Extracts concerning the Mariana Island species from Yoshio Kondo's (1955) *A Revision of the Partulidae*

Edited by

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Dankulu na Saina Ma'åse!

SUMMARY

This report provides an annotated transcription of the systematic accounts of the four then-known species of Mariana Island tree snails in the family Partulidae (*Partula gibba*, *P. radiolata*, *P. salifana*, and *Samoana fragilis*) from Kondo's (1955) unpublished and difficult to obtain Ph.D. dissertation on the systematics of Partulidae. The monograph is still a landmark study of the family, their systematics, anatomy and natural history, done at a time when most of the species of partulid were still extant and common in the wild.

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INTRODUCTION

This report has been prepared as part of a review of the biology of the terrestrial snails of the Mariana Islands, Micronesia, which are under increasing threat from human development and introduced predators (Hopper and Smith 1992). It presents a transcription of the sections on the *Partula* and *Samoana* of the Mariana Islands from Kondo (1955).

Dr. Yoshio Kondo was the Curator of Mollusks at the Bernice P. Bishop Museum in Honolulu, Hawai'i from 1935 to 1980, and served as a Malacologist Emeritus there until his passing in 1990. He has published numerous papers on the biology and systematics of terrestrial snails of Hawaii and other Pacific islands (Cowie 1993). He is perhaps best known for his exacting scholarship on the anatomy and systematics of the Partulidae, including in 1955 his landmark *A Revision of the family Partulida (Gastropoda, Pulmonata)*. This was his Ph.D. dissertation and much of it remains unpublished and difficult to obtain.

Figure 1. Dr. Yoshio "Yoshi" Kondo in the field on Oahu in 1967. Photo by Tim Ross and in the public domain.

In the monograph, he provided descriptions, including beautiful original figures of dissected reproductive tracts and notes on reproduction of nearly all species of Partulidae known at the time, including the four species from the Mariana Islands: *Samoana fragilis*, *Partula gibba*, *P. radiolata* and *P. salifana*. His work was based on his own careful dissections, often from

specimens that he had collected on expeditions throughout the western Pacific.

The family Partulidae of mostly arboreal species is largely restricted to the oceanic islands of the western Pacific Plate. The group consists of about 130 species in three genera, all endemic to single islands or a few adjacent islands on the western Pacific Plate. The smallest genus *Eua* Pilsbury & Cooke, 1934, comprised of four species, is found only in Samoa and Tonga. The genus *Samoana* Pilsbury, 1909, is of about 24 species. The largest genus *Partula* Férussac, 1821 has about 100 described species. It is also the most widely distributed, ranging from the Society Islands, French Polynesia, where species richness was highest, originally at 61 species, to the Palauan Archipelago in westernmost Micronesia with just three *Partula*. About 1300 km northeast of Palau lie the Mariana Islands with five *Partula* and one *Samoana*.

The first *Partula* described from the Mariana Islands, *P. gibba*, 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. A third species, *P. salifana* Crampton, 1925, was discovered in the southwestern highlands of Guam and is now extinct (Hopper and Smith 1992). The fourth species, *P. langfordi* Kondo, 1970, was found on the tiny island of Aguiguan and is probably also now extinct (Smith 2008; 2013). Kondo in his dissertation raised the possibility that this was a good species, but did not describe it as a new species until much later. A fifth Mariana partulid, *P. fragilis* Férussac, 1821, was transferred to *Samoana* by Kondo (1955; 1968). Adult shells of a sixth conchologically distinct species from the Marianas, the long extinct *P. desolata* Bauman & Kerr, 2013, have been collected from unconsolidated prehistoric (500–1000 YBP) cave deposits on Rota (Bauman 1996; Bauman & Kerr 2013).

ABOUT THE TRANSCRIPTION

The transcription is taken from photographs made of sections from the original copy of Kondo's dissertation held at Widener Library, Harvard University. The dissertation is an unpublished work whose copyright belongs to the original author, Dr. Kondo. The limited presentation here constitutes fair use in the service of research and education. The

original formatting, such as page layout and page numbers, was retained. I used the monospaced typeface `Courier New` to mimic the original manual typewriter font used, although Kondo applied diacritical marks by hand in black ink. The version here also retains any errors, such as double periods, misspelt words, miscapitalization of a work in French, and inconsistencies in formatting, e.g., variable spacing after periods or hyphens. Any mistakes that I have introduced tended to be double letterings for some reason; I hope I've found and removed all those. My annotations within the text are placed in **Helvetica Bold** and set off by square brackets, such as ellipses to indicate untranscribed text of irrelevant passages. The included plates are the original photos provided to me and taken with a cell-phone camera.

DISCUSSION

Kondo's (1955) section on the *Partula* and *Samoana* of the Mariana Islands provides much interesting information. Some of the material formed part of his later scientific publications, including his transfer of *Partula fragilis* to the genus *Samoana* (Kondo 1968), and his description of *P. langfordi* and, in the same paper, the sinistral population of *P. gibba* in Saipan (Kondo 1970).

Other information has not been published and hitherto difficult to obtain. For example, Kondo had found *P. salifana* as far south as Mt. Lamlam, essentially doubling its known range. Neither we (Kerr 2013; Bauman and Kerr 2013; Kerr and Fiedler 2015) nor others (Hopper and Smith 1992) studying the Mariana fauna had been aware that this fact was already known. Hence, it is probably not the Mariana species with "the most restricted distribution" (Smith et al. 2008; Bauman and Kerr 2013), after all! Rather *P. salifana*'s distribution was about equal to that of *P. langfordi*, the species once found atop the small, narrow island of Aguiguan.

This same section also discusses the unusual form of *P. gibba* also atop Mt. Lamlam. The shells lack the eponymous gibbous outline of the body whorl, so that it more resembles in silhouette *P. radiolata*.

Further, we see the development of his thoughts on the specific identity of the "small, purple race" of *P. gibba* on Aguiguan (= "Agiguan"). In his dissertation he writes

that this form could well be a separate species based on its small size alone and the sympatry of more typical *P. gibba* on the small island. Still, he did not describe this species until almost two decades later as *P. langfordi*.

Kondo also offers speculations on the evolution of the fauna. While some of this discussion is couched in the ideas of the day concerning extant species as ancestral types giving rise to other present-day species, or of 'static' and 'deteriorating' groups, much information remains relevant. For example, he considers the distribution of *P. salifana* as relictual in light of the species limited montane distribution and its conchology, which more resembles some Polynesian species than the other Marianas *Partula*. He is apparently unaware of Cockerell's (1926) earlier and similar conclusions on the subject. He also writes that knowing whether calcareous or membranous egg capsules are primitive could provide insight into phylogenetic relationship. As well, his detailed descriptions of the reproductive anatomy of the extinct *P. salifana* offers us the most detailed set of possible characters for a phylogenetic analysis, given that no DNA has, as far as is known (M. Hadfield 2014, pers. comm.), been preserved of this species.

Equally fascinating are his observations concerning the species' dispersal in the Marianas. He ventures that seabirds, perhaps dispersed by the frequent typhoons in the region, play an important role. He supports this idea by recounting his discovery while in the northern Mariana islands of two genera of native snails on a single seabird, *Succinea* (Succineidae) and *Elasmias* (Achatinellidae). All species from these genera in the Marianas were described from these islands, lending support to his hypothesis.

In sum, Kondo's (1955) dissertation remains a gold mine of information on the systematics and biology of the Partulidae. His extensive treatment of the species native to the Mariana archipelago provides much new information on the fauna, which should prove useful to biologists who study these rare and endangered animals.

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Samoana of Guam

SAMOANA FRAGILIS (Férussac)

(Pl. 1, fig. 19; pl. 13, figs. 61, 62)

Partula fragilis Férussac, Tableau Systematiques Des Animaux Mollusques En Families Naturelles, p. 66, 1821.

Partula fragilis Férussac, Crampton, Carnegie Institution of Washington, Publication no. 228A, p. 30, pl. 11, figs. 12-19, 1925.

Shell 15.4 x 10 mm., corneous, thin, fragile, translucent; lip scarcely reflected. Marianas, Guam, H. G. Hornbostel, June to August 1923. Bishop Museum no. 75354.

Genitalia (fig. 61) differing in no way from others of the genus. Hermaphrodite gland 3-lobate, very delicate, paucifolliculate (closeup shown). Albumin and prostate glands large; spermatheca long; free oviduct long; vagina long. Penis about one-half oviducal length, elongate (not stout) type; not typical; epiphallus small. Vas deferens terminal. Retractor long, thin.

Interior of penis (fig. 62). Epiphallus with thin, diaphanous, meandering low ridges of flesh arranged in about six vertical rows, one of which forms diagonally arranged steps. At base of epiphallus are faint lateral ribs which

tend to coalesce furthest below. Penis proper with one large turgid principal pilaster, greatly outcurved, with three fleshy spurs on the inside, and overhanging the usual large cavity. Secondary pilaster is a thickening of the sheath wall with a slight ridge at the free end, and also overhanging a hollow space.

Reproduction: ovoviviparous; one egg and one embryo (figured specimen); two eggs and one embryo (in another).

Crampton (p. 32) has made a statistical analysis of the fecundity in S. fragilis in which 49 gravid animals were found to contain 73 eggs and 11 embryos, an average of 1.71 per animal, a low rate of productivity even if the adolescents of the species are precocious.

Two other points of interest noted by Crampton may be touched on here, one concerning the heavily calcified egg capsule and their great size; and two, the extremely thin shell of the mollusk despite abundance of coralline limestone nearly everywhere. The egg capsule, its thickness, and great size is a characteristic of the genus and the invariability of it in the far flung areas is but another evidence of evolutionary showdown. The thickness of the shell, which eventually has to be resorbed, in order to release the embryo contained within it, undoubtedly increases the incubation period. This cursory study indicates that the eggs remain in the uterus for longer periods than in Partula. It is not

uncommon to find two, three, even four eggs with not a single capsule dissolving in the uterus while in Partula the graduations are regular and, in species with egg capsules, the egg shell begins to be absorbed at a high level in the uterus which means encapsulation is a mere formality easily dispensed with as instances of naked eggs and pseudoviviparity show. Slowdown in incubation may be one explanation to the scarcity of Samoana species.

The thin, fragile, often transparent shell is a common characteristic of Samoana, shared occasionally by some species of Partula (e.g. arguta, turgida) but only to a minor degree. Inability to take up calcium is probably another diagnostic feature of a static or a deteriorating group.

There is a remarkably close similarity between the shells of S. fragilis and S. cramptoni of Tonga which no researcher has referred to previously. In both the recurved lip end abruptly soon after reflexure as though growth were arrested abruptly and the general gross appearance of both are very similar (cf. pl. 1, figs. 4 and 19). Applying the axiom that similarity denotes relationship, we may assume that S. fragilis and S. cramptoni are not too far separated from each other on the one hand and on the other are closer to each other than each is to any of the remaining 19 species now known (total 21 in Samoana).

[end text p. 105]

[...]

Partula of Marianas

The species constituting the genus Partula in this island group are three in number, viz., P. salifana, gibba, and radiolata, named in the order of their supposed relat-tionship and possible order of derivation. P. gibba is universally distributed throughout Guam from sea level to the highest mountains and is nearly always accompanied by radiolata from which it is easily differentiated. P. salifana is a highland form and usually exists on or near the summits of the mountains and coexists with gibba in these places but seldom does radiolata occurs simultaneously to make a trio although Samoana fragilis will do so. Just below the highest peak of Guam (Mt. Lamlam, 1334 ft.) there exists a large colony of salifana together with gibba and S. fragilis. The former two resemble each other so closely here that great care must be exercised in separating one from the other. Here

the species gibba has lost much of the gibbous curvature which characterizes its ultimate whorl so that it superficially resembles salifana. The reasons behind this interesting phenomenon are principally two in number, namely, interspecific hybridization or very close relationship, probably both. Of these two reasons, if the latter is temporarily accepted for the sake of postulation, we find that it offers a clue to the origin of gibba. In other words we have a hypothesis in which salifana is a relict species once widespread over Guam but now withdrawn to a limited highland niche as a result of the appearance of a more vigorous and aggressive species to which it was parental.. This hypothesis was arrived at from comparative studies of their genitalia which will be described and discussed fully under their headings. The gist of it is this, that the penis of salifana is a reduced-modified faba type while in gibba there are two types. The commonest is the small hebe type but there also occurs a type like that of salifana. This is the evidence that links the two species in the relationship specified and is also the evidence that gives a valid explanation for their close commingling on Mt. Lamlam.

Partula gibba is of interest from another point of view. While P. salifana, P. radiolata, an S. fragilis are confined to Guam, P. gibba has invaded the remainder of the

main Marianas group (Rota, Agiguan, Tinian, Saipan) and has gone northward into some of the geologically young northern Marianas (Alamagan, Pagan).

Parenthetically, this distributional phenomenon furnishes further material on speculation as to the means of dispersal among oceanic islands. The Marianas is in the typhoon belt but more to the point is a personal experience on Alamagan in 1949 where a young sooty tern was captured carrying on its feathers a widespread species of Succinea and an equally widespread species of Elasmias, both terrestrial pulmonates, adhering fast by means of their sticky mucus. A combination of birds with typhoons makes an excellent carrier.

P. gibba has not only spread over these distantly separated islands but shows evidence of undertaking various evolutionary paths. For example, on the highest peak of Saipan (Mt. Tapochau) it has given rise to a sinistral form and on tiny Agiguan it has evolved a tiny purplish race that can easily be classified as a species due to this notable reason. In one large colony it coexists with a large yellowish race with one section of their margin fusing and commingling but without any genetic mixture whatsoever. The aforementioned large yellowish race is an interesting one for this reason, that it is the race that has found a foothold both on Alamagan and Pagan. Its presence in the middle of the northern archipelago points strongly to the possibility that it may be found to exist on four of the remaining eight islands if these were faunistically explored.

Lip of all Marianas species of Partula are slightly thickened within, without any teeth.

PARTULA GIBBA Férussac

(Pl. 4, figs. 90, 91; pl. 32, figs. 113-116)

Partula gibba Férussac, Tableau Systématiques Des Animaux Mollusques En Families Naturelles, p. 66, 1821.

Partula gibba Férussac, Pilsbry, Manual of Conchology 20: 3313, pl. 39, figs. 1 to 11, 1909.

Partula gibba Férussac, Crampton, Carnegie Institution of Washington, Publication no. 228A, pl. 12, figs. 1-56; pl. 13, figs. 1-59; pl. 14, figs. 1-57, 1925.

Shell (fig. 90) 16.4 x 11 mm., reddish brown with yellowish suffusion and subsutural white. Shell (fig. 91) 17.6 x 13 mm., similarly colored as above, the last whorl gibbous. Bishop Museum no. 152931 (fig. 90), Guam, Ritidian Point, 550 ft., Guam Girl Scouts, 22 May 1936. No. 190272, (fig. 91) Guam, Dededo - Yigo, S. L. Kimball, 23 February 1946.

Genitalia (figs. 113, 114; shell, fig. 90) typical. Hermaphrodite gland 3- to 5-lobate, spermatheca medium. small, produced; remainder of penis subcylindrical, with a

slight median bulge and curvature. Interior of penis papillose in the epiphallus, the papillae sparse and small, some on rugae, others individual; penial stalk heavily armed with pilasters of the usual kind. In some individuals the papillae are denser and larger than those figured. Vas deferens subterminal. Retractor long, medium heavy (as in figure) to light.

Genitalia (figs. 115, 116; shell fig. 91) with penial variant. Penis with enlarged head as in salifana and reminiscent of robusta (pl. 18, fig. 38, Raiatea) not in configuration but in diminution of size but retaining a distinguishable broadened epiphallus concommitant with a (relatively) richly papillose interior. Interior of penis (fig. 116) heavily papillose, with one large ruga having numerous tubercles, and with 6 to 7 other subsidiary rugae all well folded or papillate. Pilasters of stalk few, large, strong, merging above with epiphallar rugae.

While the sampling of Ritidian Point specimens (fig. 113; 152931) showed only the hebe type penis, there was one specimen of this type among the salifana type from Dededo - Yigo. There is no question as to the identity of P. gibba from these two localities and the significance of the dual-type penis has been discussed above. That this phenomenon is not isolated but has counterparts in Palau, Ponape, and

possibly will be revealed elsewhere. It shows that the genus is yet in the midst of evolutionary changes.

Dissections covering numerous populations of this species and its cospecies together with investigations of juvenile stages are indicated.

A paraneanic specimen was sampled (152933, Ritidian Pt.) but it revealed no clue on biphallism. Epiphallus very long, as long as penis, vas deferens median.

Reproduction: pseudo-viviparous; number of embryos were none (one specimen), one (in one), two (in one), and three (in three, one figured). Older embryos with portions of embryonic shells visible; earlier (younger) embryos smaller and completely enveloped in albumin.

PARTULA SALIFANA Crampton

(Pl. 4, fig. 92; pl. 32, fig. 117)

Partula salifana Crampton, 1925, loc. cit., p. 25, pl. 11, figs. 1-19.

Shell 17.7 x 11 mm., last whorl brown, penultimate reddish brown, apex reddish purple ending in vinaceous. Guam, Mt. Alifan, 800., E. H. Bryan, Jr., 20 April 1936. Bishop Museum no. 152877.

Genitalia. Spermatheca (fig. 117) medium. Penis similar to that of gibba, modified-reduced faba type, about

one-half oviducal length; epiphallus broader than stalk and forming a head, one-half penial length; stalk with upper part slightly bulging. Interior of penis as in gibba (fig. 116), one ruga thickened and multi-papillate, with about nine accompanying subsidiary rugae; pilasters six, and similar to those of gibba.

Reproduction: pseudo-viviparous; embryos counted were two (in two specimens, one figured); three (in four).

PARTULA RADIOLATA (Pfeiffer)

(Pl. 4, fig. 93; pl. 32, fig. 118)

Bulimus radiolatus Pfeiffer, Proceedings of the Zoological Society, London, p. 39, 1846.

Partula radiolata (Pfeiffer) Pilsbry, Manual of Conchology 20: 316, pl. 41, figs. 1 to 4, 1909.

Partula radiolata Pfeiffer, Crampton, 1925, loc. cit., p. 34, pl. 11, figs. 20-64.

Shell 8 x 10.8 mm., ivory with pinkish brown growth streaks, apex brown. Guam, Ritidian Pt., 100 ft., E. H. Bryan, Jr., 16 May 1936, Bishop Museum no. 188964.

Genitalia. Penis (fig. 118) hebe type, about one-fourth oviducal length, small. Epiphallus small but not greatly reduced; stalk subcylindrical, curved. Both indicate interior ornamentation to be well developed, as they are.

Interior of epiphallus with one strong ridge and six minor but well tuberculate rugae; pilasters numerous, well developed, and merging with rugae.

Reproduction: pseudo-viviparous; embryos counted were none (in one), three (in one, figured), and five (in two).

Well developed interior ornamentation of epiphallus indicates that the penis of radiolata is a modified salifana type. Dissections of larger series may indicate salifana type penis also, as in gibba.

[end text p. 203; end section on Mariana *Partula*]

Plate 4

87. Partula martensiana Pilsbry, Kusaie, Carolines.

88. P. guamensis Pfeiffer, Ponape, "

89. P. emersoni Pilsbry, " "

90. P. gibba Férussac, Ritidian Point, Guam, Marianas.

91. P. gibba, Dededo-Yigo, Guam.

92. P. salifana Crampton, Guam.

93. P. radiolata Pfeiffer, Guam.

84. P. calypso O. Semper, Babelthuap, Palau, Carolines.

85. P. thetis O. Semper, " "

96. P. leucothoe O. Semper, Peleliu, "

P. martensiana proportion: $\frac{\text{figure}}{\text{specimen}} = \frac{20}{23}$

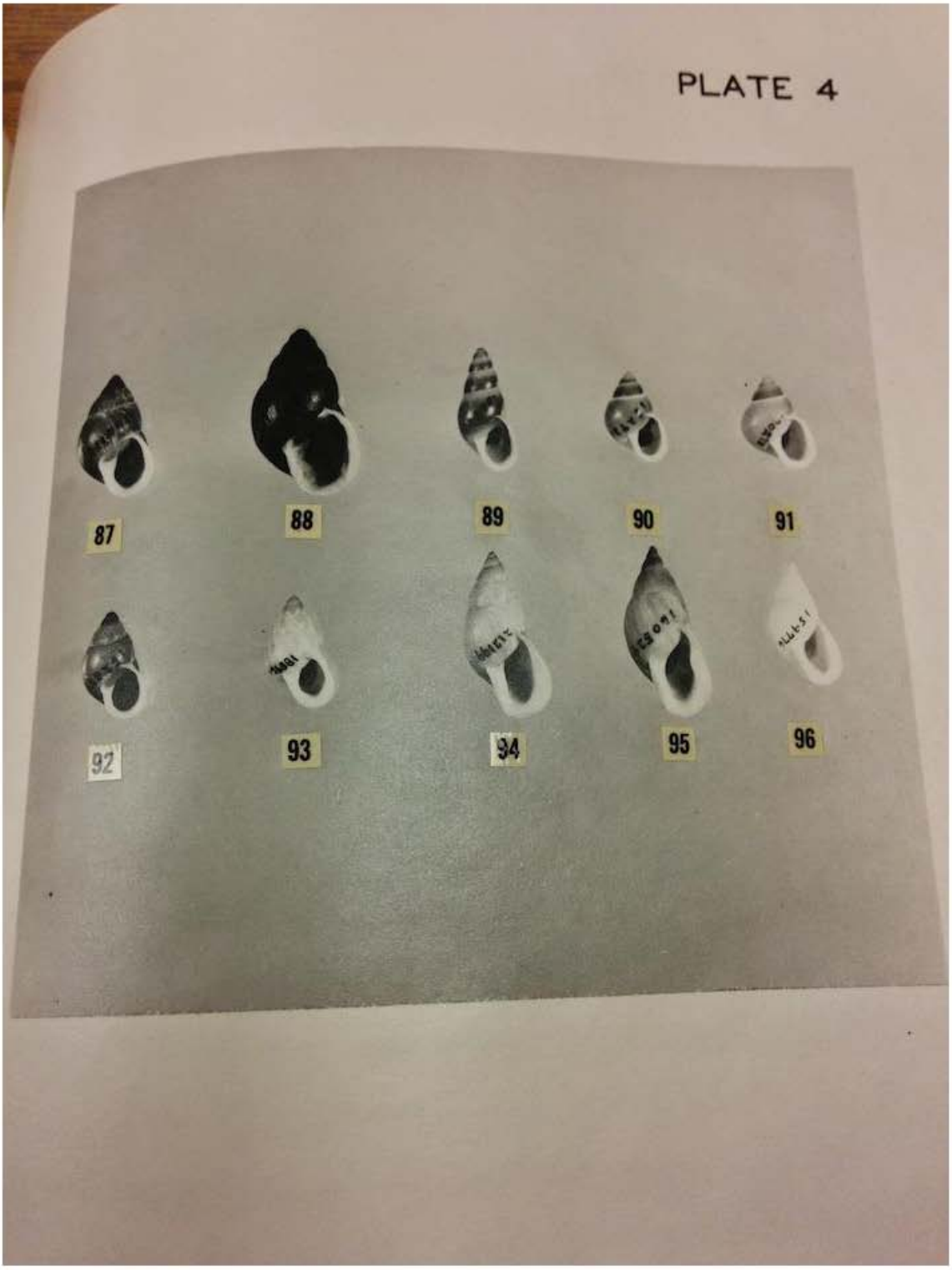
PLATE 4
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Plate 13

Samoana ganymedes

56. Genitalia.

57. Interior of penial complex.

58. Submedian flap of main pilaster.

Samoana magdalinae

59. Genitalia. Ovotestis enlarges to show follicles.

60. Interior of penial complex.

Samoana fragilis

61. Genitalia Ovotestis enlarged.

62. Interior of penial complex.

Scale for figures 56, 59, 61 same = 2 mm.

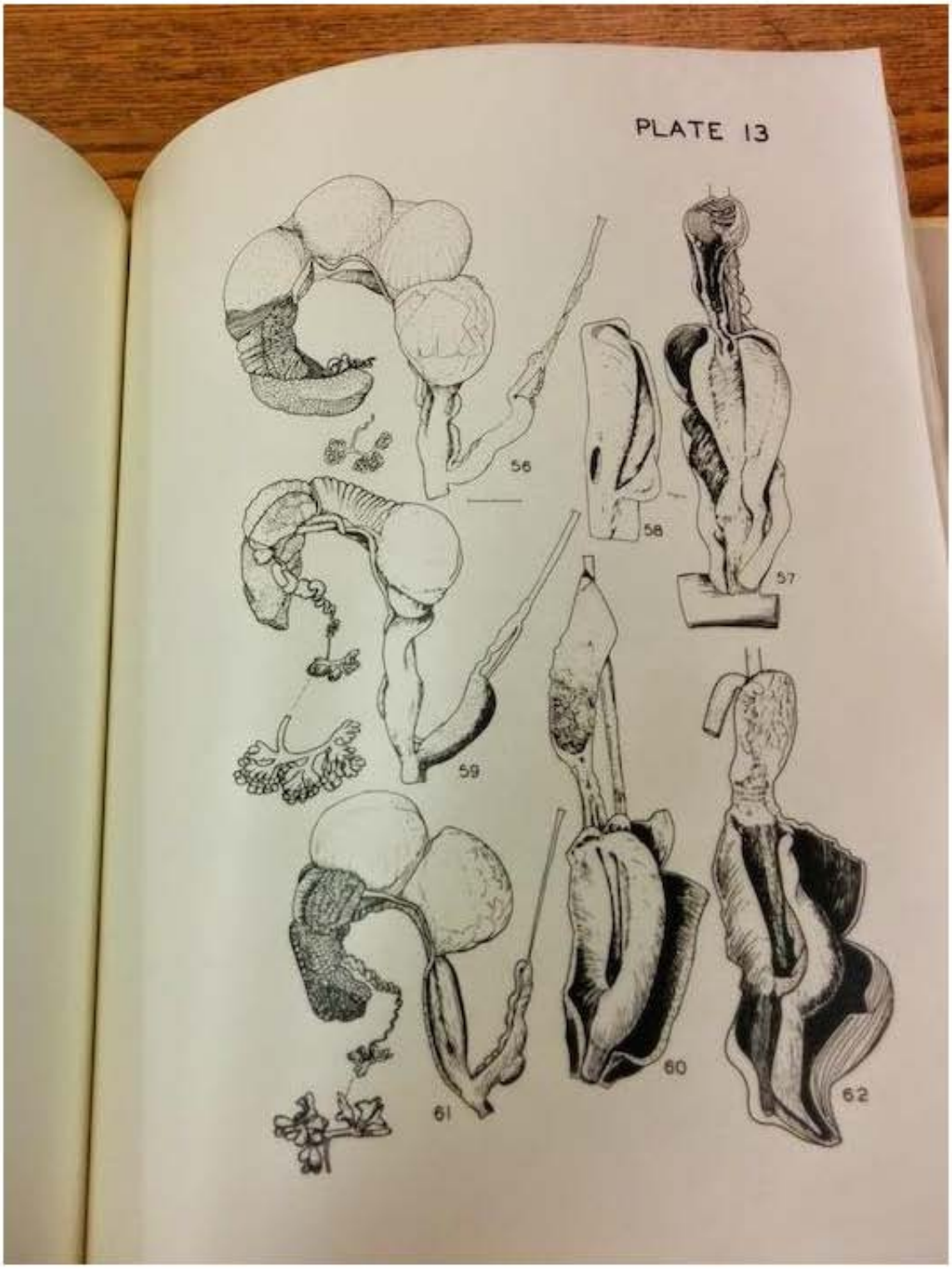
PLATE 13
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Plate 32

Partula gibba

113. Genitalia. Penis hebe type. Shell on plate 4, figure 90, Ritidian Point, Guam.

114. Interior of penial complex, hebe type penis.

115. Penis, reduced-modified faba type. Shell on plate 4, figure 91, Dededo-Yigo.

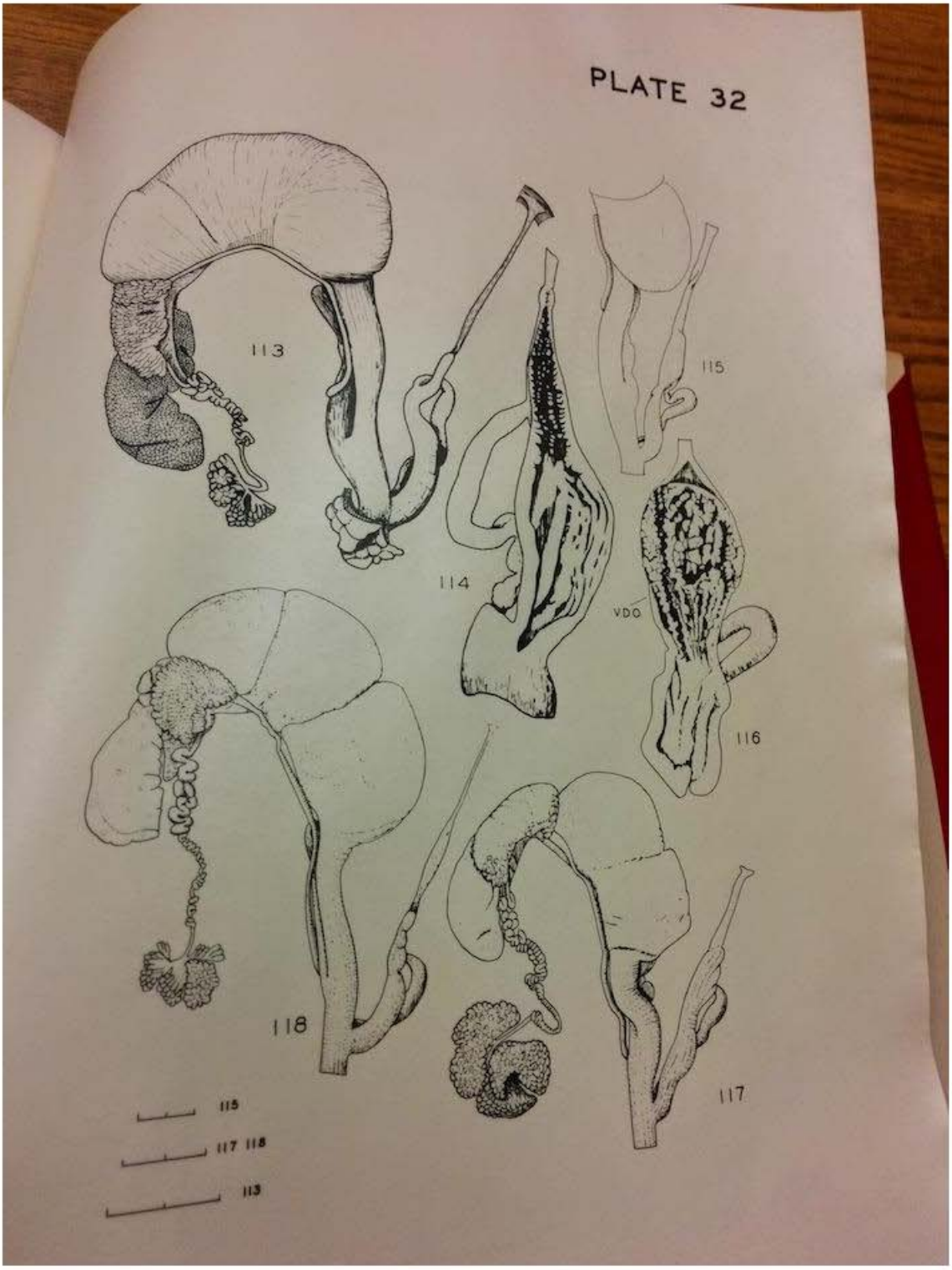
116. Interior of penial complex, reduced-modified faba type.

Partula salifana

117. Genitalia. Penis reduced-modified faba type.

Partula radiolata

118. Genitalia. Penis hebe type.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