1971.** The superfamily Trochacea. *In:* Keen, A. Myra. 1971. Sea Shells of the Tropical West America. Marine Mollusks from Baja California to Peru. Stanford University Press, Stanford California. pp. 329-349.

- McLean, J.H. 1978.** Marine Shells of Southern California. Science Series 24. Los Angeles County Museum of Natural History. pp. 104.
- McLean, J.H. 1984.** New Species of Northeast Pacific Archaeogastropods. *The Veliger* 26(3):233-239.
- McLean J.H. & T. M. Gosliner. 1996.** Taxonomic Atlas of the Benthic Fauna of the Santa Maria Basin and Western Santa Barbara Channel. The Mollusca Part 2. The Gastropods, Volume 9. Edited by Scott, P.H., J. A. Blake, & A. L. Lissner. Santa Barbara Museum of Natural History, Santa Barbara, Ca. 219 p.
- Moran, A.L. 1997.** Spawning and Larval development of the Black Turban Snail *Tegula funebris* (Prosobranchia; Trochidae). *Marine Biology* 128(1):107-114.
- Morris, P.A. 1966.** A Field Guide to Pacific Coast Shells, including shells of Hawaii and the Gulf of California. Sponsored by the National Audubon Society and National Wildlife Federation. Houghton Mifflin Company Boston. 297 p.
- Morris, R.H., D.P. Abbott & E.C. Haderlie. 1990.** Intertidal Invertebrates of California. Stanford Press, Stanford California. 689 p.
- Oldroyd, I.S. 1927.** The Marine shells of the West Coast of North America. Vol 2, Part 3. Stanford University Press, Stanford California. 393 p. + Plates 73-108.
- Perron, F. 1975.** Carnivorous *Calliostoma* (Prosobranchia: Trochidae) from the Northeastern Pacific. *The Veliger* 18(1):52-54.
- Reeve, L. 1842.** Descriptions of new species of shells belonging to the genera *Trochus* and *Turbo*. *Proceedings Zoological Society London* 10:184-186.
- Shasky, D.R. 1997.** New Range, Depth, and Size Records for some Panamic Province Gastropods. *The Festivus* 29(6):45-52.
- Skoglung, C. & R. Koch. 1993.** New Distributional Information for Panamic Province Archaeogastropoda (Mollusca). *The Festivus* 25(10):116-118.
- Stone, R.P., M.M. Masuda & J.F. Karinen. 2014.** Assessing the ecological importance of red tree coral thickets in the eastern Gulf of Alaska. *ICES Journal of Marine Sciences*; 72, 900-915. doi. 10.1093/icesjms/fsu190.
- Tuskes, P.M. (in press).** Calliostomatidae of The Northeastern Pacific. *In: Geiger, Groves, & Vendetti (Eds.). McLean's Northeastern Pacific Gastropods.* Santa Barbara Museum of Natural History. Slated for publication in 2019.
- Van Winkle Palmer, K. 1958.** Type Specimens of Marine Mollusca Described by P.P. Carpenter from the West Coast (San Diego to British Columbia). *The Memoir Series of the Geographical Society of America.* p 140-141.

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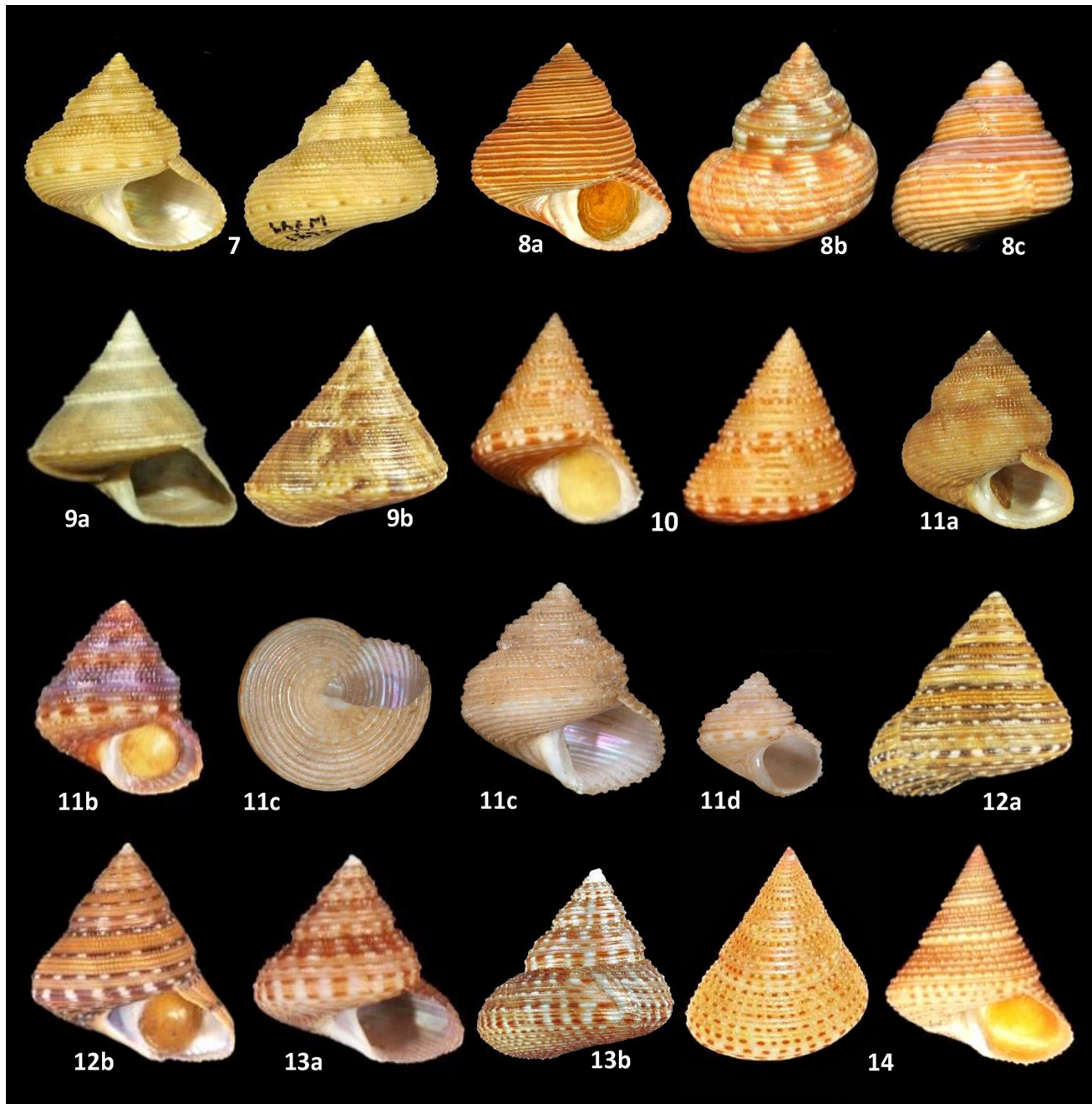
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Figures 1 - 6. Figure 1: *C. annulatum* 34 mm, Point Loma San Diego CA. Figure 2: *C. canaliculatum* 37 mm. Point Loma, San Diego, CA. Figure 3: *C. eximium* (Figure 3a) 25 mm (Figure 3b) 32 mm. Scammons Lagoon, Baja Sur, Mexico (BCS). Figure 4: *C. gemmulatum* 12.5 mm False Point, San Diego, CA. Figure 5: *C. gloriosum* (Figure 5a) 27 mm Mission Bay, San Diego, CA. (Figure 5b) 25 mm. (Figure 5c) 27.4 mm, both Morro Bay, CA. Figure 6a: *C. guerreroensis* Holotype, 32 mm, Punta Estrada, BCS. Mexico (LACM 3640). Figures 6b-6c: *C. guerreroensis* (paratypes). Figure 6b: 13.9 mm. Figure 6c: 14.9 mm subadults, both Punta Pomplente, BCS, Mexico. (LACM 71-161-16).



Figures 7 - 14. Figure 7: *C. keenae* Holotype 14.9 mm, 58 Fathom Bank, off Laguna, Orange County, CA. (LACM 1272). Figure 8: *C. ligatum* (Figure 8a) 29 mm, Morro Bay, CA. (Figure 8b) flammuled form *pictum*. (Figure 8c) purple ringed form *caeruleum*. Figure 9: *C. nepheloides* Panama Bay, Panama, (Figure 9a) 17 mm, (Figure 9b) 17.6 mm. Figure 10: *C. sanjaimense* 16 mm, 9 Mile Bank off San Diego, CA. (LaGrange). Figure 11: *C. supragranosum* Mission Bay, CA. (Figure 11a) 9.5 mm, (Figure 11b) 8.1 mm. (Figure 11c) *C. supragranosum* Holotype 14925 USNM 8.3mm. (Figure 11d) *C. splendens* Holotype 16278 USNM 4.7 mm. Figures 11c & 11d to scale. Figure 12: *C. tricolor* both Morro Bay, CA. (Figure 12a) 20.5 mm, (Figure 12b) 20.6 mm. Figure 13: *C. turbinum* both from off-shore San Diego, CA. (Figure 13a) 19.5mm, (Figure 13b) 13.4 mm. Figure 14: *C. variegatum* 19 mm, off-shore San Diego, CA.

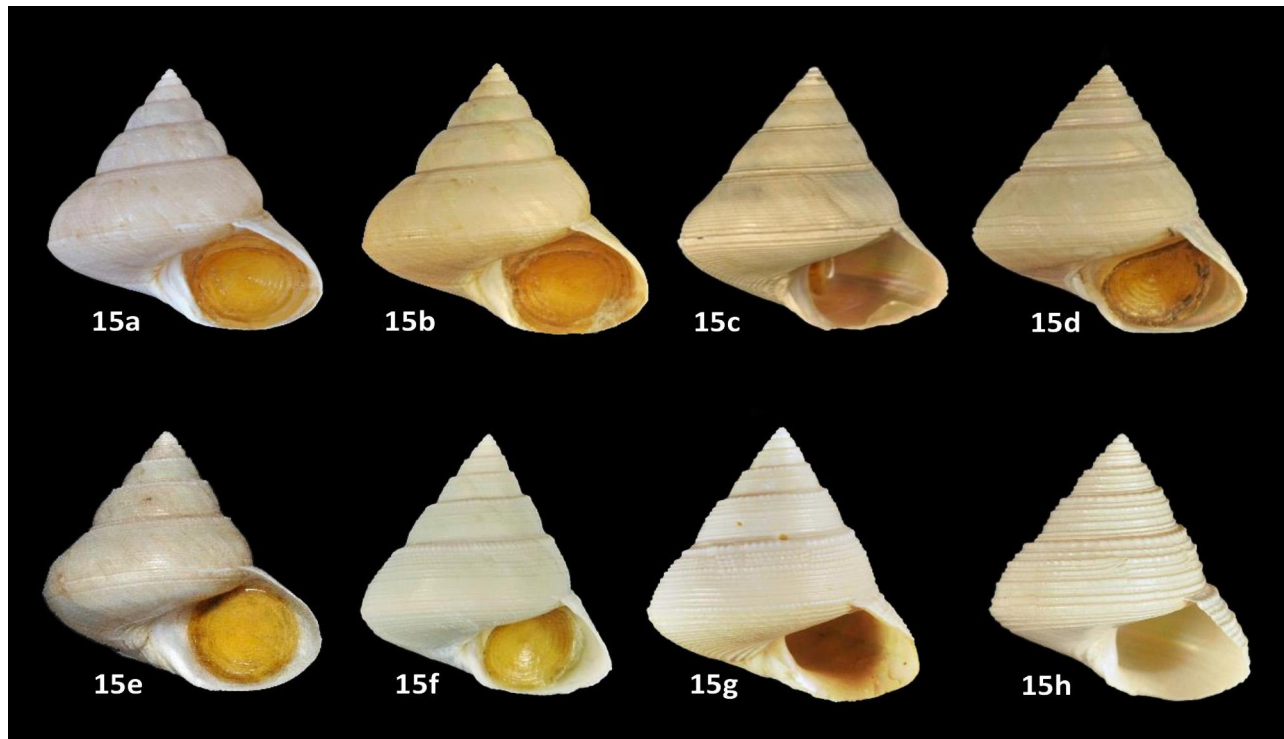


Figure 15. *Akoya platinum* complex: *A. platinum* = Figures 15a & 15b. Examples of transitional shells (Figures 15c & 15d) to form *titanium*. Form *titanium* (Figure 15e). Examples of transitional shells to form *bernardi* (Figures 15f & 15g). Extreme form of *bernardi* (Figure 15h). All eight shells measured between 31 and 33 mm in height and were collected at depths from 216 m to 350 meters off San Diego and Los Angeles, southern California. Beige shells are still covered with their periostracum.