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Native *Pteropurpura* of the Eastern Pacific (Muricidae)

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ABSTRACT Eight species in the genus *Pteropurpura* are known to occur in the Eastern Pacific, from central California to Peru. All eight species are found in the California or Panamic marine provinces. *Pteropurpura deroyana* occurs only in the southern portion of the Panamic province off the Galapagos Islands. New biological, distribution, depth, substrate, and shell length information is presented. The generic status of two species *P. leeana* and *P. festiva* are in flux, and until genetic analysis suggests otherwise they are assumed to belong to this genus.

KEY WORDS *Pteropurpura*, Muricidae, Gastropoda, Panamic Marine Province, California Marine Province.

INTRODUCTION

On a worldwide basis there are approximately 27 species in the genus *Pteropurpura.* Currently, eight native Muricidae of the genus *Pteropurpura* occur in the Eastern Pacific; *P. centrifuga* (Hinds, 1844), *P. deroyana* Berry (1968), *P. erinaceoides* (Valenciennes, 1832), *P. festiva* (Hinds, 1844), *P. leeana* (Dall, 1890), *P. macroptera* (Deshayes, 1838), *P. trialata* (Sowerby, 1841), and *P. vokesae* (Emerson, 1964). With the exception of *P. deroyana*, which is restricted to the Galapagos Islands of Ecuador, the other seven species are shared between the temperate to subtropical California marine province and the tropical Panamic marine province.

The California marine province extends from Point Conception, Santa Barbara County, southern California, past Cedros Island, Baja California to Asuncion Bay, Baja California Sur, Mexico. Seven species overlap in the southern portion of the California province and in the poorly defined transition zone between the California and Panamic marine provinces from Asuncion Bay to Magdalena Bay, Baja Sur. A review of mollusk groups such as cones, cowries, murex and cassia indicates a prevalence of tropical Panamic species at Magdalena Bay that are, for the most part, absent from the area of San Ignacio Lagoon and Asuncion Bay to the north (Keen, 1971). At Asuncion Bay many of the gastropods are typical of those found in San Diego, California. The Panamic province includes the southern tip of Baja California Sur on the Pacific side, and from the Gulf of California south to Ecuador/Peru. *Pteropurpura* are not known from the South American marine province.

The goals of this paper are to discuss the native Eastern Pacific *Pteropurpura*, provide new information regarding their biology and distribution, consolidate information, and to briefly discuss the status of *P. festivus* and *P. leeana*. *Pteropurpura falcata* (Sowerby II, 1834) (syn *P. aduncus* Sowerby II, 1834) a non-native species introduced to central California is not within the scope of this paper. This species is in a California Marine Protection Area and therefore presents regulatory and permitting issues that we have not pursued.

Materials/Methods

Museum material examined included: Natural History Museum of Los Angeles County (NHMLAC), Santa Barbara Museum of Natural History (SBMNH), San Diego Natural History Museum (SDNHM), Scripps Institution of Oceanography (SIO) and the Benthic Invertebrate Collection, California Academy of Science data base. Depth, substrate and specific locality data from museums, collectors, divers, and research vessels are quite valuable and summarized here in general terms. In addition, we have observed all of the species that typically occur at depths of less than 30 meters. Data based on material from shrimp boats is not included as they travel extensively in the Gulf, so most of those shells are labeled with the location they were purchased.

Abbreviations
Baja = Baja California, Mexico
Baja Sur = Baja California South, Mexico
CA = California, USA
m = meter
mm = millimeter

DISCUSSION

***Pteropurpura* History in the Eastern Pacific Species.** *Pteropurpura* is placed in the Subfamily Ocenebrine based primarily on characteristics of their radula, a fused siphon canal, and structure of the operculum. The genus contains four subgenera (*Pteropurpura*) Jousseaume (1880), (*Poropteron*) Jousseaume (1880), (*Ocinebrellus*) Jousseaume (1880) and (*Calictrapessa*) Berry (1959) to account for diverse morphologies. Future molecular work will be critical in defining the genus, once that data is integrated with morphological and biogeographical studies.

Past taxonomic confusion within the Eastern Pacific *Pteropurpura* is understandable. When described, *Murex macropterus* (Deshayes, 1838) was not illustrated, and no locality data was provided. That species would eventually become the type for the genus *Pteropurpura*. Dall began naming new species of three winged murex from California [*M. rhyssus* Dall, 1919 and *Pteronotus carpenteri* Dall 1899 (= *M. petri* Dall, 1902)] but issues with the descriptions raised concerns. The work of Dall was used by subsequent west coast authors (Keep, 1904, Oldroyd, 1927) but was not accepted universally. Abbott (1954) treated *Pteropurpura* as a section under the subgenus *Pterynotus* Swainson (1833), he considered *M. carpenteri* to be a subspecies of *M. trialatus,* and listed *M. rhyssus* as a subspecies of *M. erinaceoides*.

Between the works of Abbott (1954 & 1974), Emerson (1964a) located the type specimen of *M. macropterus* and provided the first illustration. He recognized *Pteropurpura* as a distinct genus and treated *M. carpenteri* and *M. petri* of Dall as junior synonymies of *P. macroptera.* Next, Emerson (1964b) realized that *M. rhyssus* was a homonym and offered the replacement name *P. vokesae,* treating it as a distinct species and pointing out how it differed from *P. erinaceoides*. Abbott (1974) later accepted the generic status of *Pteropurpura* but doubted the species status of some California material.

The *Murex Shells of the World* by Radwin & D'Attilio (1976) includes a good review of morphological information and species composition of *Pteropurpura*. It is interesting to note that they retained both *P. festiva* and *P. leeana* in *Pteropurpura,* refuting the past positions of *P. festiva* in *Jaton* Pusch (1837) and *Shaskyus* Bureh & Campbell (1963) and that of *P. leeana* in *Calcitrapessa* Berry (1959). In addition, they raised the subgenus *Poropteron* to generic status, and both *M. erinaceoides* and

M. vokesae were placed in the genus *Ocenebra* Gray (1847).

Later D'Attilio and Myers (1983), focused only on *Pteropurpura* and listed the known species. Without explanation they returned *O. erinaceoides* and *O. vokesae* to *Pteropurpura* and returned *P. festiva* to *Shaskyus* and *P. leeana* to *Calcitrapessa;* the removal of these two species was not widely accepted.

Prior to 1960 most of these shells were not common in institutional collections, as a vessel was needed to collect deeper water species. After the wide spread use of SCUBA gear, divers made many rare species common place and readily available in museum collections.

Two problem species. A review of the species illustrated (Figures 1-15) indicate how divergent *P. festiva* and *P. leeana* are from each other and other members of the genus. Mature *Pteropurpura* have three large varices (trivaricate) that extend outward from the current and previous distal aperture of the lip. The margins of the varices may be simple (*P. festiva*), scalloped (*P. macroptera, P. trialata*), have extended spurs on the margin that form distinctive recurved hook-like structures (*P. centrifuga, P. erinaceoides***,** *P. vokesae*), or have a single long heavy spine on each varices (*P. leeana*).

Pteropurpura festiva appears to have shorter varices, with a simple margin that uniformly recurves as much as 180 degrees along its entire length (Figure 7). Tuskes & Tuskes (2009) pointed out that this species can be found in surf-prone rocky coast feeding in the intertidal and subtidal zone. The curvature of the large varices effectively shortens their height and may be an adaptation to streamline the shell, thereby reducing the force of waves striking the shell. It may also allow an animal that becomes dislodged to right itself more quickly. The apparent height of the varices for *P. festiva* (ca 60 mm in length) is 4 to 5 mm but when the width is measured, over the 180 degree arc, it is 11 to 13.5 mm. The scalloped varices of similar sized *P. macroptera* varied from 9 to 15mm in height. As such, the varices of *P. festiva* are similar in width to *P. macroptera* but because they are folded, they are approximately one half to one-third the height. Unless genetic data proves otherwise, we believe that *P. festiva* is properly placed in *Pteropurpura*.

Within *Pteropurpura*, the shape of large varices found on *P. leeana* (Figures 8-9) are unique. The apex of the varices is nearly at a right angle to the columella of the shell. The spine is formed as the margins roll ventrally to produce a channel while the remainder of the varice tapers to the anterior end of the shell forming the closed siphon canal with no additional spines, and no apparent transition to form the siphon canal. All other species in the Eastern Pacific have a sharp distinctive transition from the varices to the siphon. Upon close inspection of *P. leeana*, it seems likely that if an animal were to be tipped to the side, it would be difficult for it to gain sufficient leverage to right itself. Since *P. leeana* is a deeper water species, and not likely to be significantly impacted by ocean swells**,** tipping over may be a low probability event. Holding specimens in your hand and noting the difference in shape, orientation, and strength of the spines suggest they may be a defense against large rays which typically crush a shell to feed on the animal within. When tissue is available for DNA analysis, we may have a more definitive answer as to its generic status.

Species Account

1. ***Pteropurpura centrifuga*** (Figures 1-2) is the second largest species in the region. Specimens 50 mm and greater typically express adult shell

characteristics. The final varices of all mature shells have 3 to 4 extended spines that are pinched together forming a distinctive dorsal ridge and the apical spine typically recurved by up to 90 degrees. The largest spine is at the apex with shorter spines midway to the anterior siphon. It is not unusual for the large apical spine of the varices to be broken. The shell may be white or white with distinctive yellow-brown bands Figure 1. When banding is present it is displayed on both sides of the varices.

A small cross section of records for depth and substrate in Mexico includes: Gulf of California, (Sonora) Guaymas 64-91 m, San Carlos 100 m, Doble Point also near San Carlos 95-115 m on coarse sand and dead shell; (Baja) San Juanico Bay 64-91 m in cobble, Los Angeles Bay 219-310 m; (Baja Sur Gulf) Conception Bay 46 m, Danzante Island 120 m, La Paz 45-55 m, Espirita Santos Island 164 m; (Baja Sur West Coast) Magdalena Bay 77-80 m; and (Baja West Coast) Cedros Island 76 m. Museum records indicate divers have found them on occasion in the range of 30-40 m, on sandy-mud bottoms with notable shell debris. The depth and substrate explains why specimens are taken by shrimpers. It is likely that the prey species are either bivalves or marine worms.

Range: Uncommon or absent from the northern Gulf of California. The occurrence of this species is well documented from the area of Los Angeles Bay and Guaymas in the Gulf of California south to Playa Gauyas Provence, Ecuador. Recently, Bertsch and Rosa (2016) cited a record from Caleta La Cruz, Peru. On the Pacific coast of Baja they have been collected as far north as Cedros Island.

Length: Most shells measure 60–75 mm in length, large specimens range from 80 to 90+ mm.

2. *Pteropurpura deroyana* (Figures 3-4) is endemic to the Galapagos Islands, Ecuador. When compared to *P. centrifuga* the shell of *P. deroyana* is easily distinguished as the apical spines on the varices are typically more flattened, extend upward, and are only slightly recurved; the surface of the shell is lightly but distinctly textured whereas *P. centrifuga* is smooth, larger and more robust with recurved spines on the varices. The shell of *Pteropurpura deroyana* is smaller, fragile and narrower than that of *P. centrifuga*. The species is uncommon in collections; Keen 1971 illustrated the ventral surface of a 33 mm specimen taken at 100 m. We examine two specimens collected in 1969 at a depth of 179 m off the south coast of Santa Cruz Island, in the Galapagos. Both shells are illustrated, the largest measures 58 mm the other, which had been cleaned is 43.7 mm, and are in the collection of Don Pisor. The texture of the shell surface is apparent as debris in the shallow grooves helps with the contrast on the larger individual.

Range: Restricted to the Galapagos Islands of Ecuador.

Length: 33-58 mm.

3. *Pteropurpura erinaceoides* (Figures 5-6) has mature varices with an apical spine that narrows and recurves, while the rest of the varices have five to seven short recurved spines, with a shape and size similar to those of *P. vokesae*. Shells may be white or light brown; some have contrasting banding that is dark to light brown or off-white bands present on the shell and both sides of the varices. With the exceptions of the larger apical spine, most spines measure 4 to 7 mm. Mature and juvenile animals are often found in the same environment and can be locally common. They occur both intertidal and subtidally and are found on rocks, under rocks, and occasionally attached to the base of rocks

just below the level of sand/silt. Eggs are deposited on rocks in the spring, sometimes in mass by many females. There is no parental care once the eggs are deposited.

The majority of the records are from intertidal collections, but specimens are also taken by divers and dredging. There does not appear to be a relationship between the depth and size of the shell. Specimens over 55 mm are not common. The largest intertidal shells in museum collections were 58.5 mm from Los Angeles Bay, Baja, and 61 mm from Requeson in Conception Bay, Baja Sur. Most specimens collected by divers are from less than 20 m but dredged specimens have been taken to at least 57 m. A series of 35 shells from San Luis Gonzaga, Baja, ranged from 14 to 35 mm in length, with a median size of 31 mm.

Range: Records extend from Puerto Penasco in the northern Gulf of California, south to Cabo San Lucas and north on the Pacific coast of Baja Sur to San Ignacio lagoon where they were found intertidally (ISO) and to the area of Guerreo Negro. The species is ubiquitous on the east side of the Gulf and has been found to the south in the states of Nayarit (Banderas Bay) and Oaxaca (Salina Cruz) Mexico.

Length: 25-40 mm is typical, large specimens exceed 55 mm. The largest shell measured was 64.3 mm in the collection of Larry Catarius.

4. ***Pteropurpura festiva*** (Figure 7) is found from the intertidal zone to approximately 25 meters; below that depth they are not commonly encountered. Fotheringham 1971 published a paper on a population of *P. festiva* found on the exposed rocky coast just north of San Diego, California, which provided a comparison for our later work in varied habitats. Immature and small adults are commonly found in the rocky intertidal zone. On the exposed rocky coast only 25-35% of the animals measured were greater than 30 mm in length, and no shells in a sample of 661 live animals exceeded 45 mm. While in protected areas of Quivira Basin, (Mission Bay, San Diego, California) greater than 95% of the 160 animals measured were between 31 and 55 mm.

Individuals in the intertidal zone feed primarily on barnacles during high tide and may move lower as the tide retreats, where they feed on limpets, especially the file limpet *Collisella limatula* (Carpenter, 1864). Larger adults are more often found in protected waters or in deeper water. In Mission Bay, large individuals are found on sand and measure 55 to 60+ mm. Large animals feed primarily on bivalves especially *Chione* and *Protothaca* and the attack pattern varies by prey species (Tuskes and Tuskes 2009). Adults have also been documented many times feeding with *Conus californicus* Reeve, 1844 on live bubble snails *Bulla gouldiana* Pilsbry, 1893 (Tuskes 2011). Adults breeding on the exposed rocky coast and jetty entries are smaller than breeding populations in bays. The difference in size may not be age related, but rather availability of food sources. In Mission Bay, reproduction occurs year-round, with a peak between May and August. Female *P. festiva* often lay their eggs in mass on rocks and other hard substrate. The biology of this species (prey selection, reproduction, habitat preference, *etc.*) was published by Tuskes and Tuskes 2009.

Range: Point Conception, Santa Barbara County, California south to Asuncion Bay in Baja Sur. The most southern record is from Magdalena Bay, Baja Sur. North of Point Conception, the species is infrequently found, with a record from Morro Bay and recently two specimens were documented from Monterey, California (Clark, 2016).

Length: 25 to 55mm, few shells exceed 60 mm. The largest specimen measured 67.4 mm, and collected from San Pedro Harbor, Los Angeles, California, Negus (1991).

5. *Pteropurpura leeana* (Figures 8-9) is a distinctive species and infrequently collected. They are collected by dredging, tangle nets, and occasionally by shrimpers. Battered specimens, which have lost most of their distinctive spines occasionally wash ashore. The shells of *P. leeana* are the most divergent within the genus, as the varices are modified to form large spines that surround the shell. The varices taper sharply from the spine to the body of the shell to form the closed siphon canal without the distinctive transition seen in the other species. This adaption makes the siphon much stronger and reminiscent of an additional spine. The consecutive varices of *P. leeana* do not line up; rather they are offset by 20-30 degrees distributing the spines in a greater arc. Shells with their spines intact can be as wide as the shell is long.

Range: This species is infrequently taken in the Gulf of California. Most specimens are from the Pacific side of Baja and Baja Sur primarily from Cedros Island south to Magdalena Bay. Beach worn specimens have been found further north. The most northern record is a 54 mm specimen taken NW off Anacapa Light, Anacapa Island, southern California at 86-96 m, 16 March 1941 R/V Velero (Figure 9) in the collection at NHMLAC**.**

Length: Mature shells measure 50 to 60 mm; shells 60 mm and greater are notably sturdier than smaller shells. The largest shell measured was 81.5 mm and in the collection of John LaGrange.

6. ***Pteropurpura macroptera*** (Figures 10-12). The base color of the shell varies from purple-brown , light brown, to nearly white. The color form *tremperi* (Figure 12) has white streaks across the shell and varices and are infrequently collected. The texture of the shell varies from nearly smooth to vary scaly and the margin of the varices may be deeply or moderately scalloped, or have little scalloping.

Most live specimens are less than 45 mm in length, but divers often pick up larger individuals. As a result both museum and private collections tend to have specimens 50 mm or greater. A high percentage of specimens from central California are said to have smoother margins on the varices than those from southern California, but we have not observed that based on museum material.

Bob Abel (personal communication) has taken *P. macroptera* in Fish Mill Cove, Sonoma County and noted that smaller individuals could be found at 11 m with larger specimens found deeper. In southern California, this species is taken by divers as shallow as 16 m, but more often at 20 m or greater on hard surfaces. A live 50 mm specimen was collected while dredging a rocky portion of the 9 Mile Bank, San Diego, California, at 155 m by J. LaGrange in1992, and at a depth of 100 m off Cedros Island, Baja Ca. In Baja Sur, they have been dredged at 37 m south of Point Eugenia and 99 m off Point Abreojos (NHMLAC).

Three specimens have been collected in the Gulf of California. Skoglund (1983) illustrated a live 38 mm specimen collected while dredging at a depth of 182 m off Los Angeles Bay, Baja. That specimen was deposited in the SBMNH and we have examined the shell. We found a 55 mm *P. macroptera* mixed in with a batch of *P. erinaceoides* from San Luis Gonzaga. Baja, at station #4 February 1967 by E. Hailey, the data slip did not record depth information (SBMNH). A third specimen was acquired from shrimpers

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at Loreto but the exact collection site is unknown.

Range: The species is known from Fish Mill Cove Sonoma County California south to Point Abreojos in Baja Sur. Two confirmed specimens from the upper Gulf of California may represent a relictual population.

Length: In Southern California, most specimens in collections are 50 to 55 mm, large individuals exceed 60 mm. The largest shells measured were from Santa Barbara County, California and measured 72.4 and 72.8 mm (SBMNH).

7. *Pteropurpura trialata* (Figures 13-14). Surprisingly, unlike many other *Pteropurpura* from the region, the immature stages of this species appears to be unknown. The smallest shell examined was a 29 mm sub-adult. The shell is white to off-white, with light to dark brown banding that may coalesce or remain separate. Unlike other eastern Pacific *Pteropurpura*, the banding on the shell is not expressed on the inner varices. In Mission Bay, perhaps 5% of the shells are alba. In Southern California, variation in the extent of scalloping on the margins of the varices, varices orientation, and shell length to width ratio are notably different between San Diego and Los Angeles. For more detailed information *see* Tuskes and Tuskes (2015).

Adults and sub-adults feed on the vermetid gastropod *Thylacodes* (formally *Serpulorbis*) *squamigerus* (Carpenter, 1857) which is a filter feeder found most commonly where there are notable currents. Tuskes and Tuskes (2015) published on the life history of this species. Growth occurs commonly when the water temperatures are cooler, from December through February, and tapers off with warmer water after April. Most mature animals add one varices per year until fully grown. Sub-adults may produce multiple varices per year. Based on (1) the extent of erosion on the apex, (2) the inability to replace damaged syphons, and (3) accumulation of fowling organisms; we estimate that females live to breed two additional years after growth has halted. Reproduction peaks in April and May as the water warms. Clusters of egg capsules are usually deposited on nearly vertical rock surfaces with minimal growth of red and brown algae present. Unlike *P. festiva* and *P. erinaceoides,* female *P. trialata* do not usually gather to lay egg capsules in mass. The average number of egg capsules per cluster is 60, and each capsule contained an average of 484 embryos, which emerge as veligers in 19-21 days at 70^{o}F.

Predation on adult animals has not been directly observed, but when empty shells of the species were glued to rocks and placed in the habitat near the rock-sand interface to estimate fouling rates, the vast majority of the shells were crushed and removed, probably by bat rays. We have observed and photographed bat rays feeding on other large shelled gastropods in Southern California.

Range: Point Conception Santa Barbara County, California south along rock coast and islands to similar habitat in Baja California Sur, Mexico, In Baja Sur, the species has been collected intertidally at Guerreo Negro and Point Asuncion, and Point San Pablo at 21-30 m. It would not be surprising if they occur farther south in suitable rocky habitat. Tuskes & Tuskes (2015) found that publications indicating this species occurs in Northern California are in error and based on miss-identification of *Ceratstoma foliatum* (Gmelin 1791) as *P. trialata.*

Length: 45 to 70 mm. Large shells exceed 80 mm. The largest specimen we measured was 105 mm in the SBMNH collection; very few shells exceed 90 mm. To understand the size distribution of a natural population, we dove Mission Bay, San Diego, California with a goal to measure the first 150 specimen observed regardless of size. A total of 158 specimens were measured and then released back into their environment. The size ranged from 44.1 to 74.7 mm with a mean of 63.3 mm and average of 62.4 mm.

8. *Pteropurpura vokesae* (Figure 15). Although *P. vokesae* can be taken on the same dive with *P. macroptera* they are most prevalent in sand and small rubble adjacent to rocky reef which is the preferred habitat of *P. macroptera*. Shells in small rubble at a depth 30 m off Point Loma, San Diego, are heavily encrusted, whereas, in areas where they spend time buried in sand, they are nearly free of fouling organisms. Larry Catarius (personal communication) found them buried in sand during the day with only the sponge covered dorsal varices partly exposed. Catarius noted that during dense red tide above the thermocline, dive lights were needed during the day in the clear water below. During those dives far more *P. vokesae* were found on the surface of the sand, suggesting they may be an active nocturnal predator.

Although this species has been found as shallow as 8 m in Mission Bay, that is an exception. Most specimens are taken by divers at 20-30 m and it has been dredged in Baja Sur at 99 m. It's likely that in the sand habitat the species feeds on bivalves or marine worms. It is surprising that there are no published records as to their prey species, considering the number of *P. vokesae* and *P. macroptera* that have been collected/observed. *Pteropurpura vokesae* exhibits little variation in color, other than intensity, and does not have white radial bands as do some of its close relatives, such as *P. erinaceoides.*

Range: Point Conception, southern California, south through Baja, with the southern records off Point Abreojos at 32-38 m in Baja Sur.

Length: Individuals from 35 to 45 mm are typical. Those in the range of 55 to 65 mm are less common. The largest specimen we measured was 71 mm.

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Pteropurpura* of the Eastern Pacific. Figures 1 to 15.** ***P. centrifuga Guaymas area, Sonora, Mex. (**1**) 76 mm and (**2**) 83 mm**.** ***P. deroyana*** Isla Santa Cruz, Galapagos Islands, Ecuador (**3**) Dorsal & ventral surface 58 mm and (**4**) 43.7 mm. ***P. erinaceoides*** Puertocitos, Baja Ca. Mex. (**5**) Dorsal & ventral surface 47 mm and (**6**) Isla Danzante, Baja Sur, Mex. 54 mm. ***P. festiva*** (**7**) Dorsal & ventral surface, Mission Bay, San Diego CA. 57 mm. ***P. leeana*** (**8**) Off Cabo San Lucas Baja Sur, Mex. 57 mm and (**9**) Ana Capa Island, Santa Barbara Co. CA. 54 mm. ***P. macroptera*** (**10**) Dorsal & ventral surface, Santa Barbara, CA. 54 mm, (**11**) white form, San Diego, CA. 42.9 mm and (**12**) form *tremperi,* San Diego, CA. 62 mm. ***P. trialata*** (**13**) Ventral (**14**) Dorsal, both San Pedro Breakwater, Los Angeles, CA. 86 mm. ***P. vokesae*** (**15**) Dorsal & ventral surface, Santa Barbara, CA. 53 mm.