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A Revision of the Status of Several Conoid Taxa from the Hawaiian Islands: Description of Darioconus leviteni n. sp., Pionoconus striatus oahuensis n. ssp., and Harmoniconus paukstisi n. sp. (GASTROPODA, CONIDAE)

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Systematics: The taxonomy used in the present article follows TUCKER & TENORIO (2009). For the description of the shell morphometry we use the terminology established in RÖCKEL, KORN & KOHN (1995).

Introduction:

The cone fauna of the Hawaiian Islands has been reviewed a number of times (KOHN, 1959; KOHN & WEAVER, 1962; KAY, 1979). Every new field research campaign in the area provides new findings, and expands the range of other Indo-Pacific species of cones previously unknown for the archipelago. However, even seemingly well known, common cone species long known from the Hawaiian Islands, may produce surprises when re-examined and compared to other similar taxa. Herein, we report three such surprises.

First, the presence in Hawaii of populations of cones with a brown shell marked with a white-tent pattern is well established. It had been usually treated as Conus omaria Hwass in BRUGUIÈRE, 1792. OSTERGAARD (1950), who made a thorough study of the spawning and development of some Hawaiian marine gastropods including a number of species of cones, used this nomenclature. KOHN (1959a, 1959b) noticed that the Hawaiian individuals were different from typical Darioconus omaria, which has a much narrower last whorl, a lower spire, and a multispiral protoconch, and identified them as Conus pennaceus BORN, 1778. If these Hawaiian populations are considered conspecific with Darioconus *pennaceus*, then they would be geographically isolated from the other populations of *D. pennaceus* that are distributed throughout the Indian Ocean. This suggests that these marginal populations deserve subspecific status (RÖCKEL, KORN & KOHN, 1995; KORN, NIEDERHÖFER & BLÖCHER, 2000; PAGANELLI, 2009). Apart from the geographical isolation, which clearly suggests an allopatric speciation process, there are a number of constant features that from our point of view justify the consideration of these *pennaceus*-like cones as members of a new, separate species, which is hereby introduced: D. leviteni n. sp. The specific names Conus stellatus G. B. SOWERBY III, 1874, and Conus racemosus KIENER, 1845 which have been sometimes used to denote the Hawaiian populations of *Conus pennaceus* (= D. leviteni) were reviewed in RÖCKEL, KORN & KOHN (1995). They concluded that these names can not be unequivocally applied to the Hawaiian specimens, and hence the introduction of a new name seems appropriate at this stage. Second, local populations of Pionoconus striatus LINNAEUS, 1758 in the Hawaiian Islands differ statistically in shell length, maximum diameter and spire height when compared to individuals from other Indo-Pacific localities. These constant features found in the Hawaiian P. striatus have prompted us to introduce a new subspecies, P. striatus oahuensis n. ssp. for this population.

Finally, a new species of Harmoniconus related to H. nanus has been identified. We have determined that there are at least four conchologically recognizable species of Harmoniconus (see TUCKER & TENORIO, 2009) in the Hawaiian Islands. Despite extensive molecular study the identities of these were not completely clarified by DUDA & al. (2008). We recognize the following three known species: Harmoniconus mcbridei (LORENZ, 2005), H. nanus (G. B. SOWERBY I, 1833) (sensu stricto), and H. sponsalis (Hwass, 1792) and describe Harmoniconus paukstisi n. sp. as the fourth species that has somehow escaped notice until now.

> Family Conidae FLEMING, 1822 Subfamily Coninae FLEMING, 1822 Darioconus leviteni n. sp.

Type material: Holotype and 14 paratypes in collections of the Santa Barbara Museum of Natural History SBMNH as follows: holotype-SBMNH 423910, 64.4 x 38.1 mm, Hauula, Oahu, Hawaii, in sand under dead coral, 0-2 m, 21°36'N, 157°54', collected by BOB PURTYMUM, 29 December 1973; SBMNH 423492: paratype 1, 49.8 x 30.6, same data as holotype; SBMNH 423472: paratype 2, 51.8 x 32.7 mm, Diamond Head Beach Park, Oahu, Hawaii, in sand under coral head, 0-2 m, 21°15'18"N, 157°48'20"W, collected by BOB PURTYMUM, October, 1969; SBMNH 423474: paratype 3, 61.0 x 36.5 mm, Diamond Head Beach Park, Oahu, Hawaii, in sand under coral slab, 0-2 m, 21°15'18"N, 157°48'20"W, collected by BOB PURTYMUM, 31 January 1971; SBMNH 423471: paratype 4, 54.4 x 32.2 mm, Waikiki Beach, Oahu,

Hawaii, in sand under coral head, 0-2 m, 21°16'06"N, 157°50'30"W, collected by BOB PURTYMUM, 18 February 1974; SBMNH 88483: paratype 5, 41.5 x 20.3 mm, paratype 6, 30.5 x 16.8 mm, paratype 7, 21.2 x 11.5 mm, all Port Allen, Kauai, Hawaii, at night, low tide, intertidal, 21°54'10"N, 159°35'25"W, collected by TWILA BRATCHER, February 1961; SBMNH 88478: paratype 8, 38.3 x 22.5 mm, paratype 9, 37.9 x 20.8 mm, Ewa Beach, off Keahi Point, Oahu, Hawaii, in sand under coral. 10-25 m, 21°17'12"N, 157°58'24"W, collected by RAY A. MCKINSEY, 1 May 1976; SBMNH 88484 paratype 10, 53.3 x 31.0 mm, paratype 11, 49.5 x 29.0 mm, both Hauula Beach Park, Oahu, Hawaii, in sand under coral on low reef, by diving, 0-2 m, 21°36'N, 157°54', collected by RAY A. MCKINSEY, 15 March 1980; SBMNH 99556: paratype 12, 42.2 x 26.0 mm, Kahuku, Oahu, Hawaii, 0-2 m, 21°41'12"N, 157°56'48"W, collected by RAY A. McKINSEY, 12 May 1957; SBMNH 99548: paratype 13, 38.1 x 20.9 mm, paratype 14, 31.1 x 17.1 mm, both Kailua Bay, Hawaii, Hawaii, by diving, in sand and rubble under rock, 0-2 m, 19°38'N, 155°59'55"W, collected by HENRY W. CHANEY, 12 September 1982. Additional paratypes: Museo Nacional de Ciencias Naturales (MNCN 15.05/53.566), Madrid: paratype 15, 49.8 x 29.7 mm, Haleiwa, Oahu, Hawaii, on reef in sand under rocks, 0.5 m depth, collected 3 November 1974; Natural History Museum (NHM), London: paratype 16, 51.05 x 30.60 mm, Hauulu, Oahu, Hawaii, 2-6 feet, under dead coral on sand on reef; Musée Nationale d'Histoire Naturelle (MNHN 22800), Paris: paratype 17, 36.4 x 23.9 mm, Kuhuku, Oahu, Hawaii, on sand pockets and channels on reef (w/p, w/o), collected 2 March, 1975; US National Museum (USNM 338584), Washington DC, paratype 18, 69.2 x 37.3 mm, Keaukaha Pond, Hilo, Hawaii, Hawaii (ex-THAANUM collection).

Type locality: The type locality is Hauula, Oahu, Hawaii, in sand under dead coral, 0-2 m, 21°36'N, 157°54', the collecting site for the holotype and one of the paratypes.

Geographical distribution: At present, the species is known from the Hawaiian Islands including the islands of Oahu (e.g. SBMNH 423492, SBMNH 423471, SBMNH 423472, etc), Hawaii (SBMNH 99548), Molokai (one specimen from this locality is hosted at the Academy of Natural Sciences of Philadelphia, ANSP 116366, from Moomomi, Molokai), Kauai (SBMNH 88483), and Maui (SBMNH 423491, SBMNH 423469, SBMNH 99547) along with one or more specimens from Midway Island (SBMNH 125377) and Johnson Atoll (SBMNH 88498). It is likely that *Darioconus leviteni* is distributed throughout the Hawaiian Islands including the northwestern Hawaiian Islands, atolls and banks. Other specimens of the *D. pennaceus* complex of species (see RÖCKEL, KORN & KOHN, 1995) occur in the Indo-Pacific region. These and *D. leviteni* are all allopatric with each other.

Diagnosis: Medium-sized, solid shells, ventricosely conical with a low to moderate spire; shells broader than *Darioconus omaria* and typical *D. pennaceus*; sutural ramps flat to concave, with two or three weak cords disappearing in later whorls; protoconch paucispiral, pink, mamillated; ground color white; last whorl and spire patterned with different shades of brown overlaid with white tent markings; aperture white; radular tooth of the molluscivorous type, with one barb, a blade, a serration and a terminating cusp; basal spur absent; relative barb and blade lengths, and relative shaft width larger than in the radular tooth of *D. pennaceus*; direct benthic development, with larvae metamorphosing within 24 hours of hatching.

Description: More than 170 specimens were examined. Shell morphometry: L = 30 to 57 mm (mean 42 mm, max. L measured 65.2 mm); RD = 0.56 to 0.72 (mean 0.65); RSH = 0.08 to 0.15 (mean 0.10); PMD = 0.75 to 0.92 (mean 0.82). The holotype and a series of paratypes are illustrated in Plate 1. The shell is solid and medium-sized. The profile of the last whorl is ventricosely conical to broadly and ventricosely conical (conical in some specimens), with a low to moderate spire. The spire has usually a straight profile, but it can be slightly concave or slightly convex. The early sutural ramps are flat, slightly concave to concave in later whorls, with two or three weak cords becoming obsolete or absent. The protoconch is paucispiral (1.75 whorls), pink, mamillated. The shoulder is subangulate to rounded. The sides of the last whorl are usually convex, but straight in some populations. It appears to exist a consistent variability in shell shape according to the particular island, or even to particular populations within an island. Thus, certain populations (i.e. specimens from Kauai) tend to have a more ovate shape, whereas other are more elongated (i.e specimens from Maui). Ground color white, with pinkish shades specially in younger specimens. Last whorl overlaid with tones of brown color ranging from yellowish to almost black, sometimes with fine dotted spiral bands, and with a distinctive pattern of white tent markings. The triangular tent markings are edged with a dark brown line, and are usually arranged in three spiral bands of variable width around the last whorl, one below the shoulder, another at the center and at the base. In certain populations the tent markings might be more scarce and brown color predominates over white, whereas in others (i.e. shells from Kauai), the tented pattern is replaced by a fine axially reticulated pattern giving a darker appearance. The spire sutural ramps are patterned like the last whorl. The aperture is pure white. The periostracum is yellow, thin and translucent.

Living animal and radula: The foot is white to tan, mottled with reddish-brown. The siphon is white with a red tip and a black ring near the end. The radular tooth is of the molluscivorous type, elongated, with one barb opposite to a small pointed blade (Figure 1). The anterior portion of the tooth is distinctively longer than the posterior section, representing 65 to 70 % of the total length of the tooth. There is a serration with small denticles in a single row extending from the apex to the indistinct waist, ending in a rounded cusp. The posterior section has a C-fold, and the base does not have a basal spur.



Darioconus leviteni n. sp.

Fig. 1: Paratype 2, Diamond Head Beach Park, Oahu, 51.8 mm, SBMNH 423472. Fig. 2: Paratype 3, Diamond Head Beach Park, Oahu, 61.0 mm, SBMNH 423474. Fig. 3: Paratype 8, Ewa Beach, off Keahi Point, Oahu, 38.3 mm, SBMNH 88478. Fig. 4: Paratype 15, Haleiwa, Oahu, 49.8 mm, MNCN 15.05-53.566. Fig. 5: Paratype 11, Hauula Beach Park, Oahu, 49.8 mm, SBMNH 88484. Fig. 6: Holotype, Hauula Beach Park, Oahu, 64.4 mm, SBMNH 423492.
Fig. 7: Paratype 12, Kahuku, Oahu, 42.2 mm, SBMNH 88488. Fig. 8: Paratype 17, Kahuku, Oahu, 36.4 mm, MNHN 22800. Fig. 9: Paratype 14, Kailua Bay, Hawaii, 31.1 mm, SBMNH 99548. Fig. 10: Paratype 5, Port Allen, Kauai, 41.5 mm, SBMNH 88483.





Fig. 1. Radular tooth of D. leviteni (extracted from paratype 13, SBMNH 99548, 38.1 x 20.9 mm, Kailua Bay, Hawaii).

Comparison and Remarks: Darioconus leviteni has been extensively studied under a variety of names: Conus omaria (OSTERGAARD 1959), Conus pennaceus (KOHN 1959; PERRON 1981, 1983), or even Conus elisae (KOHN 1959b; PERRON 1979). It has a benthic reproductive development (unique among the cone fauna of the Hawaiian Islands) compared to the planktonic development for the Indian Ocean populations of D. pennaceus (Röckel, Korn & Kohn 1995, and references therein). The average egg diameter (470-520 um for D. leviteni) as well as the number of eggs per capsule (25 to 250) differs significantly from the values observed for Indian Ocean D. pennaceus populations. There are also significant differences in shell and radula morphology which allow separation of D. leviteni from D. pennaceus. The shell of D. leviteni is significantly broader than any other form of D. pennaceus. We have measured the maximum diameter and the shell length of 184 specimens of D. leviteni from different populations in Hawaii, 29 D. behelokensis, 20 D. lohri, 55 D. pennaceus, and 31 D. pennaceus f. quasimagnificus totalising 319 shells. An analysis of covariance (ANCOVA) using maximum diameter (MD) as variable, taxon (behelokensis from Madagascar, leviteni from Hawaii, lohri from South Africa/Southern Mozambique, pennaceus from Northern Mozambique/other East Africa localities, quasimagnificus from Oman/Red Sea) as factor, and shell length as covariate yielded highly significant differences (99 % probability level) between the maximum diameter of Hawaiian shells (D. leviteni) compared to the shells of taxa from localities in the Indian Ocean corrected for differences in length (F-score = 63.81, p = 0.0000), with the only exception of D. lohri. The least-squares mean maximum diameter for D. leviteni is 25.8 mm (std error 0.1 mm) versus 22.0 mm (std error 0.2 mm) for *D. pennaceus* (Figures 2 and 3).



Fig. 2. Least-squares mean maximum diameters and 99 % BONFERRONI intervals for taxa in the D. pennaceus complex.



Fig. 3. Plot of maximum diameter versus shell length for D. leviteni (o) from Hawaii, and D. pennaceus (\blacktriangle) from northern Mozambique/East Africa, showing the differences in relative maximum diameter.

The most similar taxa in maximum diameter are D. lohri (LS mean MD = 25.7 mm, std error 0.3 mm) and D. pennaceus f. quasimagnificus (LS mean MD 24.8 mm, std error 0.3 mm). However, the pairwise comparison of the maximum diameter between D. leviteni and D. pennaceus f. quasimagnificus is still significant at 99 % probability level. A similar ANCOVA using spire height (SH) as variable, taxon as factor and length as covariate for a total of 301 specimens compared, yielded statistically significant differences (F-score = 18.20, p = 0). The pairwise comparison between mean spire heights of *D. leviteni* (LS mean SH = 5.3 mm) and *D. lohri* (LS mean SH = 3.7 mm) is significant at 99 % probability. The differences in spire height between D. leviteni and D. pennaceus (LS mean SH = 3.7 mm) and D. pennaceus f. quasimagnificus (LS mean SH = 4.3 mm) are also significant at 99 % probability level. Hence, D. leviteni has the largest maximum diameter and spire height compared to other taxa in the D. pennaceus group, with few exceptions. See Plate 4 for shell comparison.

Nishi and KOHN (1999) have studied the variability of several quantitative characters for the radular teeth of separate populations of *Conus pennaceus* from Hawaii (= D. leviteni), Maldives and Sumatra. By means of an analysis of variance (ANOVA) these authors concluded that the ratios barb length/tooth length ($B_{1,}/T_{1,}$), blade length/tooth length ($B_{2,}/T_{1,}$) and shaft width/tooth length (SH_w/T_i) varied significantly among these populations of taxa. Pairwise comparison tests differentiated the Hawaiian specimens from those of the Maldives and from Sumatra. Hence, the relative barb and blade lengths for D. leviteni (B1,/T, = 0.043 to 0.076, B2,/T, = 0.081 to 0.116) are larger than in specimens of D. pennaceus from Indian Ocean localities (Maldives and Sumatra). We have additionally compared with the relative blade lengths B2,/T, of three specimens of D. pennaceus f. rubropennatus from Réunion (from EMILIO ROLÁN radula collection), which ranged from 0.075 to 0.09 versus 0.081 to 0.116 for D. leviteni. Unfortunately, there are insufficient data on the morphometric parameters of radular teeth of Indian Ocean specimens of D. pennaceus from other localities, and hence a statistical comparison having a wider scope was not feasible at this stage. The different populations of *D. leviteni* in Hawaii are very variable in shape, color and pattern. This is a direct consequence of its benthic mode of reproduction, as previously reported (OSTERGAARD 1959; KOHN 1959a; PERRON 1979, 1981, 1983). Certain populations are strikingly different and would suggest that D. leviteni is actually a superspecies composed of several taxa. One of these cases is the form referred to as Conus elisae KIENER, 1845. This name is applied to shells with a rather ovate shape, most typically from Kauai, with a characteristic reticulate pattern of fine axial lines. However, PERRON (1979) showed in laboratory experiments that shells with the "elisae" pattern are a color form due to a recessive allele combination, and co-occur with the standard patterned individuals from Oahu. We have studied the variability of shell shape in 172 specimens of D. leviteni by means of ANCOVA using either MD or SH as variable, island (Hawaii-Big Island: 50 specimens, Oahu: 104 specimens, Kauai: 18 specimens) as factor, and shell length as covariate (Figure 4). Specimens from other islands such as Maui, Molokai or the Northwestern Hawaiian Islands were excluded due to insufficient sampling.



Fig. 4. Least-squares mean maximum diameter and spire height and 99 % BONFERRONI intervals for *D. leviteni* from different islands.

The results indicate highly significant differences in maximum diameter (F-score = 72.78, p = 0) depending on the island. The specimens from Oahu exhibit the largest LS mean maximum diameter, whereas specimens from Hawaii (Big Island) are the narrowest. In addition to this, significant differences were also found in spire height (F-score = 19.76, p = 0). Specimens from Hawaii (Big Island) are significantly higher spired than individuals from Oahu or Kauai. No differences in spire height were found between Kauai and Oahu individuals. Specimens of *D. leviteni* from different localities showing species variability are shown in Plate 4. Clearly, more thorough morphometric and molecular studies are needed in order to clarify the taxonomic status of the different populations of *D. leviteni* in each of the islands of the Hawaiian archipelago.

Ecology: Most of the specimens of *Darioconus leviteni* were collected intertidally and most under rocks or coral heads in sand and rubble.

Etymology: This species is named for the late PAUL J. LEVITEN a gifted ecologist who succumbed to cancer at age 36. PAUL was a student of the Hawaiian cone fauna.

Pionoconus striatus oahuensis n. ssp.

Type material: Holotype and 12 paratypes in collections of SBMNH as follows: holotype-SBMNH 90431, 106.8 x 50.9 mm, Maile Point, Oahu, Hawaii, in sand, under rock by SCUBA, 30-45 m, 21°24'N, 158°11'42"W, collected by RAY A. McKINSEY,16 June 1981; SBMNH 90436: paratype 1, 36.1 x 15.8 mm, Kawailoa, Oahu, Hawaii, N offshore, in sand, by SCUBA, 30-45 m, 21°37'06"N, 158°16'42"W, collected by RAY A. MCKINSEY, 27 August 1979; SBMNH 368144: paratype 2, 96.1 x 45.0 mm, off Makua, Oahu, Hawaii, on flat reef, scattered coral, 35 feet, 21°31'42"N, 158°14'06"W, collected by JOHN W. SENDER, 20 August 1955; SBMNH 90430: paratype 3, 101.7 x 49.0 mm, and paratype 4, 95.6 x 45.0 mm, both from Haleiwa, Oahu, Hawaii, near breakwater, buried in sand, 3-6 m, 21°36'N, 158°06'24'W, collected by RAY A. MCKINSEY, 15 June 1956; SBMNH 90440: paratype 5, 92.6 x 41.9 mm, Kihei, off Maui Lou Harbor, Maui, Hawaii, in sand under coral, 5-10 m, 20°47'N, 156°27'W, collected by RAY A. MCKINSEY, 27 August 1972; SBMNH 423909: paratype 6, 77.1 x 34.8 mm, off Honolulu, Oahu, Hawaii, by SCUBA, 10-25 m, 21°18'N, 157°52'W, collected by DAVID MULLINER, 3 September 1987; SBMNH (formerly 423586): paratype 7, 84.8 x 37.5 mm, Ewa Beach, Oahu, SCUBA, under dead coral head, 10-25 m, 21°17'12"N, 157°59'24"W, collected by BOB PURTYMUM, 14 March 1976; SBMNH 90433: paratype 8, 99.5 x 45.1 mm, Kaanapali, Maui, Hawaii, by SCUBA, buried under coral rubble, 3-6 m, 20°56'N, 156°41'W, collected by Christopher Cleaver, May 1970; SBMNH 90432: paratype 9, 110.9 x 48.8 mm, Kailua Bay, Hawaii, Hawaii, by SCUBA, buried under coral rubble, 10-25 m, 19°38'19"N, 155°59'48"W, collected by James Robinson, 1970; SBMNH 423573 paratype 10, 98.6 x 48.0 mm, Haleiwa Beach, Oahu, Hawaii, SCUBA, on reef, crabbed, 10-25 m, 21°35'25"N, 158°06'45"W, collected by BOB PURTYMUM, 25 August 1974; SBMNH 90442: paratype 11, 60.2 x 27.9 mm, Maunalua Bay, Oahu, Hawaii, off Niu, in sand, uder rubble, by SCUBA, 10-25 m, 21°16'06"N, 157°44'12"W, collected by RAY A. MCKINSEY, 27 November 1978; SBMNH 85452: paratype 12, 96.5 x 43.5 mm, McGregor Point, Pali Lookout, Maui, Hawaii, on sand, 10-25 m, 20°46'40"N, 156°31'26"W, collected by EDWIN B. WOMACK, 26 April 1970. Additional paratypes: Museo Nacional de Ciencias Naturales (MNCN 15.05/53.567), Madrid:



Pionoconus striatus oahuensis n. ssp.

Fig. 1: Paratype 7, Ewa Beach, Oahu, 84.8 mm, SBMNH 423586. Fig. 2: Paratype 3, Haleiwa, Oahu, 95.6 mm, SBMNH 90430. Fig. 3: Paratype 10, Haleiwa, Oahu, 98.6 mm, SBMNH 423573. Fig. 4: Paratype 3, Haleiwa, Oahu, 101.7 mm, SBMNH 90430. Fig. 5: Paratype 5, off Maui Lou Harbor, Kihei, Maui, 92.6 mm, SBMNH 90440. Fig. 6: Holotype, Maile Point, Oahu, 106.8 mm, SBMNH 90431. Fig. 7: Paratype 1, Kawailoa, Oahu, 36.1 mm, SBMNH 90436 (x 2). Fig. 8: Paratype 12, McGregor Point, Maui, 96.5 mm, SBMNH 85452.



Addendum 2

paratype 13, 90.7 x 43.3 mm, Makaha, Oahu, Hawaii, 60-75 feet under dead coral on reef and sand; Natural History Museum (NHM), London: paratype 14, 65.88 x 28.29 mm, Makaha, Oahu, Hawaii, 60-75 feet under dead coral on reef and sand; Musée Nationale d'Histoire Naturelle (MNHN 22801), Paris: paratype 15, 99.8 x 45.2 mm, Makaha, Oahu, Hawaii, 60-75 feet under dead coral on reef and sand; US National Museum (USNM 338580, lot of 3 specimens), Washington DC, paratypes 16 to 18, Keaukaha Pond, Hilo, Hawaii, Hawaii (ex-Thaanum collection).

Type locality: The type locality is Maile Point, Oahu, Hawaii, in sand, under rock, 30-45 m, 21°24'N, 158°11'42"W, the collecting site for the holotype.

Geographical distribution: At present, the species is known from the Hawaiian Islands including the islands of Oahu, Hawaii, Kauai, and Maui along with one specimen from Johnston Atoll (SBMNH 90429). It is likely that the subspecies is distributed throughout the Hawaiian Islands. The nominate subspecies occur in the Indo-Pacific region. However, intergrades between P. s. oahuensis and P. s. striatus are not known.

Diagnosis: Average adult size of the shell larger than in the nominate subspecies; last whorl narrowly conoid-cylindrical, distinctively elongated; shoulder smooth and sharply carinate; spire low or very low, very often depressed below the shoulder; teleoconch sutural ramps concave in latest whorls; protoconch pale pink; color pattern of the last whorl very much like in the nominate subspecies; aperture white; radular tooth of the piscivorous type, with one barb, a blade and an accessory process.

Description: 48 specimens examined. Morphometric parameters: L = 55 to 129 mm (mean 98 mm); RD = 0.44 to 0.54 (mean 0.48); RSH = 0.00 to 0.12 (mean 0.04); PMD = 0.76 to 0.82 (mean 0.76). The holotype and a series of paratypes are illustrated in Plate 2. Shell large to very large. The last whorl is narrowly conoid-cylindrical, with an almost straight outline, very often with nearly parallel sides specially in larger specimens. The general appearance is more elongated than the nominate subspecies. The shoulder is smooth and sharply carinate. The spire is low or very low, with a spire outline concave to extremely concave. The spire is very often depressed below the shoulder. This is a feature characteristic of this subspecies. The early teleoconch sutural ramps are flat, concave in latest whorls. The spire whorls have cords becoming obsolete in latest ramps. The siphonal fasciole bears distinct spiral ribs. The protoconch is pale pink. The ground color of the shell is pinkish white. The spire is patterned with brown and white blotches. The color pattern of the last whorl is very much like in the nominate subspecies, consisting of brown or purplish brown blotches composed of closely spaced transverse lines. The aperture is white. The periostracum is thin, yellow, smooth and translucent.

Living animal and radula: The foot, rostrum and siphon is tan mottled with brown (KOHN 1959B; RÖCKEL, KORN & KOHN 1995). Radular tooth essentially identical to that of the nominate subspecies. Tooth of the piscivorous type, large and elongated, with a barb, a blade and an accessory process in the apical portion (Figure 5). Base small. Basal spur absent.



Fig. 5. Radular tooth of *P. striatus oahuensis* (extracted from paratype 11, SBMNH 90442, 60.2 x 27.9 mm, Maunalua Bay, Oahu).

Comparison and Remarks: Pionoconus striatus oahuensis is very similar to the nominate subspecies P. striatus striatus in color pattern (see Plate 4 for comparison). However, they differ in shape, as well as in average adult size. The shells of Hawaiian P. s. oahuensis are significantly more elongated than the shells P. s. striatus from other Indo-Pacific localities. We have measured the maximum diameter and the length of 236 shells of P. striatus, 47 specimens from Hawaii (P. s. oahuensis) and 189 specimens from several localities scattered throughout the Pacific and Indian Ocean (P. s. striatus). An ANCOVA using maximum diameter as variable, taxon (oahuensis or striatus) as factor, and length as covariate vielded highly significant differences between the maximum diameter of Hawaiian shells compared to the shells from other Indo-Pacific localities corrected for differences in length (F-score = 36.57, p = 0.0000). The least-squares mean maximum diameter for P. s. oahuensis is 35.6 mm (std error 0.25 mm) versus 37.3 mm (std error 0.12 mm) for P. s. striatus (Figure 6).

In analogous fashion, an ANCOVA (185 specimens, 38 P. s. oahuensis and 147 P. s. striatus) on spire height using taxon as factor and length as covariate also yielded significant differences (F-score = 130.06, p = 0.0000) between P. s. oahuensis (least squares mean spire height 2.9 mm, std error 0.16 mm) and P. s. striatus (least-squares mean spire height 5.02 mm, std error 0.08 mm) for this trait (Figure 7). Hence, P. s. oahuensis is narrower and has a lower spire than P. s. striatus. The Hawaiian subspecies also attains a larger mean adult size. Thus, the mean shell length for P. s. oahuensis is 98 \pm 5 mm (N = 38), whereas for *P. s. striatus* is 75 \pm 2 mm (N = 175). These differences are statistically significant $(t = 9.00472, p = 2 \times 10^{-7}).$



Fig. 6. Plot of maximum diameter versus shell length Fig. 7. Plot of spire height versus shell length for P. for P. striatus striatus (o) from different localities in the striatus striatus (o) from different localities in the Indo-Indo-Pacific, and *P. striatus oahuensis* (▲) from Hawaii. Pacific, and *P. striatus oahuensis* (▲) from Hawaii.

Another feature which is very characteristic of the Hawaiian P. s. oahuensis is the appearance of the spire, very often sunken below the large carina of the last whorl, and sometimes depressed below the shoulder (Fig. 8).



This feature was already pointed out by KOHN (1959). This is occasionally observed in some specimens of P. s. striatus from other Indo-pacific localities, but never with the frequency as expressed in P. s. oahuensis. Interestingly, other species of the genus *Pionoconus* such as *P. gubernator* or *P. magus* also exhibit in exceptional cases of depressed spires. In fact, this is the most distinctive character of the "mysterious" Conus boivini KIENER, 1845 (= P. gubernator), recently re-discovered in Madagascar (BOZZETI 2008)..

Ecology: Most of the specimens of Pionoconus striatus oahuensis were collected subtidally in depths between 3 and 45 m and most were in sand under rocks or coral heads.

Etymology: This subspecies is named for the island of Oahu (type locality) in the Hawaiian Islands.

Fig. 8. Sunken spire in a specimen of P. striatus oahuensis from Kaena Point, Oahu (95.2 mm, M. J. TENORIO Coll.).

Subfamily PUNCTICULIINAE Tucker & Tenorio, 2009

Harmoniconus paukstisi n. sp.

Type material: Holotype and 14 paratypes in collections of SBMNH as follows: holotype-SBMNH 99555, 25.0 x 16.0 mm, Kahuku, Oahu, Hawaii, bench reef off golf course, in sand on reef, 0-2 m, 21°41'12"N, 157°56'48"W, collected by RAY A. MCKINSEY, March 1957; SBMNH 90226: paratype 1, 15.7 x 9.8 mm and paratype 2, 14.3 x 8.9 mm, same data as holotype; SBMNH 423607: paratype 3, 18.5 x 10.0 mm, paratype 4, 15.1 x 9.2 mm, paratype 5, 15.1 x 8.9 mm, paratype 6, 13.9 x 8.4 mm, all from Magic Island, Oahu, Hawaii, SCUBA in rubble under coral head, 30-45 m, 21°16'56"N, 157°50'50"W, collected by BOB PURTYMUM, 22 April 1976; SBMNH 90222: paratype 7, 15.1 x 9.6 mm, Makua, Oahu, Hawaii, on bench reef, 0-2 m, 21°31'42"N, 158°14'06"W, collected by RAY A. MCKINSEY, 25 October 1971; SBMNH 90219: paratype 8, 23.6 x 13.9 mm, paratype 9, 18.2 x 11.3 mm, paratype 10, 16.1 x 9.6 mm, Sandy Beach, Oahu, Hawaii, in sand on shallow reef, 0-2 m, 21°17'06"N, 157°39'36"W, collected by RAY A. MCKINSEY, 5 December 1955; SBMNH 85289: paratype 11, 18.7 x 11.4 mm, Waialua, Oahu, Hawaii, outside inner reef, exposed on reef, 0-2 m, 21°35'54"N, 158°08'30"W, collected by EDWIN B. WOMACK, 24 July 1967; SBMNH 423580: paratype 12, 29.7 x 20.0 mm, Diamond Head Beach Park, Oahu, Hawaii, on hard coral reef, 0-2 m, 21°15'18"N, 157°48'20"W, collected by BOB PURTYMUM, 17 January 1972; SBMNH 90231: paratype 13, 17.7 x 11.0 mm, paratype 14, 12.6 x 7.6 mm, Kaupulehu, Hawaii, Hawaii, diving exposed by fanning sand on hard terraces, 1-2 m, 19°50'N, 155°59'W, collected by HENRY W. CHANEY, 8 August 1969. Additional paratypes: Museo Nacional de Ciencias Naturales (MNCN 15.05/53.568), Madrid: paratype 15, 25.5 x 14.5 mm, Kahuku, Oahu, Hawaii, on sand patched in tidal pools, collected 8th March 1975; Natural History Museum (NHM), London: paratype 16, 19.36 x 11.94 mm, Kahuku, Oahu, Hawaii, on sand patched in tidal pools, collected 18th May 1975; Musée nationale d'Histoire naturelle (MNHN 22802), Paris: paratype 17, 23.4 x 14.8 mm, Kahuku, Oahu, Hawaii, on sand patched in tidal pools, collected 8th March 1975; US National Museum (USNM), Washington DC: paratype 18, 19.7 x 11.5 mm, Haleiwa, Oahu, Hawaii, crawling on sand in tide pools on reef, 2-3 feet, collected 3rd November 1973; American Museum of Natural History (AMNH 301722), New York: paratype 19, 20.0 x 17.0 mm, Kauai, Hawaii.

Type locality: The type locality is Kahuku, Oahu, Hawaii, bench reef off golf course, in sand on reef, 0-2 m, 21°41'12"N, 157°56'48"W, the collecting site for the holotype and two of the paratypes.

Geographical distribution: At present, the species is known from two of the Hawaiian Islands (Oahu and Hawaii). It is likely distributed throughout the Hawaiian Islands but has not been differentiated from Harmoniconus nanus by previous authors.

Diagnosis: Shell small reaching about 35 mm in length; conical in shape but with slightly convex sides in small shells (< 20 mm); sides become very convex in larger shells and the shoulders of these are swollen looking with indistinct shoulders; 13 to 22 nodules are present on shells up to 18 mm after reaching this sides nodules may become irregular or fade out; whorl tops of the first 2 or 3 whorls have 2 cords but these increase in number to five or more; cords spread from the whorl tops over the nodules on to the body whorl; cords well developed between adjacent nodules; cords may be obsolete in the largest specimens; anterior end and interior of the aperture colored brown, rarely purple brown; a strong constriction present inside the aperture at about midbody; coloration highly variable depending on growth stage; smaller shells (< 18 mm) can be all blue-white, marked with brown irregular blotches, have brown spiral lines on the body whorl, or be mottled brown over the body whorl; spire coloration can be uniform blue-white or have brown markings, in which case these are best developed between the nodules; coloration generally lost in larger shells, which are mostly blue-white in color; operculum about 1/4 of the aperture length; periostracum varies in thickness; areas at shoulder and midbody may have the periostracum thin and transparent but thicker between these yielding a banded appearance.

Description: 100 specimens examined. Shell morphometry: L = 9 to 26 mm (mean 16.7 mm, max. L measured 32 mm); RD = 0.61 to 0.73 (mean 0.66); RSH = 0.02 to 0.14 (mean 0.08); PMD = 0.77 to 0.85 (mean 0.81). The holotype and a series of paratypes are illustrated in Plate 3. The shell is small with the largest specimen observed being 32 mm in length and 19 mm in width. The body is conical with slightly convex sides in small specimens (< 20 mm). However, with growth the shoulders become convex and swollen giving the shell a more ventricose appearance. The shoulder of all but the large specimens are nodulose. In these large specimens the nodules may fade out or be reduced to short axial ridges at the shoulder. At this stage the shoulder is rounded swollen and indistinct. The shoulder is rounded but not indistinct in small specimens. There are 2 cords on the whorl tops of the first 2 or 3 whorls. These increase in number to five or more in the middle and outer whorls. The cords in this species are not limited to the whorl tops. Instead they spread from the whorl tops over the nodules on to the body whorl. This results in well developed cords between adjacent nodules. The cords may be obsolete in the largest specimens. The body whorl is often ornamented with sulci or ridges in smaller specimens. These may reach the shoulder and are not possible to differentiate from the cords. Larger specimens have the sulci and ridges restricted to the anterior third of the shell. The cords, however, remain present between the nodules and anterior to the shoulder angle in smooth bodied specimens. The anterior end and the interior of the aperture is colored brown. Rarely this coloration is shaded slightly by purple tinting but it is not blue. There is a strong constriction present



Harmoniconus paukstisi n. sp.

Fig. 1: Paratype 3, Kahuku, Oahu, 18.5 mm, SBMNH 90226. Fig. 2: Paratype 2, Kahuku, Oahu, 14.3 mm, SBMNH 90226. Fig. 3: Paratype 15, Kahuku, Oahu, 25.5 mm, MNCN 15.0553.568. Fig. 4: Paratype 4, Kahuku, Oahu, 15.1 mm, SBMNH 90226. Fig. 5: Paratype 12, Diamond Head Beach Park, Oahu, 12.6 mm, SBMNH 423580. Fig. 6: Holotype, Kahuku, Oahu, 25.0 mm, SBMNH 99555. Fig. 7: Paratype 17, Kahuku, Oahu, 23.4 mm, MNHN 22802. Fig. 8: Paratype 19, Kauai, 20.0 mm, AMNH 301722. Fig. 9: Paratype 14, Kaupulehu, Hawaii, 12.6 mm, SBMNH 90231. Fig. 10: Paratype 13, Kaupulehu, Hawaii, 20.0 mm, SBMNH 90231. Fig. 11: Paratype 9, Sandy Beach, Oahu, 20.0 mm, SBMNH 90219. Fig. 12: Paratype 10, Sandy Beach, Oahu, 16.1 mm, SBMNH 90219.



inside the aperture at about midbody region. This ridge is not colored effectively dividing the interior into anterior and posterior halves. The coloration is highly variable depending on growth stage. Smaller shells (< 18 mm) can be all blue-white, marked with brown irregular blotches, have brown spiral lines on the body whorl, or be mottled brown over the body whorl. Similarly, spire coloration is variable and can be uniformly blue-white or have brown markings, in which case these are best developed between the nodules. Coloration generally lost on the body whorl and spire of larger shells, which are mostly blue-white in color. The operculum is about 1/4 of the aperture length. The periostracum is distinctive and varies in thickness over the body and spire. Areas at shoulder and midbody may have the periostracum thin and transparent but the periostracum thickens in between these two areas yielding a banded appearance.

Living animal and radula: These were not observed by us.

Comparison and Remarks: *Harmoniconus paukstisi* is superficially similar to *H. nanus* but differs in several remarkable ways. First the new species has unique spire morphology. In *H. paukstisi* the cords on the whorl tops cross over onto the body whorl and are thus traced over the tops of the nodules and between them (Fig. 9). In *H. nanus*, the cords are limited to the whorl tops.



Fig. 9. Close-up of the spire and shoulder region of *H. paukstisi* (paratype 11, SBMNH 85289) showing the characteristic cords on the whorl tops and onto the body whorl.

Besides this difference, the cord pattern in *H. paukstisi* is one of increasing numbers of cords reaching a total of 4 to 8 in mid-sized specimens. In *H. nanus*, initially these are a single central cord that splits into two or rarely three cords in these smaller specimens. However, these cords then fade out and become obsolete. The two species differ in coloration of the aperture and the anterior end. In *H. paukstisi*, the anterior end and the aperture are brown colored. They are blue colored in *H. nanus* (see Plate 4 for comparison). This trait seems highly reliable: only one of more than 50 *H. nanus* from Hawaii that we examined had any brown shading at all. Finally, the periostracum of *H. paukstisi* seems to be characteristic. It is variable in thickness, which produces bands of thick and thin areas of periostracum. In *H. nanus*, the periostracum is of uniform thickness. ANCOVA has shown that the shells of *H. paukstisi* do not differ statistically in maximum diameter or spire height from those of *H. nanus*, and hence they can not be differentiated each other by shell shape.

Recently, DUDA & al. (2008) examined the molecular biology of the *Harmoniconus*. This study uncovered unexpected differentiation in these species especially for Hawaiian specimens. We originally suspected that their '*nanus* VI' was *H. paukstisi*. However, we examined voucher specimens of *nanus* VI and they are not *H. paukstisi*. If *H. paukstisi* is not included in DUDA & al.'s *nanus* I, then there are two molecularly distinct forms of *H. nanus* in the Hawaiian Islands. We consider it unlikely that *nanus* I includes *H. paukstisi* because the geographic distribution of specimens of *nanus* VI do not resemble the lectotype of *H. nanus* (KOHN, 1992: fig. 455). In the later species, the nodules are large and project upward. In similar sized specimens of *nanus* VI, the nodules are smaller and closer together. They point towards the coiling axis as though bent downward on the shoulder angle. The anterior end coloration and that inside the aperture of *nanus* VI and *H. nanus* (sensu stricto) are blue distinguishing them from *H. paukstisi*.

Ecology: Most of the specimens of *Harmoniconus paukstisi* were collected intertidally and most often on hard reef or terrace sorts of habitats. These might have been exposed or covered by sand at the time of collection. Of the lots that we examined from SBMNH several were mixed with *H. paukstisi* collected with *H. nanus* or *H. sponsalis* indicating that all of these species may occur sympatrically. We do note that *H. paukstisi* is most commonly collected in shallow water. However, one lot was collected subtidally in water deeper than 30 m (SBMNH 423697 above).

Etymology: This species is named for the late GARY L. PAUKSTIS, a dear friend and colleague of the first author. GARY provided much encouragement and support for these malacological studies including gifts of equipment and specimens. He also did important herpetological work on temperature dependent sex determination in turtles and turtle life history strategies, many co-authored with JKT.

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Fig. 1: Darioconus behelokensis (LAUER, 1989): Tuléar, Madagascar, 55.9 mm, TENORIO Coll. Fig. 2: Darioconus leviteni n. sp.: Paratype 13, Kailua Bay, Hawaii, 38.1 mm, SBMNH 99548. Fig. 3: Darioconus leviteni n. sp.: Maalaea Bay, Maui, 63.0 mm, SBMNH 423469. Fig. 4: Darioconus leviteni n. sp.: Kauai, 37.0 mm, TENORIO Coll. Fig. 5: Darioconus leviteni n. sp.: Midway Islands, NW Hawaiian Islands, 46.3 mm, SBMNH 125377. Fig. 6: Darioconus leviteni n. sp.: Moomomi, Molokai, 34.8 mm, ANSP 116366. Fig. 7: Darioconus pennaceus (BORN, 1778): Fernão Veloso, Nacala, Mozambique, 57.0 mm, TENORIO Coll. Fig. 8: Darioconus pennaceus (BORN, 1778): Fernão Veloso, Nacala, Mozambique, 57.0 mm, TENORIO Coll. Fig. 8: Darioconus pennaceus f. quasimagnificus (REEVE, 1843): Oman, 63.4 mm, TENORIO Coll. Fig. 9: Harmoniconus nanus (G. B. SOWERBY I, 1833): Kahulu, Oahu, 17.3 mm, SBMNH 90226 (x 2). Fig. 10: Harmoniconus paukstisi n. sp.: Paratype 11, Waialua, Oahu, 18.7 mm, SBMNH 85289 (x 2). Fig. 11: Harmoniconus sponsalis (Hwass in BRUGUIÈRE, 1792): Stanton Beach, N Queensland, Australia, 18.9 mm, TENORIO Coll. (x 2). Fig. 12: Pionoconus striatus striatus (LINNAEUS, 1758): Philippines, 83.3 mm, TENORIO Coll. Fig. 12: Pionoconus striatus striatus (LINNAEUS, 1758): Philippines, 83.3 mm, TENORIO Coll. Fig. 12: Pionoconus striatus striatus (LINNAEUS, 1758): Philippines, 83.3 mm, TENORIO Coll. Fig. 12: Pionoconus striatus striatus (LINNAEUS, 1758): Philippines, 83.3 mm, TENORIO Coll. Fig. 12: Pionoconus striatus striatus (LINNAEUS, 1758): Philippines, 83.3 mm, TENORIO Coll. Fig. 12: Pionoconus striatus striatus striatus (LINNAEUS, 1758): Philippines, 83.3 mm, TENORIO Coll. Fig. 12: Pionoconus striatus striatus (LINNAEUS, 1758): Philippines, 83.3 mm, TENORIO Coll. Fig. 12: Pionoconus striatus striatus (LINNAEUS, 1758): Philippines, 83.3 mm, TENORIO Coll. Fig. 12: Pionoconus striatus striatus striatus (LINNAEUS, 1758): Philippines, 83.3 mm, TENORIO Coll. Fig. 12: Pionoconus striatus striatus striatus (LINNAEUS, 1758): Philippines, 83.3 mm, TE

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A New Subspecies of Nucleolaria nucleus (LINNAEUS, 1758) (GASTROPODA: CYPRAEIDAE) from the Hawaiian Islands

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Abstract:

A new subspecies of the kernel cowrie, Nucleolaria nucleus (LINNAEUS, 1758), is described from the Hawaiian Islands on the basis of conchological characters. N. nucleus hapa n. ssp. resembles both N. nucleus and N. granulata (PEASE, 1832). It can be separated from most specimens of the former by its broadly ovate shell and usually darker coloration; it differs from the latter by having a glossy shell and more numerous basal ridges. Introduction:

C. M. BURGESS collected, in the mid 1940's, the first known live specimen of Nucleolaria nucleus in Hawaii (KAY & WEAVER 1963). BURGESS (1985) states that only two or three live specimens, and perhaps half-dozen beach-worn were known from Hawaii by the mid 1980's. With the increase in popularity of scuba diving more specimens have come to light since then.

Nucleolaria granulata is the only known cowrie to have a dull shell when fully adult; the juvenile has a glossy shell, but it is thin-walled, lighter in color, the ridges on the base are not well formed, and the dorsal nodules are small, compared to those of adults. BURGESS (1960) explains that only beach-worn shells of N. granulata may become shiny. However, DAYLE (1990) documented the first live-collected glossy "grannie." Short color videos now available on YouTube (DAYLE 2007) show the living specimen, labeled a "cross-breed" between N. granulata and N. nucleus. LORENZ & HUBERT (2000) also mention Hawaiian intergrades.

Since 2006, this author has gathered material of the Hawaiian N. nucleus, and thanks to the efforts of CHRIS TAKAHASHI and other diver friends from the Hawaiian Malacological Society, now enough material has been assembled to study the Hawaiian population of N. nucleus: 27 shells usually identified as N. nucleus or nucleus × granulata; 65 N. granulata, 57 N. nucleus from outside of Hawaii, including N. n. gemmosa (PERRY, 1811) and N. n. madagascariensis (GMELIN, 1791), one N. cassiaui (BURGESS, 1965). Most specimens were borrowed from private collections and museums (Houston Museum of Natural Science and the Field Museum of Natural History); about one third of the material is in the author's collection. Field observations from divers suggest that more typical N. nucleus is very rare in Hawaii, but shells resembling N. granulata are more common. The author believes that like in other cowries (e.g. see MORETZSOHN 2007), because of isolation, the Hawaiian population of N. nucleus has diverged enough from other populations to be recognized as a geographic subspecies.

Nucleolaria nucleus hapa n. ssp.

Type material: Holotype: ANSP 423878, shell size (mm): $24.27 \times 16.38 \times 11.70$; 13 and 22 (columellar and labral teeth), from Makaha, Oahu, under rock at 90 ft, collected and donated by CHRIS TAKAHASHI. Paratypes: 26 paratypes (Table 1, Figs. 7–16), all from the main Hawaii Islands, except for one specimen from Midway Atoll. Paratypes range in size from 18.00 to 29.34 mm.

Table 1: List of the holotype and first 10 paratypes with measurements and locality.

Гуре #	Collection	L	W	H	СТ	LT	Locality
Holotype	ANSP 423878	24.27	16.38	11.70	13	22	Oahu, Makaha, 90 ft.
Paratype 1	C. Takahashi	27.81	17.38	13.65	16	18	Oahu, Ft. Kamehameha, 20 ft.
Paratype 2	J. AUFRANZ	23.84	16.15	11.22	17	21	Oahu, West side, 8–10 m
Paratype 3	FMNH 159984	20.08	12.31	9.92	17	23	Midway Atoll
Paratype 4	FMNH 77718	18.68	11.71	9.15	16	26	Hawaiian Islands
Paratype 5	D. Lum	25.72	17.49	11.88	16	23	Oahu, Waimea Bay, 50 ft.
Paratype 6	J. AuFranz	24.25	15.65	11.83	15	23	Oahu, Makaha caverns, 20 ft.
Paratype 7	C. Takahashi	25.95	17.88	12.70	15	23	Oahu, Mokuleia, 20 ft.
Paratype 8	M. PANG	19.97	13.01	9.65	18	25	Oahu, Makaha, 15 ft.
Paratype 9	D. WATTS	26.71	17.26	12.34	16	20	Oahu, Makaha, 30 ft.
Paratype 10	USNM 1135986	22.42	14.41	9.99	15	20	Oahu, Pearl Harbor

Type locality: Makaha, Oahu, Hawaii (aprox. 21°28'7"N, 158°13'8"W) (Fig. 17)

Diagnosis: The new subspecies can be separated from *N. granulata* by a glossy shell (dorsal tubercles, basal ridges, and interspaces) that is smooth to the touch, has more numerous basal ridges, and rostrate extremities. N. nucleus hapa can be distinguished from typical N. nucleus by having a broader shell, basal ridges lined in red-brown, and sometimes by having rosy-brown or brown dorsal color.