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Partula desolata sp. nov. (Pulmonata: Partulidae), an extinct land snail from Rota, Mariana Islands, Micronesia¹

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Abstract.—*Partula desolata* sp. nov. is described from two partial and two complete shells recovered from Late Holocene subfossil cave deposits on the island of Rota, Mariana Islands, in western Micronesia. The species is most similar to its presumed sister, the sympatric and still extant *P. gibba* Férussac, 1821, but is distinct from this and all other partulids by its more robust shell and exceptionally expanded and thickened peristome. *Partula desolata* sp. nov. appears to have survived to at least the late prehistoric human settlement of the island, ca. 1000 yr BP.

Sumåria.—Hami in na'fanmalitråtu kuåttro na karakot siha nu i på'go masodda' na akaleha' ginen Luta gi iya Marianas, ni mafana'an *Partula desolata* n. sp. Ti lå'lala' på'go este na akaleha', ya siña ha' masodda' i karakot-ña gi amkoko' na pigo gi ge'halom liyang siha. Kulan umachule' ha' este na akaleha' yan i che'lu-ña, *P. gibba* Férussac, 1821, lao metgotña i karakot-ña, yan la'fedda' yan la'potpot i pachot i karakot-ña, lokkue'. I pine'lon-måmi na ginen manlå'lala' i *P. desolata* n. sp. meggaiña nu i mit na såkkan tåtte annai i Mañamoru ha' nu i mañåsaga gi iya Marianas.

Index terms: arboreal snail, extinction, fino' Chamoru, Holocene, Mollusca, Oceania, subfossil, zooarchaeology.

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Introduction

The tropical, arboreal snail family Partulidae Pilsbry, 1900 consists of about 130 species in three genera, all endemic to single islands or a few adjacent islands on the western Pacific Plate. The largest genus *Partula* Férussac, 1821 is the most widely distributed, with about 100 described species, ranging from the Society Islands, French Polynesia, where species richness is highest at 61 species, to the Palauan Archipelago in westernmost Micronesia with just three species (Cowie 1992). About 1300 km northeast of Palau lie the Mariana Islands, also in Micronesia, with four endemic species.

The first *Partula* described from the Mariana Islands, *P. gibba* Férussac, 1821, is the most widely distributed in the archipelago. Another species, *P. radiolata* (Pfeiffer, 1846), is endemic to, and still widely distributed within, the largest and southernmost island of Guam. Another species, *P. salifana* Crampton, 1925, was discovered in the forests surrounding the summit of Mt. Alifan of Guam. The fourth species, *P. langfordi* Kondo, 1970, is restricted to the tiny island of Aguiguan. A fifth Marianas partulid *P. fragilis* Férussac, 1821 was transferred to *Samoana* by Kondo (1968).

As with nearly all native snails across the Pacific (Cowie 1992; Lydeard et al. 2004), the numbers of most Marianas snails, including its partulids, have declined precipitously beginning in the latter half of the 20th century (Hopper & Smith, 1992; Bauman 1996) due to habitat destruction and a series of imprudent introductions of generalist predators to control the invasive gastropod and agricultural pest *Achatina fulica* (Férussac, 1821) (Achatinidae). Declines of partulids have been of the order that the two Marianas *Partula* having the most restricted distributions, *P. salifana* and *P. langfordi*, are now undoubtedly extinct (Hopper & Smith 1992; Smith 2008a), and even *P. gibba* no longer occurs in vast areas of its former broad range (Bauman 1996; Smith 2008b).

Adult shells of a fifth conchologically distinct *Partula* sp. from the Marianas were collected by one of us (SB) in 1994 from unconsolidated Late Holocene deposits on the island of Rota, Commonwealth of the Northern Mariana Islands (85 km²; 14° N, 145° E; Fig. 1). The species has been figured and briefly discussed by Bauman (1996) as *P*. c.f./aff. *gibba*. The shells were recovered from excavations in Payapai Cave (Test Pit 3, Layer III, Level 4) and nearby Alaguan Rock Shelter (Test Pit 1) on the south-central coast (14° 8' 35" N, 145° 13' 38" E), and at As Matmos Cliffside Cave (Test Pit 1) from the northeastern coast (14° 11' 41" N, 145° 16' 25" E). These excavations were initiated as part of a broader study of the vertebrate faunas extant during early human settlement of the Mariana Islands (e.g., Pregill 1998; Steadman 1999). Land snails from the collection sites were retrieved from sediments by dry-sieving in the field through 1.6-mm mesh screens. The uncalibrated radiocarbon age of associated, ostensibly

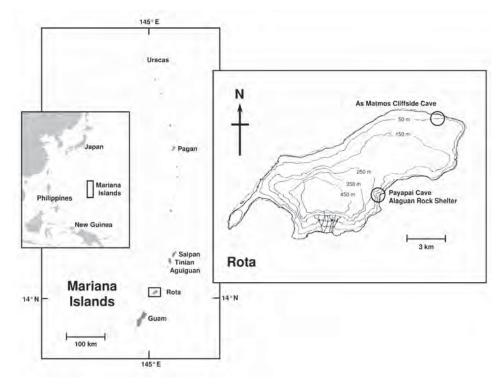


Figure 1. Map of the Mariana Islands with islands mentioned in the text labeled and a map of Rota showing approximate locations of the collecting sites (see text for coordinates).

anthropogenic charcoal in the deepest and *Partula*-bearing layer at Payapai Cave, the only ¹⁴C-dated site, is 400 ± 60 yr BP (Steadman 1999).

The following abbreviations are used in this paper: BPBM, Bernice P. Bishop Museum, Honolulu, Hawaii; UF, Florida Museum of Natural History, Gainesville, Florida; UGI, University of Guam Marine Laboratory. Definitions of shell characters and measurements follow Perez & Cordeiro (2008).

Systematics Clade Stylommatophora *sensu* Bouchet & Rocroi (2005) Family Partulidae Pilsbry, 1900 Genus *Partula* Férussac, 1821

Type species: *Helix faba* Gmelin, 1791 via suppression of *Limax faba* Martyn, 1784 (see ICZN 1957). Type locality: Raiatea, Society Islands, French Polynesia.

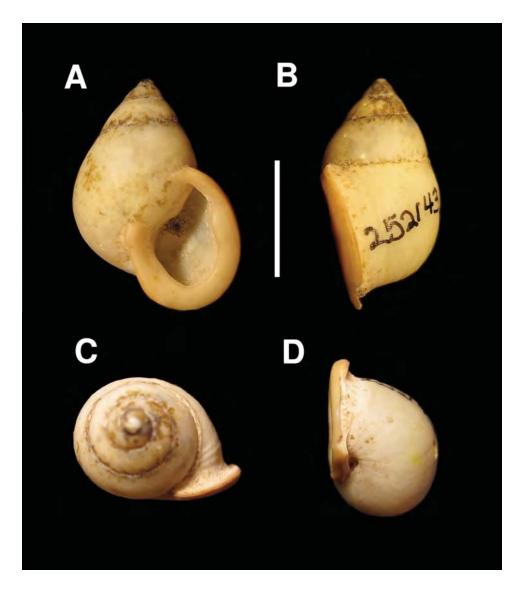


Figure 2. *Partula desolata* Bauman & Kerr, sp. nov. Holotype, BPBM 252143-A, Payapai Cave, Alaguan region, Rota Island, Mariana Islands. Scale bar = 10 mm. A.–C. Apertural, adapertural, apical views, respectively. **D.** Slightly oblique basal view exposing the umbilical pit and a thickened and reflexed, but damaged, basal peristome.

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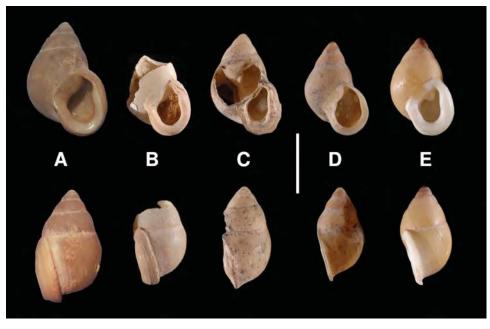


Figure 3. Comparison of *Partula desolata* sp. nov. to *P. gibba* and *P. thalia*, showing disparity in size and development of peristome. Scale bar = 10 mm. *P. desolata* sp. nov., Rota, Mariana Islands, paratypes: **A.** UGI 3001, **B.** UF 449332 and **C.** UF 449333. **D.** *P. gibba*, Rota, UF 449334. **E.** *P. thalia*, Raiatea, Society Islands, UF 112145.

Partula desolata sp. nov.

(Figs. 2–3)

Partula cf./aff. gibba, Bauman 1996: 21, fig. 32.

Material examined. Holotype: BPBM 252143-A, complete shell, Payapai Cave (Test Pit 3, Layer III, level 4), Rota, Collector: S. Bauman, July 1994. Paratypes: UF 449333, partial shell, Alaguan Rock Shelter (Test Pit 1), Rota, Collector: S. Bauman, 21 July 1994; UF 449332, partial shell, As Matmos Cliffside Cave (Test Pit 1), Rota, Collector: S. Bauman, 23 July 1994. UGI 3001, complete shell, Payapai Cave (Test Pit 3, Layer III, level 4), Rota, Collector: S. Bauman, July 1994.

Comparative material. *Partula gibba*, BPBM 252143-B, complete shell, Payapai Cave (Test Pit 3, Layer III, level 4), Rota, Collector: S. Bauman, July 1994; UF 449334, partial shell, Alaguan Rock Shelter (Test Pit 1), Rota, Collector: S. Bauman, 21 July 1994; UF 449335, partial shell, As Matmos Cliffside Cave (Test Pit 1), Rota, Collector: S. Bauman, 23 July 1994; *Partula thalia* Garrett, 1884 UF 112145, complete shell, Raiatea, Society Islands, French Polynesia, Collector: W. J. Clench, no collection date.

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Diagnosis. A *Partula* from the Mariana Islands with a robust shell and an expanded, reflexed and thickened peristome.

Description. Shells dextral, heavy, opaque, ovate conical, colour altered taphonomically in at least some specimens, but in the holotype both externally and internally light brown, darker near sutures, protoconch whorl and peristome lighter. The following measurement ranges are drawn from three to, when possible, all four specimens and always include the complete shell of the holotype: Shell height 17.2–19.5 mm (holotype 19.5 mm), width 13.8–14.8 mm (holotype 14.5 mm), aperture height 9.8–12.5 mm (holotype 12.5 mm), aperture width 8.5–10.1 mm (holotype 10.1 mm), peristome width at parietal margin 2.0– 2.3 mm (holotype 2.0 mm), peristome thickness at parietal margin 2.2-3.0 mm (holotype 2.2 mm), shell height/width ratio 1.10–1.43 (holotype 1.10), apertural height/width ratio 0.71-1.10 (holotype 0.74); about one protoconch whorl and 3.5 teleoconch whorls. Spire conical, apex somewhat obtuse, whorls evenly descending, basal whorl ca. 60% of shell height, protoconch whorl smooth, postembryonic whorls nearly shiny in some specimens, nearly flattened, numerous prosoclinic growth striae at irregular intervals checking or offsetting fine, evenly spaced appressed spiral striae, suture distinct, emarginate, impressed, aperture slightly oblique, squarish to auriculate, non-labiate, with a thick, reflexed, flattened and polished peristome, columellar margin straight and flared against the body whorl, almost circular in outline through the basal and mid-palatal margin, then angling adaxially while narrowing suddenly so as to form a low, rounded sub-denticulate inner border, the aperture's entire margin thick, from 2.5-3.0 mm (holotype 3.0 mm) at the peripheral palatal margin, with distinct multiple growth lamellae, parietal callus present, opaque, thin, of uniform thickness, undenticulated, umbilicus typically Partula-like: narrow, deep, and partially eclipsed by the reflexed columellar lip.

Etymology. This snail was discovered and is being described at a time when over half of the Partulidae are now extinct (Cowie 1992), including two of the five species inhabiting the Mariana Islands (Hopper & Smith 1992; Smith 2008a). The remaining three species, as well as most other partulids Pacific-wide, are seriously threatened with extinction (IUCN 2012). Hence, the specific epithet *desolata* (the singular feminine adjectival form of the Latin present infinitive *desolare* = to render forsaken or, as in the sense intended here, to have been rendered forsaken) is chosen to indicate that the excavated shells have reemerged in a time quite apart from that in which they once coursed, to a world now desolate of most members of the formerly diverse family Partulidae.

Distribution. Known only from four shells recovered from Late Holocene (< 1000 yr BP) deposits in caves from the Alaguan and As Matmos regions of Rota, Mariana Islands. The distance between these localities spans roughly half the length of the island (6.5 km), as well as straddles the northern and southern coasts, indicating that the species was probably widely distributed within Rota.

Table 1. Comparison of shell dimensions of Mariana Island *Partula* spp. Measurements in millimeters are expressed as a sample mean (and one standard deviation). A hyphen indicates no published data. n = sample size. For *P. desolata* n. sp., shell height based on n = 3. The two-sample *t* tests compare *P. desolata* sp. nov. and the Mariana partulid most similar in size, *P. salifana*, where $t_s =$ Student's *t* value for the minimum degrees of freedom df = 18, and p = tail probability of t_s .

Species	Shell height	Shell width	Aperture height	Aperture width	п	Reference
P. desolata sp. nov.	18.7 (1.30)	14.4 (.513)	11.3 (1.17)	9.4 (.660)	3–4	This study
P. gibba (Guam)	17.1 (.767)	11.9 (.571)	9.7 (.401)	7.3 (.309)	291	Crampton 1925
P. gibba (Rota)	16.6 (.792)	11.2 (.681)	9.4 (.590)	6.8 (.526)	21	This study
P. gibba (Saipan)	17.1 (.770)	12.0 (.573)	9.7 (.434)	7.2 (.358)	2586	Crampton 1925
P. langfordi	13.9 (.465)	-	-	-	73	Kondo 1970
P. radiolata	16.6 (.019)	10.2 (.012)	9.3 (.011)	6.7 (.008)	1416	Crampton 1925
P. salifana	18.0 (.151)	11.0 (.063)	10.2 (.055)	7.2 (.034)	17	Crampton 1925
t_s p	6.65 <<0.001	82.0 <<0.001	11.6 <<0.001	40.3 <<0.001		

Excavations in similarly aged deposits on the two adjacent and larger islands, Guam and Tinian, have as yet not turned up this *Partula* (S. Bauman, unpubl.; J.A. Starmer, pers. comm.; C. Christensen, pers. comm.). Further, extensive searches by us and others (Crampton 1925; Kondo 1970; Kurozumi 1994; Smith 2008a–b, Smith et al. 2008; D.R. Hopper, pers. comm.; J.A. Starmer, pers. comm.) for living *Partula* in Rota and the other Mariana Islands have not discovered contemporary specimens with this morphology. We, therefore, consider this species an endemic of Rota, Mariana Islands, and one now extinct.

Remarks. Partula desolata sp. nov. differs from other Mariana Partula, including the sympatric *P. gibba*, in multiple respects. To more rigorously assess the distinctiveness of the new species' shell, we used two-sample t tests to compare shell height, shell width, apertural height, and apertural width to the respective measures taken from other Mariana Partula. All tests were performed against the measurements taken by Crampton (1925) of the Mariana partulid species most similar in size, the now extinct *P. salifana*. This comparison was

preferable since it rendered our tests maximally conservative, i.e., it decreased the chance of finding a statistically significant difference among all the species, and for two important reasons. First, *P. salifana*, while somewhat smaller on average than the new species, is nevertheless most similar to the new species in all tested dimensions (Table 1). Thus, a finding of a significant difference indicates that the other and even smaller species, including *P. gibba* sampled from Guam, Rota and Saipan, must also be smaller than expected by chance sampling. Second, *P. salifana* also had the smallest sample size (n = 17), which thus provided the least statistical power to uncover a genuine difference. Still, despite our conservative tack, *P. desolata* sp. nov. is on average significantly larger than all other Mariana *Partula* (Table 1).

The development of the peristome also shows much more expansion and thickening, to 3 mm (Table 1; Figs. 2–3). In fact, this appears unprecedented among the Partulidae Pacific-wide. Expansion, recurving and thickening of the lip approaching that in *P. desolata* sp. nov. has previously been seen only in a few of the geographically remote species, notably the Raiatean P. thalia in the Society Islands (Fig. 3E). However, even the latter species' lip tends to one-half to one-third as thick (to 1.2 mm), its parietal callus is thinner and transparent, prominently denticulate, and its shell less gibbous with stronger and more numerous growth striae. Crampton's (1925) plates of P. gibba in apertural view occasionally give the appearance of having a peristome approaching the breadth of the new species. However, Crampton (1925) does not mention that any specimens of P. gibba have an unusually thickened peristome. Instead. Crampton (p. 26) writes that the Marianas *Partula* most similar to the thicklipped forms of the Society Islands is Guam's P. salifana, which we show to be, nevertheless, statistically smaller (Table 1). Finally, the new species is bigger than shells of *P. gibba* also recovered from the excavations (e.g., Fig. 3D), thus ruling out the possibility that its more robust form is ancestral to the latter species.

We also considered the possibility that *P. desolata* sp. nov. was a hypercalcified ecophenotype of *P. gibba*. Shell thickening occurs among terrestrial pulmonate snails inhabiting environments with high-calcium soils (Solem 1988, p. 522) or pathologically *via* infection with digenean trematodes (Żbikowska 2003), but never to the degree required here of any Marianas partulid to emulate *P. desolata* sp. nov. We and others (Crampton 1925; Kondo 1970; D.R. Hopper, pers. comm.; J.A. Starmer, pers. comm.) have collectively examined many thousands of living and subfossil *P. gibba*, but specimens approaching this morphology have not been observed to our knowledge. As well, *P. desolata* sp. nov. with its well-developed lip is known from multiple specimens only recovered from sediments of similar age at widely separated sites on one island, Rota, consistent with a wide intra- and singular-island distribution typical of *Partula* spp. (Crampton 1916, 1925, 1932). Finally, the thickened, more reflexed lip covaries with other distinctive shell characters, such as a more circular peristomal margin, larger shell size, flatter whorls, more ovate outline, less gibbous body whorl, and thicker shell.

While *P. desolata* sp. nov. has likely been extinct for upwards of a millennium, tentative remarks on its biology are possible. All members of the family Partulidae, as far as is known, are long-lived, fungivorous, simultaneous hermaphrodites, bearing a few live young from lightly calcified egg capsules retained inside a brood chamber (Barker 2001). Hence, *P. desolata* sp. nov. also likely displayed these traits. Indeed, a large protoconch implicates ovoviviparous reproduction in snails (Barker 2001) and the holotype's protoconch appears to be at least as broad as those from modern *P. gibba* from Rota and Saipan. Finally, all *Partula*, whether arboreal or strictly terrestrial, inhabit the leafy, humid and shaded understorey of native forest. However, the size, shape and robustness of the *Partula*'s shell is, as far as is known, not unambiguously linked to a treeversus ground-dwelling lifestyle (Cowie 1992).

Damage to two of the paratypes of the new species (e.g., Fig. 3B–C), appears consistent with that of predation by rats (Hadfield et al. 1993; Meyer & Shiels 2009), or more speculatively, the large native terrestrial crabs, *Coenobita* spp. and *Birgus latro* (Linné, 1767). Rat damage to *Partula gibba* is seen in shells recently collected from Rota (A. Gawel, pers. comm.). The radiocarbon date (< 1000 yr BP) of charcoal associated with the shells (Steadman 1999), as well as the abundance of fish bones (Pregill 1998) and at one site (Alaguan Rock Shelter), human burials, indicate that *P. desolata* sp. nov. was extant until at least late prehistoric human occupation of Rota. Initial human settlement of the Marianas occurred ca. 4000 BP (Athens & Ward 2004). Unlike the many bird bones recovered from the same stratum at Payapai Cave (Steadman 1999), none of the shells show evidence of charring or other modification by extreme heat that would unambiguously implicate the shells' damage as being a consequence of human consumption.

In conclusion, *Partula desolata* sp. nov. represents the first member of the Partulidae known only from the sub-fossil record. Other identifiable zooarchaeological *Partula* material has been assignable to modern taxa (e.g., Sinoto & McCoy 1975; Kirch et al. 1995; Lee et al. 2007). Hence, it will be interesting to learn whether further investigations of prehistoric deposits turn up more extinct species of land snails, just as such work has many extinct vertebrates whose demise has been linked with early human occupation of the islands.

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