The *Talostolida pellucens* Complex in the Tropical Eastern Pacific: In Perspective (Mollusca: Gastropoda: Cypraeidae)

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ABSTRACT The Tropical Eastern Pacific (TEP) stretches south from the Gulf of California along the west American mainland and the adjacent coastal areas, and then continues to its terminus in northern Peru. There are also five deep water oceanic islands within the TEP. The TEP coastal area encompasses the coast to the edge of the continental shelf and includes the coastal offshore islands in the Gulf of Panama. The Gulf of California and the Gulf of Panama constitute separate sub-basins within the TEP and contain the greatest diversity of molluscan fauna within the coastal area. The five TEP oceanic islands are defined as: (1) the near atoll of Clipperton, and the islands of Cocos and Malpelo which are centered in the region and (2) the two archipelagos, Revillagigedo and Galapagos which are on the northern and southern peripheries of the TEP. Clipperton is the furthest of the five main oceanic islands from the American mainland at 1,100 km, while Malpelo is the closest at 435 km. All five are volcanic and are separated by abyssal depths from the mainland and each other, and have never been connected.

The Cypraeidae of the TEP, including the *Talostolida pellucens* (Melville, 1888) complex, have only received the attention of scientists in relatively recent times, and only on a sporadic basis. This is due to the remote location of the offshore oceanic islands they inhabit, the difficulty of access, and the challenging collecting conditions which limit that activity. The literature is sparse and, with respect to the *T. pellucens* complex, confusing. While the description of the populations at Clipperton and Cocos Islands provided much current information, some additional perspective will hopefully shed more light on the status of the populations.

INTRODUCTION

The First Records and Reports

Even today, the 1905-1906 Galapagos Expedition of the California Academy of Sciences is regarded as a landmark in our understanding of those islands. However, stops at Clipperton Island on August 10 and at Cocos Island, from September 3 through September 13, 1905, were often overlooked as little of the findings were published. While there was no malacologist among the scientific members of

the expedition, the geologist, Washington Henry Ochsner, collected and documented both land and marine shells from the Galapagos Islands. He also collected and recorded *Talostolida* Iredale, 1931 from both Clipperton and Cocos Islands.

L. G. Hertlein first reported Ochsner's 1905 *Talosolida* finding at Clipperton as *Cypraea teres* (Gmelin, 1791) in 1937. Subsequently, he reported *C. teres* among the specimens collected during the 1954 Acapulco Trench

Expedition of the Scripps Institution of Oceanography (Hertlein & Emerson, 1957). Thereafter, the population was referred to as *C. teres*, *C. t. pellucens* or *Blasicrura alisonae* (Burgess, 1983) by various authors. Note: *Blasicrura* Iredale 1930 was changed to *Talostolida* by C. Meyer in 2003 and will be used in this paper throughout, unless quoting other authors. Lorenz & Hubert (1993) preferred *T. pellucens* for the Clipperton population while Emerson & Chaney (1995) preferred *T. alisonae*.

W. H. Ingram reported Ochsner's 1905 Cocos Island find in 1945. He had found a specimen of *Talostolida rashleighana* (Melvill, 1888) "while arranging the Cypraeidae collection of the California Academy of Sciences, Golden Gate Park, San Francisco, California." He noted that "It is a beach shell. The dorsal pattern and coloring are well preserved, and the shell is but slightly eroded."

He wrote: "To date there are two general widely separated areas from which specimens of C. rashleighana Melvill have been reported: one of these areas is the Hawaiian Archipelago and the other is New Caledonia and the Loyality Islands, Schilder, 1939. The writer has never seen specimens from the latter area but has collected beach shells of this species from the dredgings of Honolulu Harbor, Oahu, Hawaiian Islands, Ingram, 1937. The Cocos Island record extends the range of this species several hundreds of miles eastward and southward from the Hawaiian Islands and brings it into the fauna of the Western Americas. A close relative of this species, and one found with it in the Hawaiian Islands, is Cypraea teres Gmelin, reported earlier from the Western Americas on Clipperton Island, Hertlein, 1937" (Ingram, 1945).

Ingram clearly believed the specimen was synonymous with *T. rashleighana*, one of the most distinctive members of the genus. He also noted its separation from *T. teres*, also found in the Hawaiian Islands. Ingram repeated his findings in 1947.

As no further recorded collecting activities took place at Cocos Island until the early 1980s, all reports prior to then of *T. rashleighana* from Cocos are based on Ingram's finding. Note: By the mid 1980s, based on additional findings and research, it was apparent that Ingram's attribution of the Cocos Island population of *T. pellucens* to *T. rashleighana* was incorrect.

Emerson & Old (1968) figured a *Talostolida* specimen from Panama, one of a number collected in the 1930s by the Allen Hancock Pacific Expedition. They were a small, narrow form, collected alive in association with corals. This population was named *Talostolida pellucens panamensis* (Lorenz, 2002).

Subsequent Developments

In both of Burgess's publications (1970, p. 115, 1985, pp. 148-9), the range of T. rashleighana was extended to include Cocos Island. Kay (1979, pp. 197-199) maintains Cocos Island within the distribution of T. rashleighana. However, Burgess (1985) states that "Dr Kay does not believe it (T. rashleighana) exists as a breeding population outside of the Hawaiian Chain." This must have been based on personal communication because Kay does not hold that position in her 1979 publication as stated by Burgess. Further confusing the issue, Burgess (1985) includes Cocos Island in the distribution map of T. rashleighana while, at the same time, introducing Talostolida alisonae. He further notes "I have seen conchologically similar cowries from ... Cocos Island off Central America (Dr. D. R. Shasky)."

Talostolida alisonae (Burgess, 1983) was proposed almost entirely on the basis of differences with anatomical Т. Differences in the papillae were cited as the main difference between the two species, adding that the two species are not separable on conchological characters alone. In addition, Burgess stated that "Shells collected by Emerson and Old in the eastern Pacific are conchologically *alisonae*, but as in other cases animal studies are not recorded" (Hawaiian Shell News, 1984). Emerson & Old (1968, Plate 12, Figures 1 to 9) figured a specimen from the Galapagos along with the Holotype of T. alisonae. The latter is also pictured in the HSN article (p. 3) and Burgess (1985, p. 148). The Holotype bears a striking resemblance to Talostolida from Cocos Island. The HSN article and Burgess (1985) formed the basis for collectors of Talostolida from Cocos Island to label them *T. alisonae*.

However, descriptions of a species/subspecies on the basis of anatomical characteristics, without supporting consistent conchological characteristics, are problematic at best. Not surprisingly, Lorenz & Hubert (1993) placed *T. alisonae* in synonymy with *T. teres pellucens*, treating the latter as an ecological subspecies. All *teres* complex populations in the TEP were attributed to this subspecies while giving the population from Panama the varietal name *panamensis*.

Emerson & Chaney (1995), while acknowledging Lorenz & Hubert's work, retained the use of *T. alisonae* for TEP populations, pending further elaboration of the characteristics of *T. alisonae* in the TEP. Dr. Chaney's collecting at Cocos Island (1991-1992) and on the offshore islands of western Panama (1993) produced a significant number of specimens of the *T. teres* complex. On that basis, the authors wrote: "All of these cowries had the

mantle characters of *B. alisonae* and not of *B. teres*, even though there was considerable variation in shell morphology, expressed as differences in color pattern, growth form, or most importantly, sexual dimorphism. Populations from Cocos Island and western Panama have a similar radular morphology (*teste* Hugh Bradner, June 26, 1993)."

At this point, the Cocos Island population of *T. pellucens* had competing classifications, both of which needed further study and elaboration.

Lorenz (2002, p. 107) elevated T. teres and T. pellucens to separate species status. He also described T. p. panamensis, elevating the variety to subspecies status. The distribution of the subspecies was listed as "Panama, Costa Rica, Mexico and Galapagos." It was further noted that "Shells from Clipperton Is. and Cocos Is. may resemble either typical teres, pellucens or even latior. Their animal characteristics are so far poorly documented. ... Particular attention should be paid to the populations of this species from Natal, the Red Sea, Cocos Is., Clipperton Island, and the Marquesas all of which show subtle features which might indicate validity on some relevant level" (pp. 122-3).

Elaboration and Clarification

Up until 2011, the study of the Cocos Island Talostolida population, as well as other TEP populations, had been precluded by a lack of sufficient available specimens with reliable collection data. The exception was specimens from the Panamanian population which became widely available prior to Lorenz (2002). By 2011, the authors had accumulated sufficient specimens from the 1994 Clipperton Island Expedition and the 1980s/90s Expeditions to Cocos Island for a comparative study (Daughenbaugh Beals, 2013). These &

specimens, coupled with the holdings of the Santa Barbara Museum of Natural History, formed the basis for the descriptions of *Talostolida pellucens jacksoni* Daughenbaugh & Beals, 2013 and *Talostolida pellucens sumeihoae* Daughenbaugh & Beals, 2013.

Based on a number of factors which led to the Divergent Evolution of the *T. pellucens* populations in the region (see below), these two new subspecies were described in addition to the subspecies previously described. The distinct conchological features of the individual populations supported subspecies recognition. The features of and holotype photos of each of the subspecies are provided below:

• Talostolida pellucens jacksoni (Figure 1) are callous/heavy and oval/cylindrical. Embryonal bands are not visible through the thick basal callus. The labral margin is slightly stepped, the columellar margin mostly well produced with a slightly upturned marginal edge. The aperture is narrow throughout and the peristome concave with a serrated edge at its inner edge. Marginal spotting is distinct and mostly profuse. Dorsal ground coloration pale blue/green.

- Talostolida pellucens sumeihoae (Figure 2) are callous/heavy and oval/pyriform. Embryonal bands are not visible through the thick basal callus. The labral groove is stepped; the columellar margin calloused, produced and slightly upturned. The aperture is of intermediate width throughout and the peristome distinct. Marginal spotting is distinct and profuse, especially on the columellar side. Dorsal ground coloration pale blue/green.
- Talostolida pellucens panamensis (Figure 3) are lightweight and slender, and nearly cylindrical. Embryonal bands are visible through the thin basal callus. The labral groove is shallow, the columeller margin not calloused. The aperture is wide throughout and the peristome indistinctly ribbed. Marginal spotting is distinct but sparse. Dorsal ground coloration greenish. (Lorenz, pp. 106-7).



Figure 1. T. p. jacksoni holotype



Figure 2. T. p. sumeihoae holotype



Figure 3. T. p. Panamensis holotype

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	Mantle	Papillae	Siphon
T. p. jacksoni	orange to orange/red, faint lighter blotches, thick/slightly rough	mostly small to large, sparse, light gray to grayish white, banded, slightly tapered, few blunt but mostly 2-4 white or white tipped branches	light orange, translucent, fringed w/ white tips, orange ringed
T. p. sumeihoae	orange/red to red, faint lighter blotches, orange/ brown flecked, thick/slightly rough	large, sparse, grayish white to white, banded, mixture of tapered blunt, and complex white branches	light orange, translucent, fringed
T. p. panamensis	orange/red to red, faint lighter blotches, dark flecked, thick/slightly rough	large, sparse, dark, banded, few blunt but mostly numerous, complex white branches	light orange, translucent, fringed, orange/brown ringed

Prior to the 2013 paper, the animal characteristics of the three subspecies were poorly documented. Fortunately, Dr. Henry Chaney, Santa Barbara Museum of Natural istory (SBMNH), was able to provide excellent animal photos of all three subspecies taken by him on his trips to the region (Figures 4-6). The characteristics are distinct as shown in the table above.

As of 2013, the known distribution for each subspecies was noted as: 1. *T. p. jacksoni* is restricted to Clipperton Island, 2. *T. p. sumeihoae* is restricted to Cocos and Malpelo Islands with the latter likely representing down stream migrants from Cocos, and 3. per Lorenz (2002, p. 107), *T. p. panamensis* ranges from Panama, Costa, Rica, Mexico and Galapagos. However, the authors are not aware of any records or evidence of *T. pellucens* from either Mexico or the Revillagigedo Archipelago.

From the above, one could be forgiven for believing that the taxonomy of the three subspecies is clear cut and not controversial. This would be true for specimens from the type localities of Clipperton Island and Cocos/Malpelo Islands. However, nature conforms to its own rules which do not necessarily align with those of man.

There has been a recent report of a specimen closely resembling *T. p. sumeihoae* from the coast of Costa Rica (Lorenz, pers. comm.). While we have not examined the specimen, nor verified the accuracy of the collection data, it is possible that this could be a migrant from the Cocos Island population. We would not be surprised if other isolated specimens were found down stream or in areas adjacent to the island. However, there is no indication that this represents a viable population, but is probably a migrant.

Talostolida pellucens panamensis Elaborated

Along with specimens whose features align with those of the type species, there are specimens which do not align with the description of T. p. panamensis at the type locality of Cebaco Island and in the type habitat of "depths between 2 and 15 m among rocks and sponges" (Lorenz, p. 107). At Cebaco Island and the adjacent islands in the Gulf of Panama, there are shells which retain the nearly cylindrical shape of T. p. panamensis but have a callous base with the callosity extending up onto the margins in some instances. When this occurs, the shape of the shell is extended somewhat laterally and the shell is heavier, but still retains the nearly cylindrical shape of the subspecies. In addition, the marginal spotting is distinct and dense. Some of these shells are noticeably elongate while others more truncated. In all other respects, the shells conform to the type. While relatively rare, these are probably more mature specimens of *T. p. panamensis*.

In addition, there are two specimens in the second author's collection which are similar to T. p. sumeihoae. They were collected in 1993 following the moderate 1991-1992 El Nino-Southern Oscillation (ENSO) event. ENSO events result in stronger, faster currents albeit along their normal trajectory. One specimen was collected at Ladrones Island, Panama in January and is indistinguishable from T. p. sumeihoae. The other specimen was collected on a seamount off Ladrones Island in April. It shares the features of both T. p. sumeihoae and T. p. panamensis with the callosity of the former and the elongate shape and coloration of the latter. The authors believe that this specimen represents a hybrid of the two subspecies. The former is a likely migrant from Cocos Island. This hybrid likely represents an early stage of integration into the *T. p. panamensis* gene pool. These are the only two such specimens known

to the authors. The authors are not aware of any evidence that a population of *T. p. sumeihoae* has established itself in Panama.

Does the range of *T. p. panamensis* extend to the Galapagos Islands? From February to April each year, the downstream Panama Current flows from the Gulf of Panama to the Galapagos where the molluscan fauna is primarily Panamic (Daughenbaugh & Beals, 2013). As such, one could expect that to find *T. p. panamensis* in the Galapagos. In fact, they are there. While verified *Talostolida* specimens from the Galapagos Islands are rare, the authors have examined six verified specimens (Beals, pers. comm.).

Four specimens were collected at Wolf Island in March, 2005. Two of the specimens align with the description of T. p. panamensis, while the other two align more closely with the callous form from the Gulf of Panama. The two callous shells were found under one rock, one is elongate and over 40 mm in length while the other is more truncated. This probably represents sexual dimorphism. Of note, one of the non-callous shells is also over 40 mm in length. In addition to the four Wolf Island shells, two additional specimens were collected on the same trip. One was collected at Cousins Rock while the other was collected at Cape Marshall. Isabella Island. Both shells are the callous form. All six specimens were collected at 6-10 meters, under rocks.

An additional specimen is illustrated by Emerson & Old (1968, Plate 12, Figures 1 to 9) as *Cypraea (Talostolida) teres*. The specimen was reported to have been collected fresh dead off Sombrero, Isla San Salvador, Galapagos Islands at a depth of two fathoms. The specimen is very large at 50 mm and appears to be the callous form of *T. p. panamensis*.

Divergent Evolution

There are three *T. pellucens* subspecies in the TEP, a relatively compact, end of range region. This somewhat surprising happenstance is the result of a number of factors:

- 1. DNA studies of two *T. p. jacksoni* showed that the Clipperton population had been colonized multiple times from at least two different closely related groups from a southwest (Thailand, Phuket, Marquesas) minor trajectory, meaning that the TEP populations are likely not a single lineage (C. Meyer, pers. comm.).
- 2. The populations are isolated by:
 - Biogeography. The TEP islands are separated by abyssal depths from the mainland and each other and have never been connected.
 - **Distance.** From the Line Islands to Clipperton is 5,700km, from Clipperton to Cocos is 2,375km, from Cocos to the Galapagos is 673km.
 - Oceanography. The North Equatorial Counter Current (NECC) flows from the central Pacific Line Islands downstream into the TEP through Clipperton, Cocos, Malpelo and the Gulf of Panama in seriatim. There is little upstream current. However, currents do flow seasonally toward Malpelo Island from the Gulf of Panama and then flow onward to the Galapagos Islands (Glynn, et al.).
- 3. The short life of the *Erroneinae* Troschel, 1863 lineage larvae in general, and *T. pellucens* specifically (Pauley & Meyer), limits present day dispersal of *T. pellucens* within the TEP.
- 4. Present day currents are relatively stable and predictable, fostering genetic isolation.

5. The Panama/Galapagos populations inhabit depths between 1-10 meters while the Clipperton and Cocos/Malpelo populations inhabit depths of 10 meters or greater in open ocean settings.

These factors and conditions set the stage for the Divergent Evolution of populations of *T. pellucens* at distinct, separate locales within the TEP. In this case, it is likely that the small number of individual *T. pellucens* veligers which survived to form viable populations were the survivors of a larger influx from a different ecological environment (coral reefs) who were able to adapt to the challenging, largely volcanic conditions existing at varied locales within the TEP. This probably occurred over a relatively short evolutionary time span.

ACKNOWLEDGEMENTS

Dr. Henry Chaney, SBMNH, provided the holotype and a paratype for both *T. p jacksoni* n. ssp. and *T. p. sumeihoae* n. ssp. as well as excellent photos of live *T. pellucens* from the Clipperton, Cocos and Panama populations. We are also indebted to Dr. Chaney for his review of the manuscript, and Virginie Heros of the MNHN in France for images of the *T. p. panamensis* holotype.

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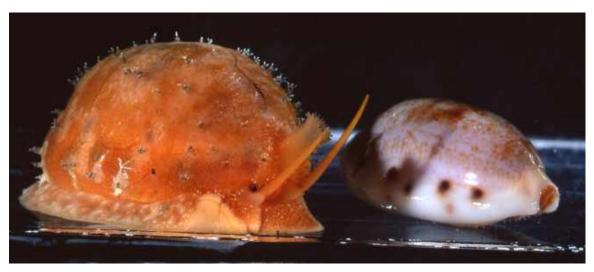
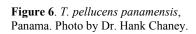




Figure 4. *T. pellucens jacksoni,* Clipperton Island. Photo by Dr. Hank Chaney.

Figure 5. *T. pellucens sumeihoae*, Cocos Island. Photo by Dr. Hank Chaney.





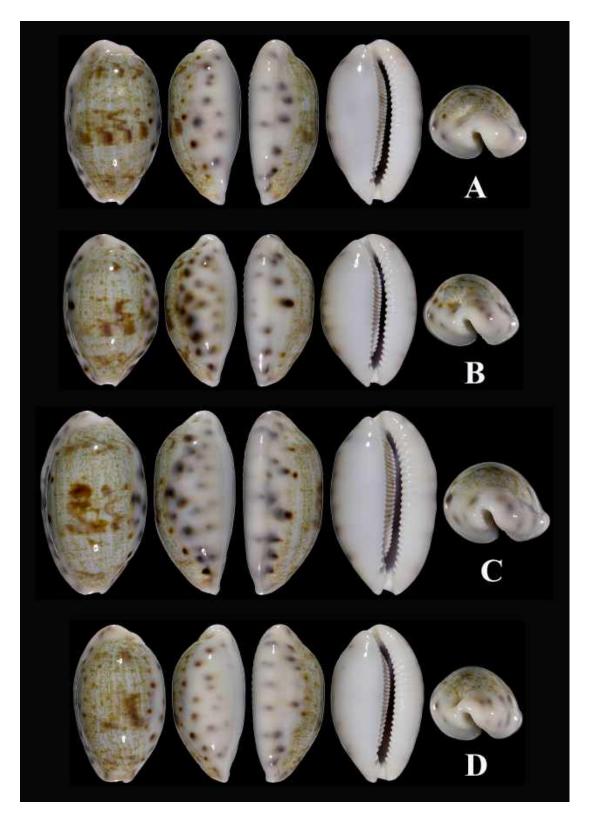


Figure 7: *T. pellucens jacksoni* specimens. A = holotype 34.8mm; B = paratype 2, 32.0mm; C = paratype 3, 38.7mm; D = paratype 5, 33.2mm.

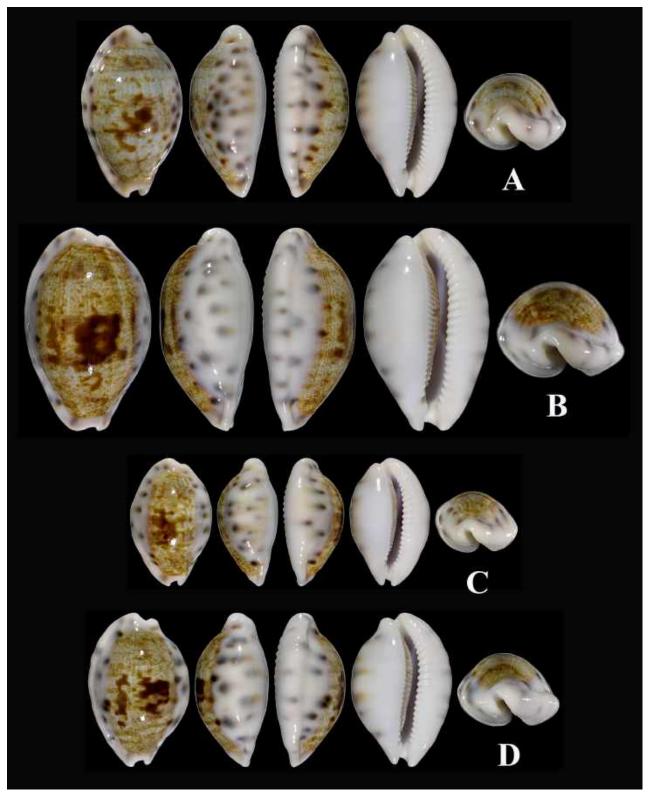


Figure 8: *T. pellucens sumeihoae* specimens. A = holotype 35.4mm, B = paratype 2, 42.0mm, C = paratype 6, 26.7mm, D = *T. pellucens sumeihoae* paratype 9, 32.0mm.



Figure 9: *T. pellucens panamensis* specimens. Top row = holotype, 26.8mm, dorsal, ventral and side views; Second row = Sebaco Island 27.3mm, Contreras Island 34.9mm, Contreras Island 30.8mm dorsal and ventral views; Third row = Sebaco Island 42.1mm, Sebaco Island 35.0mm, Secas Island 41.5mm dorsal and ventral views; Fourth row = Sebaco Island 34.6mm dorsal and ventral views, off Ladrones Island 38.1mm dorsal and ventral views.



Figure 10: Top row = *T. pellucens sumeihoae* Cocos Island 37.6mm, *T. pellucens sumeihoae* x *T. pellucens panamensis* off Ladrones Island, Panama 38.7mm, *T. pellucens sumeihoae* Ladrones Island, Panama 34.2mm; Second row = *T. pellucens panamensis* Las Perlas Islands, Panama 38.0mm and 34.1mm, Wolf Island, Galapagos 44.2mm and 34.4mm; Third row = *T. pellucens panamensis* Wolf Island, Galapagos 43.3mm dorsal and ventral views, Cousins Rock, Galapagos 36.1mm, and Isabella Island, Galapagos 33.3mm.