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The tree snail on Rota Island, Northern Mariana Islands, long identified as *Partula gibba* (Partulidae), is a different species

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Abstract

Tree snails in the family Partulidae are widespread across the tropical Pacific, with endemic species occurring on most high islands. Partulid species have faced catastrophic range reductions and extinctions due primarily to introduced predators. Consequently, most extant species are threatened with imminent extinction. The U.S. administered Mariana Islands, consisting of Guam in the South and the Commonwealth of the Northern Mariana Islands (CNMI) in the north, historically harbored six endemic partulid species, half of which are thought to be extinct. While conducting a phylogenetic assessment of *Partula gibba*, an extant tree-snail with a range spanning at least seven islands within the archipelago, it was discovered that what has been identified as *P. gibba* on the island of Rota is a misidentified cryptic species. Here we use molecular phylogenetics, shell morphometrics and reproductive anatomy to describe it as a new species, *Partula lutaensis* **sp. nov.**. Because the new species has suffered population declines and has a restricted range, consisting solely of the small island of Rota, we highlight the urgent need for conservation measures.

Keywords

Cryptic species, Mariana Islands, Micronesia, Mollusca, narrow-range endemic, systematics

Introduction

The tree-snail family Partulidae is known from islands across the tropical Pacific (Cowie 1992). While most of the known diversity occurs in the eastern portion of the family's range, particularly the Society Islands for the genus *Partula* and the Samoan Islands for the genus *Samoana*, the progenitors of both genera likely came from further west (Lee et al. 2014). The 15 islands of the Mariana Archipelago in the western Pacific (Fig. 1) historically harbored six described species. Two of them, *Partula radiolata* (Pfeiffer, 1846), and *Partula salifana* Crampton, 1925, were known only from the island of Guam, while *Partula desolata* Bauman & Kerr, 2013, described from sub-fossil shells, and *Partula langfordi* Kondo, 1970, were described as single-island endemics from Rota and Aguigan, respectively. The only two Mariana species with multi-island distributions are *Samoana fragilis* (Férussac, 1821), known from both Guam and Rota, and *Partula gibba* Férussac, 1821, known from seven islands, from Guam, in the south, to Pagan Island in the north. In a recent publication, we described the discovery of a cryptic species of *Partula* on the island of Rota, based on molecular evidence (Sischo and Hadfield 2017). Due to greatly similar shell shape, this species had been identified as *Partula gibba* in prior surveys and publications (Kondo 1970; Bauman 1996; Bauman and Kerr 2013; Hadfield 2015). Adding further taxonomic confusion, a colony of *Partula* once maintained at the Invertebrate Conservation Center, Zoological Society of London in London, was labeled *Partula langfordi*, although it was originally collected on Rota (Goodacre and Wade 2001; Sischo and Hadfield 2017). Because *P. langfordi* was described as endemic to the island of Aguigan, snails bearing that name in the London collection were likely not *P. langfordi* (Kondo 1970). Unfortunately, *P. langfordi* is now thought to be extinct (Smith 2013; J. Liske-Clark, Northern Mariana Department of Fish and Wildlife, personal communication). The name of Aguigan Island is variously spelled on different maps and in different resources, including: Agiguan, Agijuan and Aguijan. We apply here the spelling currently in use by CNMI bureaus, the NOAA and elected officials in the CNMI.

To distinguish the new Rota *Partula* species from other extant species in the Mariana Archipelago, we paired our previously published phylogeny (Sischo and Hadfield 2017) with anatomy of the male reproductive tract, the latter having been used extensively as a diagnostic trait for *Partula* species (Pilsbry 1909; Pilsbry and Cooke 1934; Kondo 1955, 1968, 1970; Gerlach 2016; Slapcinsky and Kraus 2016). Because we were not able to extract useful DNA from preserved tissue of *Partula langfordi*, we were unable to carry out molecular phylogenetics with that species. In addition to anatomy of the male reproductive tract, we further distinguished *P. langfordi* from the species on Rota by replicating the shell morphometric analysis originally conducted by Kondo (1970) in his study of *P. langfordi* and co-occurring *Partula gibba* on the island of Aguigan. Here we describe *Partula lutaensis* sp. nov. and designate type material.

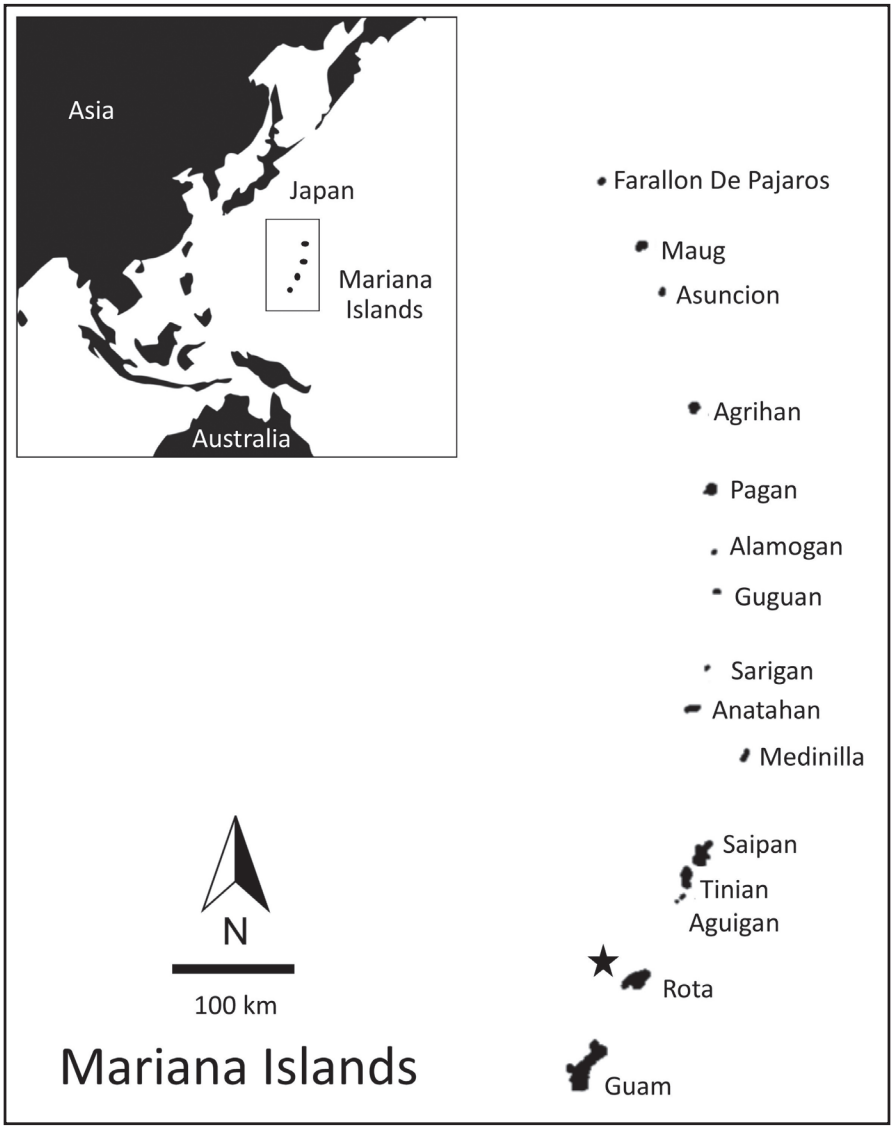

Figure 1. Map of the Mariana Archipelago with a star indicating the location of Rota Island.

Material and methods

Due to the endangered status of all partulid species from Guam and the Commonwealth of the Northern Mariana Islands, we have elected to not include specific location information of any of the extant colonies or type specimen material in this paper. However, this information has been deposited in the Bernice Pauahi Bishop Museum with each specimen.

Shell morphological assessment

Kondo (1970) found no differences in conchology, aside from non-overlapping shell sizes, between *P. langfordi* and sympatric *P. gibba* on the island of Aguigan. Because *Partula* from Rota had been mistakenly identified as *P. langfordi*, we carried out a similar comparison. Shells of *P. langfordi* from the mollusc collection housed at the Bernice Pauahi Bishop Museum (**BPBM**) in Honolulu, Hawai'i were used for analysis. BPBM lot numbers 213092, 21309, 213104, 213012, 213024, originally collected by Y. Kondo from Aguigan Island were compared with shells from what was then labeled as *P. gibba* (BPBM lot numbers, 217155, 213251, 213248, 213151, 213241) originally collected on Rota (Fig. 2). Lengths and widths were measured to 0.01 mm from 48 shells of *P. langfordi* and 47 shells of *P. gibba* with precision calipers. Shell length was measured parallel to the shell axis from the apex to the base of the aperture, and width was measured perpendicular to the shell axis across the widest portion of the shell. Means (M) and standard deviations (s.d.) are reported. Adult *Partula* spp.

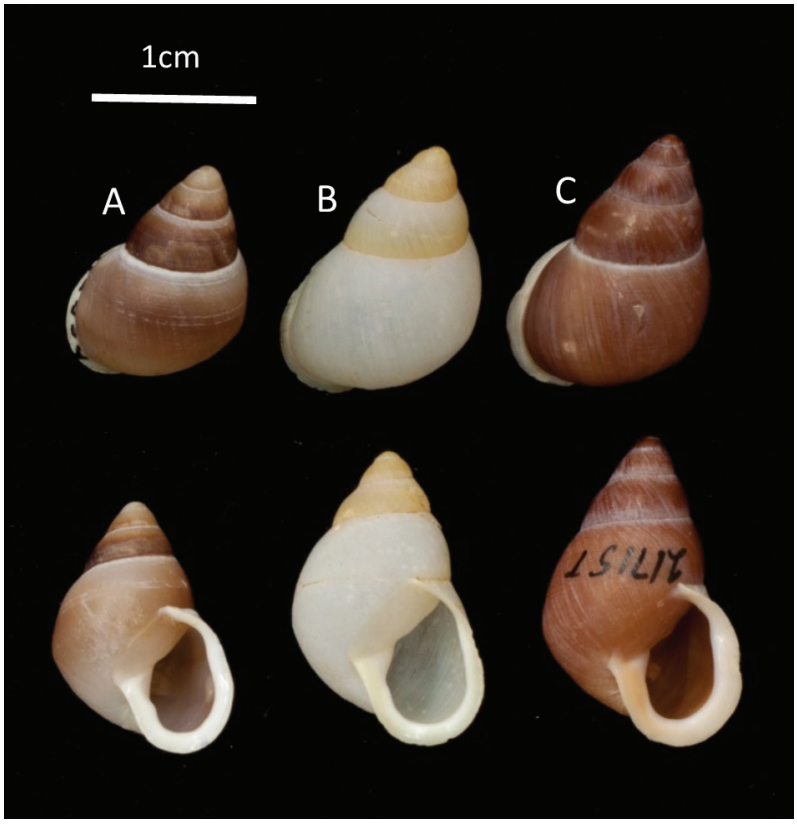

Figure 2. A typical shell of *P. langfordi* from Aguigan (**A**) compared to light and dark shell morphs of *P. lutaensis* sp. nov. from Rota (**B** and **C**). The three shells are shown in abapertural view in the upper row and apertural view below.

stop growing and become sexually mature when they form a characteristic thickened flare around the aperture of their shells, here referred to as a lip. All shells measured were lipped, indicating they were mature adults (Cowie 1992). Mean shell length and width were compared with independent-samples, two-sided t-tests, assuming unequal variances, using Microsoft Excel (version 16.44). Extensive shell metrics and comparisons for all partulid species of the Mariana Islands are found in historical publications (Crampton 1925; Kondo 1955, 1970). More recently Gerlach (2016) carried out extensive morphometric analyses of partulid shells, including *P. lutaensis* sp. nov., there referred to as *Partula* sp. (Rota). We therefore have made no other shell size comparisons. Lacking phylogenetic data for *P. langfordi*, our objective here was to replicate Kondo's shell size comparison between *P. langfordi* and sympatric *P. gibba* to determine whether *P. langfordi* and *P. lutaensis* sp. nov. are similarly distinct.

Morphology of the male reproductive tract

Many taxonomic descriptions of partulid snails have emphasized reproductive anatomy, particularly differences in the male part of the reproductive tract, to differentiate species (Pilsbry 1909; Pilsbry and Cooke 1934; Kondo 1955, 1968; Gerlach 2016; Slapcinsky and Kraus 2016). For this purpose, we obtained preserved specimens of *Partula radiolata* (lot nos. 21462 [2] and 213605 [1]) and *P. gibba* (lot nos. 214256 [2] and 214179 [1]) from Guam and those recorded as *P. gibba* from Rota (lot nos. 188958 [2], 213131 [2], 213152 [3]) from the extensive collections of the BPBM in Honolulu, Hawai'i. In selecting preserved museum specimens from Rota, we endeavored to obtain snails from the same or very near sites where snail tissue samples were collected for DNA analysis. Kondo and others who collected at these sites separated 'soft parts' from many shells for inclusion in the Bishop Museum collections and maintained the same lot numbers for the shells and preserved bodies for snails collected at one site at the same time. This allowed us to examine the shells before carrying out the dissections to make certain that the shells matched the shells of the snails from which we had collected small tissue samples for DNA analyses. In all cases, we were successful in this matching. Kondo (1970) found no difference in the male reproductive tracts of *P. langfordi* and *P. gibba*. We therefore did not dissect specimens of *P. langfordi*.

The following specimens were dissected.

- *Partula radiolata* (Pfeiffer, 1846) from Guam: BPBM no. 214262, 2 spms; BPBM no. 213605, 1 spm.
- *Partula gibba* Férussac, 1821 from Guam: BPBM no. 214256, 2 spms; 214179, 1 spm.
- *Partula* sp. nov. from Rota, as *P. gibba* in BPBM collections: BPBM no. 213151, 3 spms; 188958, 1 spm.; 213132, 2 spms; 213128, 1 spm.

The museum specimens were stored in 90% ethanol. Before dissecting them, we transferred them to three changes of fresh water and carried out the dissections under

water. The reproductive tracts of the snails were exposed by cutting the right-dorsal wall of the snail with a fine scalpel. Then, using fine forceps, the reproductive tract was carefully exposed and the ducts teased apart. Dissections were photographed with a Canon camera mounted on a Zeiss dissection microscope. Outline drawings were made by tracing duct contours from photos using Adobe Illustrator.

DNA analysis

During our collecting trip to Rota in 2010 only small tissue samples were collected for DNA analysis. Following the discovery of a cryptic species on Rota described in Sischo and Hadfield (2017), we were sent five newly collected voucher specimens from Rota by the CNMI Division of Fish and Wildlife to serve as type material for this new cryptic species. Unfortunately, our attempts to extract DNA from these ethanol-preserved specimens failed for unknown reasons. In the interim, all *Partula* species from Guam and the Commonwealth of the Northern Mariana Islands were listed as Endangered under the U.S. Endangered Species Act (US Fish and Wildlife Service 2015). Due to the rarity of the new species and its listing status, we have been unable to obtain another full voucher specimen. To move forward with describing this species, three non-lethal tissue samples were collected from individuals of the same population as the original shell vouchers provided by the CNMI Division of Fish and Wildlife, as well as three samples from a new site not visited by Sischo and Hadfield (2017). Non-lethal tissue samples were collected following the methodology of Thacker and Hadfield (2000), originally developed for sampling Hawaiian tree snails. These tissue vouchers were used to confirm that the shell vouchers are *P. lutaensis* and not *P. gibba*. Tissue sample collection, tissue preservation, total cell DNA extraction, CO1 DNA amplification and CO1 phylogenetic analyses were carried out using the methods described by Sischo and Hadfield (2017).

Results

Systematics

Class Gastropoda Cuvier, 1795

Subclass Heterobranchia Burmeister, 1837
Order Stylommatophora A. Schmidt, 1855
Superfamily Pupilloidea W. Turton, 1831
Family Partulidae Pilsbry, 1900

Genus *Partula* Férussac, 1821

Type species. *Helix faba* Gmelin, 1791.

***Partula lutaensis* sp. nov.**
http://zoobank.org/65D4AC75-488B-4A29-9773-5E0F5FB25449

Type material. ***Holotype*.** Bishop Museum BPBM 284888 Fig. 3. Entire specimen collected by Jill Liske-Clark, 20/11/2014 from type locality. ***Paratypes*.** BPBM 284889, 2 specimens collected by Jill Liske-Clark, 20/11/2014, from type locality, and BPBM 284890, 3 specimens collected by Jill Liske-Clark, same date, from a second location on Rota Island, Commonwealth of the Northern Mariana Islands.

Type locality. Rota Island, Commonwealth of the Northern Mariana Islands (CNMI).

Diagnosis. ***Shell*.** Shell dextral, moderately thin, ovate-conic, slightly perforate; umbilicus open; whorls moderately convex, suture adpressed; aperture ovate-elongate, slightly oblique; outer lip reflexed, thick, glossy; parietal lip glossy with light or dark coloration; color of embryonic whorls and post-embryonic whorls variable from shades of brown, buff, white and yellow with prominent white subsutural band; Measurements (N = 48 specimens from five lots in BPBM collections from Rota): height (= length) 15.98 mm, s.d. 0.75 mm; width, 10.64 mm, s.d., 0.24 mm. See Figure 4 for examples of shell color variation. Shell greatly resembles those of *Partula gibba* on Guam and Saipan (Crampton 1925).

Distinguishing shells of *P. lutaensis* from those of *P. langfordi*. Shell length of *P. langfordi* (M = 13.83 mm, s.d. = 0.37 mm, N = 47) was significantly shorter than the length of *P. lutaensis* sp. nov. (M = 15.98 mm, s.d. = 0.75 mm, N = 48), t(82) = -13.91,

Figure 3. Shell holotype of *P. lutaensis* sp. nov.

Figure 4. Left – Color morphs of *Partula lutaensis* sp. nov. found within a 10 × 10-meter quadrat. Right – Closeup of a *Partula lutaensis* sp. nov. with a dark shell.

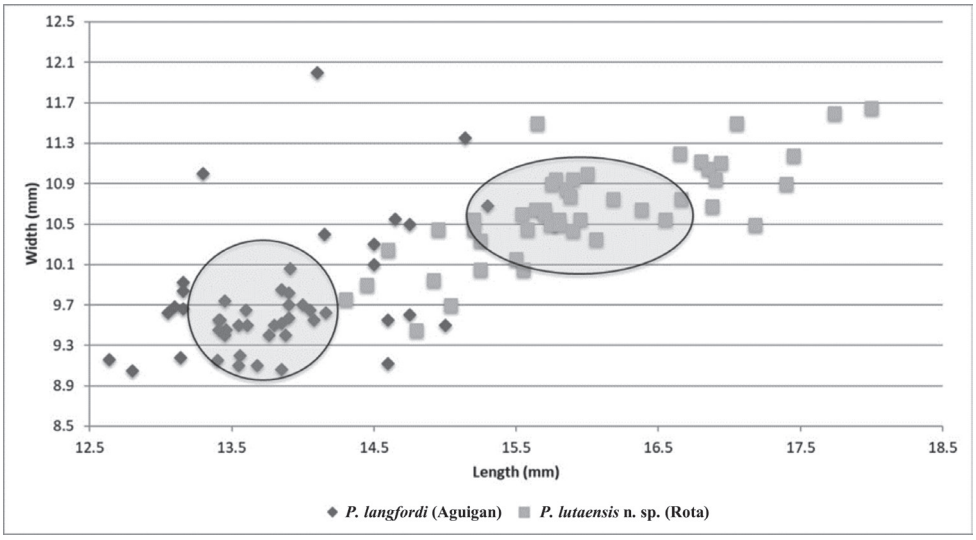

Figure 5. Scattergram of Bishop Museum shell measurements comparing shell width (y-axis) by shell length (x-axis) of 48 *P. langfordi* from Aguigan and 47 *P. lutaensis* sp. nov. from Rota. The mean shell length and width plus standard deviation of each species are encircled. All shells were lipped indicating snails were mature and had reached terminal growth.

$P < 0.001$. Similarly, shell width of *P. langfordi* (M = 9.74 mm, s.d = 0.36 mm) was significantly less than that of *P. lutaensis* sp. nov. (M = 10.64 mm, s.d = 0.24 mm), $t(90) = -8.02$, $P < 0.001$ (Fig. 5).

Male reproductive system. The male reproductive system of *Partula gibba* figured by Kondo (1955, 1970) and Gerlach (2016) is highly variable. In specimens we examined (Fig. 6A), the vas deferens entered the penis very near its top, leaving the upper

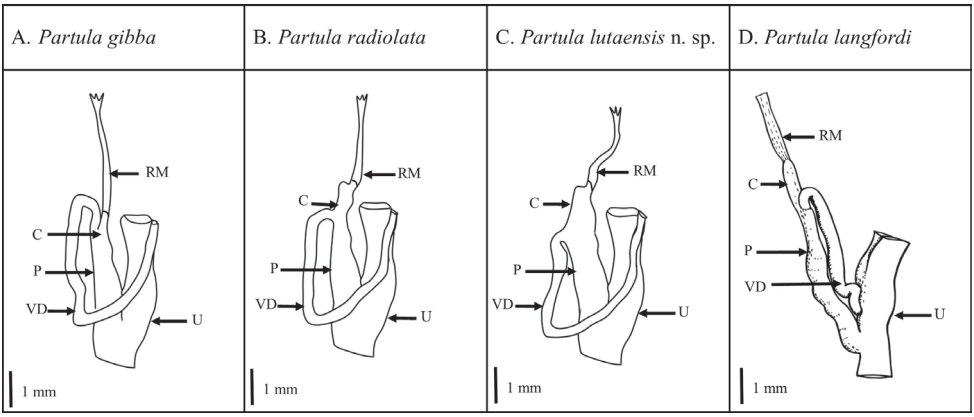

Figure 6. Outline drawings comparing the male reproductive tracks of four extant *Partula* species from the Mariana Islands. Male anatomy abbreviations are as follows: retractor muscle (RM), caecum (C), penis (P), vas deferens (VD), uterus (U). The figure of *Partula langfordi* is adapted from figure 5 of Kondo (1970). Note, Kondo found no difference between the male reproductive tracts of *P. gibba* and *P. langfordi*.

portion of the penis, attached to the retractor muscle and called the caecum by Gerlach (2016), to be very short. In specimens of *P. radiolata*, the entry of the vas deferens was about 1/5 to 1/4 of the length of the penis below the retractor-muscle attachment (Fig. 6B). However, the male duct was distinctive in *P. lutaensis* sp. nov. by the bulge or shoulder at the top of an expanded caecum, proximal to the vas deferens. In the male system of *P. lutaensis* sp. nov., the attachment of the vas deferens was consistently more distal than in either *P. gibba* or *P. radiolata* (Fig. 6C); the insertion was close to 1/3 of the length of the penis below the retractor-muscle attachment. In no other regard were there any distinctive differences among the penial structures of these three species. The lower attachment of the vas deferens to the retractor muscle in both *P. lutaensis* sp. nov. and *P. radiolata* is concordant with their placement as sister taxa in phylogenetic reconstructions of the group. Kondo (1970) found no differences between the male reproductive tract of *P. langfordi* and *P. gibba*. We include a modified version of his drawing with ours for comparison (Fig. 6D).

Ecology. Type and paratype specimens were found on *Epiprenmum aureum* and *Tectaria crenata* (J. Liske-Clark, Northern Mariana Department of Fish and Wildlife, personal communication).

Etymology. The specific epithet *lutaensis* recognizes Luta, the indigenous Chamorro name for the island of Rota.

DNA analyses

Analyses of the mitochondrial CO1 fragment confirmed that the tissue samples collected from the two type and paratype collection localities on Rota are *P. lutaensis* sp. nov. From the six tissue samples collected, two additional CO1 haplotypes were recovered (GenBank Accession numbers MT720839 and MT720840). As described in

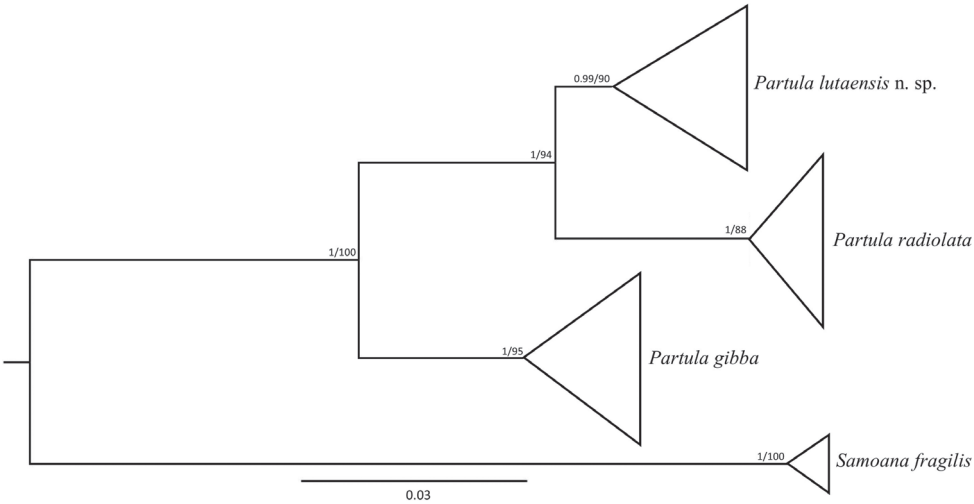

Figure 7. Bayesian phylogenetic tree representing the relationships between extant species in the family Partulidae from the Mariana Archipelago. This figure is an adaptation from one published in Sischo and Hadfield (2017). The phylogeny contains sequences from 24 individuals with unique haplotypes from seven islands and is based on a concatenated alignment of three genes (CO1, 16S and ITS2). The combined sequence length was 1683 base pairs. Maximum likelihood and Bayesian analyses recovered comparable topologies. Therefore, Bayesian posterior probabilities and maximum likelihood bootstrap values are reported on all nodes greater than 0.80 or 80% respectively. Branch ends have been collapsed to emphasize support for the species groups, rather than within group relationships. Also, note that this phylogeny does not include the newly sequenced haplotypes of *Partula lutaensis* sp. nov. mentioned above.

Sischo and Hadfield (2017), *P. lutaensis* sp. nov. is sister to *P. radiolata* from Guam despite having a shell more similar in appearance to *P. gibba* than to *P. radiolata* (Fig. 7). Currently all known extant colonies of *Partula* on Rota are *P. lutaensis* sp. nov.

Discussion

The phylogeographic assessment of the extant partulids in the Mariana Islands reported by Sischo and Hadfield (2017) strongly supports the presence of a cryptic species on Rota and is concordant with further analyses of the male reproductive tracts, with *P. lutaensis* sp. nov. and *P. radiolata* sharing a lower attachment of the vas deferens in relation to the retractor muscle. Because this cryptic species was not found on any other islands, we conclude it is endemic to the island of Rota and have given it the name *Partula lutaensis* sp. nov. to recognize the indigenous Chamorro name for the island.

Available data indicate that all known populations of the genus *Partula* on Rota are *P. lutaensis* sp. nov.. This does not rule out the possibility that *P. gibba* once was, or currently is, on the island. Further surveys for extant partulid populations and analysis of sub-fossil shell remains on Rota may provide further evidence as to the present and

Figure 8. A *Partula lutaensis* sp. nov. freshly depredated by *Platydemus manokwari* observed by authors on Rota.

historical distribution of these two species on the island. Moving forward, we strongly encourage that DNA barcoding be employed to determine species identification of any new living populations of *Partula* spp. discovered on Rota and elsewhere in the Mariana Islands. Furthermore, should *P. gibba* be located on Rota it should be attempted to find shell or body characters that might aid in distinguishing the two species without dissection or tissue sample collection.

Partula lutaensis sp. nov. was observed in locally high abundance on Rota, similar to observations of *P. radiolata* on Guam (Sischo and Hadfield 2017). Unfortunately, *P. gibba*, once the most abundant partulid on Guam, is now almost entirely extirpated (Hopper and Smith 1992; Sischo and Hadfield 2017; C. Fiedler personal communication June 2018). Persistence despite depredation by introduced predators may be further evidence of the shared ancestry between *P. lutaensis* sp. nov. and *P. radiolata*. Possibly, the *P. lutaensis* – *P. radiolata* clade shares behavioral and or life-history traits that have allowed the species to persist despite significant threats. For

example, a recent study found that *P. radiolata* has a higher reproductive rate than *P. gibba* (Bick et al. 2018).

Across the Pacific, partulid species have been driven to extinction by introduced predators, most notably North American carnivorous snail species in the genus *Euglandina*, and the New Guinea flatworm *Platydemus manokwari* (Clarke, Murray and Johnson 1984; Murray et al. 1988; Hopper and Smith 1992; Bauman 1996; Coote et al. 1999; Cowie and Cook 2001; Régnier, Fontaine and Bouchet 2009; Pelep and Hadfield 2011; Meyer et al. 2017; Sischo and Hadfield 2017; Hadfield 2020; Gerlach et al. 2020). This has been particularly true in the Mariana Islands where half of the described partulid species are thought to be extinct, and the remaining species are imperiled across their ranges. While we observed *P. lutaensis* sp. nov. in locally high numbers in 2010, known populations are few and geographically discrete. Sub-fossil shells of partulids are ubiquitous on Rota (Bauman 1996) and Saipan (personal observations, October 2014), suggesting severe range reductions (Bauman 1996). Additionally, we observed *Platydemus manokwari* depredating *P. lutaensis* sp. nov. while collecting tissue samples on Rota (Fig. 8). Because *P. lutaensis* sp. nov. is an island-endemic species with a very restricted range and is clearly under significant predation pressure from introduced species, its existence is imperiled. When the Rota populations were considered to be *Partula gibba*, they were protected by a federal Endangered Species declaration. For these reasons, it is imperative that *Partula lutaensis* sp. nov. be listed as Endangered as soon as possible.

Acknowledgements

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References

Bauman S (1996) Diversity and decline of land snails on Rota, Mariana Islands. American Malacological Bulletin 12: 13–27. https://www.biodiversitylibrary.org/part/143145#/summary

Bauman S, Kerr AM (2013) *Partula desolata* sp. nov. (Pulmonata: Partulidae), an extinct land snail from Rota. Mariana Islands Micronesia. Micronesica 5: 1–12. http://micronesica.org/sites/default/files/2013-05_bauman-kerr_partula.pdf

Bick CS, Pearce-Kelly P, Coote T, Ó Foighil D (2018) Survival among critically endangered partulid tree snails is correlated with higher clutch sizes in the wild and higher reproductive rates in captivity. Biological Journal of the Linnean Society 125(3): 508–520. https://doi.org/10.1093/biolinnean/bly124

Clarke B, Murray J, Johnson MS (1984) The extinction of endemic species by a program of biological control. Pacific Science 38(2): 97–104. http://hdl.handle.net/10125/844

Coote T, Clarke D, Loeve E, Meyer JY (1999) Extant populations of endemic partulids on Tahiti, French Polynesia. Oryx 33(3): 215–222. https://doi.org/10.1046/j.1365-3008.1999.00065.x

Cowie RH (1992) Evolution and extinction of Partulidae, endemic Pacific island land snails. Philosophical Transactions of the Royal Society of London B – Biological Sciences 335: 167–191. https://doi.org/10.1098/rstb.1992.0017

Cowie RH, Cook RP (2001) Extinction or survival: partulid tree snails in American Samoa. Biodiversity and Conservation 10: 143–159. https://doi.org/10.1023/A:1008950123126

Crampton HE (1925) Studies on the variation, distribution, and evolution of the genus *Partula*. The species of the Mariana Islands, Guam and Saipan. Carnegie Institution of Washington Publication 228a: 1–116.

Gerlach J (2016) Icons of evolution: Pacific Island tree-snails, family Partulidae. Cambridge Phelsuma Press, 336 pp.

Gerlach J, Barker GM, Bick CS, Bouchet P, Brodie G, Cristensen CC, Collins T, Coote T, Cowie RH, Fiedler CG, Griffiths OL, Florens FBV, Hayes K, Kim J, Meyer J, Meyer WM, Richling I, Slapcinsky JD, Winsor L, Yeung NW (2020) Negative impacts of invasive predators used as biological control agents against the pest snail *Lissachatina fulica*: the snail *Euglandina* '*rosea*' and the flatworm *Platydemus manokwari*. Biological Invasions 23: 997–1031. https://doi.org/10.1007/s10530-020-02436-w

Goodacre SL, Wade CM (2001) Molecular evolutionary relationships between partulid land snails of the Pacific. Proceedings of the Royal Society B – Biological Sciences 268(1462): 1–7. https://doi.org/10.1098/rspb.2000.1322

Hadfield MG (2015) The occurrence of the endangered tree snail *Partula gibba* in the Mariana Islands, with a focus on Pagan Island. Bishop Museum Bulletin in Zoology 9: 147–167. http://hbs.bishopmuseum.org/pubs-online/pdf/bz9-10.pdf

Hadfield MG (2020) Snails that eat snails. The Feral Atlas (Stanford University Press). https://feralatlas.supdigital.org/poster/snails-that-eat-snails

Hopper DR, Smith BD (1992) Status of Tree Snails (Gastropoda: Partulidae) on Guam, with a Resurvey of Sites Studied by HE Crampton in 1920. Pacific Science 46: 77–85. https://scholarspace.manoa.hawaii.edu/bitstream/10125/1675/v46n1-77-85.pdf

Kondo Y (1955) A revision of the family Partulidae (Gastropoda Pulmonata). PhD Thesis, Cambridge, Harvard University, Massachusetts.

Kondo Y (1968) Partulidae: preview of anatomical revision. Nautilus 81: 73–77.

Kondo Y (1970) Some aspects of Mariana Islands Partulidae (Mollusca, Pulmonata). Bishop Museum Occasional Papers 24(5): 73–90. http://hbs.bishopmuseum.org/pubs-online/pdf/op24-5.pdf

Lee T, Li J, Churchill CK, Ó Foighil D (2014) Evolutionary history of a vanishing radiation: isolation-dependent persistence and diversification in Pacific Island partulid tree snails. BMC Evolutionary Biology 14: e202. https://doi.org/10.1186/s12862-014-0202-3

Meyer WM, Yeung NW, Slapcinsky J, Hayes KA (2017) Two for one: inadvertent introduction of *Euglandina* species during failed bio-control efforts in Hawaii. Biological Invasions 19: 1399–1405. https://doi.org/10.1007/s10530-016-1354-4

Murray J, Murray E, Johnson M, Clarke B (1988) The extinction of *Partula* on Moorea. Pacific Science 42: 150–153.

Pelep PO, Hadfield MG (2011) The status of the endemic snails of the genus *Partula* (Gastropoda: Partulidae) on Pohnpei, Federated States of Micronesia. Micronesica 41(2): 253–262. https://micronesica.org/sites/default/files/17_pelep-hadfield_pp_253-262.pdf

Pilsbry HA (1909–1910) Manual of Conchology, Structural and Systematic vol 20: *Caecilioides*, *Glessula* and Partulidae. Academy of Natural Sciences, Philadelphia, 154 pp.

Pilsbry HA, Cooke CM (1934) Partulidae of Tonga and related forms. Occasional Papers of the Bernice P. Bishop Museum 10: 3–22. http://hbs.bishopmuseum.org/pubs-online/pdf/op10-14.pdf

Régnier C, Fontaine B, Bouchet P (2009) Not knowing, not recording, not listing: numerous unnoticed mollusk extinctions. Conservation Biology 23(5): 1214–1221. https://doi.org/10.1111/j.1523-1739.2009.01245.x

Slapcinsky J, Kraus F (2016) Revision of Partulidae (Gastropoda, Stylommatophora) of Palau, with description of a new genus for an unusual ground-dwelling species. ZooKeys 614: 27–49. https://doi.org/10.3897/zookeys.614.8807

Sischo DR, Hadfield MG (2017) Phylogeographic relationships among multi-island populations of the tree snail *Partula gibba* (Partulidae) in the Mariana Islands. Biological Journal of the Linnean Society 121: 731–740. https://doi.org/10.1093/biolinnean/blx031

Smith BD (2013) Taxonomic inventories and assessments of terrestrial snails on the islands of Tinian and Aguiguan in the Commonwealth of the Northern Mariana Islands. University of Guam Marine Laboratory Technical Report 154.

Thacker RW, Hadfield MG (2000) Mitochondrial phylogeny of extant Hawaiian tree snails (Achatinellinae). Molecular Phylogenetics and Evolution 16: 263–270. https://doi.org/10.1006/mpev.2000.0793

US Fish and Wildlife Service (2015) Endangered and Threatened Wildlife and Plants; Endangered Status for 16 Species and Threatened Status for 7 Species in Micronesia. Federal Register 80: 59424–59497. https://www.govinfo.gov/content/pkg/FR-2015-10-01/pdf/2015-24443.pdf